SEASONAL AND ONTOGENETIC MOVEMENTS OF LINGCOD (*OPHIODON ELONGATUS*) IN CENTRAL CALIFORNIA, WITH IMPLICATIONS FOR MARINE PROTECTED AREA MANAGEMENT

ASHLEY GREENLEY
FishWise
PO Box 233
Santa Cruz, CA 95061
ph: (831) 427-1707
a.greenley@fishwise.org

KRISTEN GREEN
Alaska Department of Fish and Game
304 Lake St. Rm. 103
Sitka, AK 99835
ph: (907) 747-2683
kristen.green@alaska.gov

RICHARD M. STARR
California Sea Grant
Moss Landing Marine Laboratories
8272 Moss Landing Road
Moss Landing, CA 95039
ph: (831) 771-4442
starr@mlml.calstate.edu

ABSTRACT

Movements of lingcod implanted with acoustic transmitters were monitored for a year in central California. Half of the tagged lingcod remained within 5 km of coastline for at least 50% of days in the year, and 30% of lingcod were detected for >80% of the study days. Lingcod demonstrated distinct patterns in residency that were correlated to sex, fish length, and season. Residence times of females decreased with total length; female lingcod >90% maturity were present during the fall spawning season and briefly during the spring. Size-specific movements were less pronounced for males, but daily detections of males declined in spring, at the end of the winter nest-guarding season. The majority of lingcod detections were constrained to a limited area, however a few lingcod exhibited movements up to several kilometers. These results indicate that marine reserves can serve to both protect lingcod and also provide fisheries benefits via spillover.

INTRODUCTION

In recent years, ecosystem-based management approaches such as the use of marine protected areas (MPAs) have augmented traditional fishery management strategies that set harvest guidelines based on fishing mortality rates over large geographic distances (Lester et al. 2009). Meta analyses of field studies have shown that on average, MPAs yield positive results with respect to an increase in biomass, density, species richness, and size of individual organisms protected (e.g., Lester et al. 2009). The magnitude of changes in response variables, however, varies greatly and is dependent upon management parameters (MPA size and protection level, enforcement, and time since MPA was established), environmental conditions (habitat characteristics, oceanographic regimes), species' life histories, and ecological factors (Molloy et al. 2009). For managers, an equally important response variable to measure is the degree to which MPAs result in fisheries benefits via adult "spillover" from reserve boundaries. To determine the latter, it is essential to understand movement patterns of species, how they vary in relation to oceanographic seasons and life stages, and the likelihood to which species movements may extend beyond reserve boundaries (Kramer and Chapman 1999).

Lingcod (*Ophiodon elongatus*) are targeted by commercial and recreational fisheries throughout their range from Alaska to Baja California, Mexico. In 1999, the Pacific Fisheries Management Council officially declared lingcod stocks along the US West Coast to be overfished (Jagielo et al. 2000), prompting a rebuilding phase that included stringent harvest restrictions. Aided by strong recruitment events from 2000–02 and again in 2006, lingcod populations rapidly recovered, first in Oregon and Washington (Jagielo 2005), and later in California (Hamel et al. 2009).

As lingcod populations increased in California, a parallel increase in lingcod abundances in MPAs have been recorded relative to adjacent fished areas (Caselle et al. 2015; Starr et al. 2015). This indicates that lingcod are benefiting from MPA protection, but also leads to questions as to whether lingcod are moving beyond MPA boundaries and thus contributing to increased catches outside of MPAs. Existing movement information for lingcod in California is primarily based on recapture information from external tagging studies (Miller and Geibel 1973; Lea et al. 1999), however these data provide limited movement information and may not capture the nuances of certain life-history attributes of lingcod, such as seasonal migrations and reproductive behaviors.

We designed a project to determine the amount of time that tagged lingcod of different sizes and sexes remained within a continuous stretch of coastline in central California, an area that is now largely encompassed by two separate MPAs. Our primary goal for this study was to determine if lingcod in central California are highly residential, and therefore more likely to remain within an MPA boundary, or if lingcod are characterized by intermediate spatial scales of movements that would allow for partial protection via MPAs while offering some potential for adult spillover to adjacent fishing grounds. We were also interested in determining if movement patterns and residency differed by sex and size class of lingcod, to better understand how MPAs might be best designed to protect critical life stages. Specifically, we hypothesized that female lingcod would be less residential than males in the nearshore areas we monitored, due to sex-related differences in depth distributions (Jagielo 1990; Gordon 1994). Lingcod migrate to deeper waters at the onset of maturity (Miller and Geibel 1973; Gordon 1994), and thus we hypothesized that smaller lingcod tagged in Carmel Bay would occupy shallower depths than their larger conspecifics. Based on a hypothesis proposed by Matthews (1992), we also examined if smaller, possibly immature lingcod were less site-specific than larger fish. Finally, we hypothesized that movements of all sizes and sexes of lingcod would be stimulated by environmental factors, i.e., that increased upwelling and subsequent food availability would lead to an expansion of movements related to foraging. In short, our study contained three main objectives: 1) determine the residence time of lingcod tagged with acoustic transmitters in the nearshore environment in Carmel Bay for one year; 2) compare movements among sexes and size classes of lingcod; and 3) determine if movements varied with season and or environmental conditions.

MATERIALS AND METHODS

Study Site

Carmel Bay is located on the southwestern side of the Monterey Peninsula in central California coast, near 36°32'N, 121°57'W. Our study site in Carmel Bay was located north of the Carmel Canyon head, from Carmel Point to approximately 1 km northwest of Pescadero Point (fig. 1). The nearshore environment in Carmel Bay is characterized by the seasonal presence of giant kelp (*Macrocystis pyrifera*) and seafloor habitat comprised of contiguous high-relief granite outcrops, patchy areas of low-relief bedrock, and sand bottom. Four separate MPAs are located within or in close proximity of Carmel Bay, however only the Carmel Bay State Marine Conservation Area (SMCA) and the Carmel Pinnacles State Marine Reserve (SMR) were encompassed within the study area.

Fishing and Tagging

We tagged 30 lingcod with acoustic transmitters during two time periods: 8/18/2005–9/8/2005 and 8/21/2006–10/7/2006. Lingcod were caught by hook and line and implanted with sterilized acoustic transmitters (Vemco V13P-1H-S256) using standard surgical techniques for fishes (e.g., Lowe et al. 2009). Each transmitter was programmed to send a signal with a unique identification code along with fish depth at a random interval between 90–270 seconds. Transmitter battery life was estimated to be one year, although some tags were detected for >700 days. For external identification, a t-bar anchor tag was implanted into the dorsal musculature of each fish. Similar procedures have been successful in other lingcod tagging studies (Starr et al. 2004; Lowe et al. 2009; Tolimieri et al. 2009; Bishop et al. 2010).

Two large male lingcod tagged in 2005 were never detected after release and were excluded from the analyses. Another fish (tag #66, male, 62 cm TL) was caught by a spear fisherman after 246 days at liberty, within 500 m of its original tagging location. Residence time for this fish was calculated for the percentage of days detected until the day it was caught (% days at liberty). A second confirmed fishing mortality was tag #71 (female, 94 cm TL), caught by an angler in August 2008, after 702 days at liberty and 371 days since its last detection within the array. The angler reported catching this large female within close proximity (<300 m) to the original tagging location. No adjustments were made to the residence time analysis for tag #71 as this fish was captured after the study had concluded.

Of the 30 fish we tagged, 17 were male and 10 were female lingcod. The sex of three lingcod tagged in 2005 was unidentified and these fish were excluded from sex-specific analyses. For both sexes, we targeted fish in two size classes: fish between the lengths of 50%–90% maturity (five females, eight males, three with unknown gender), and fish at lengths ≥90% percent maturity (five females, nine males). We based our estimates of lengths at 50% maturity (males 47 cm TL; females 57 cm TL) and 90% maturity (males 61 cm TL; females 67 cm TL) on calculations by Silberberg et al. (2001) and Laidig et al. (1997) for lingcod in central California. From age-length relationships, we estimated that the lingcod tagged in this study were between 3–12 years of age.

Receiver Array

We monitored lingcod movements using an array of 30 acoustic receivers (Vemco, Inc. VR-2, 69 kHz) moored parallel to the coastline in Carmel Bay in depths ranging from 7–40 m (fig. 1, fig. 2). Along with a time and date stamp for each signal received, the receivers recorded transmitter IDs and depths of tagged fish swimming within the receiver's detection range. Most of the receivers were deployed 5 m from the seafloor except in areas greater than 30 m depth, where the receivers were elevated 10–15 m from the seafloor to limit SCUBA diving depths during retrieval. Receivers were collected, serviced, and redeployed every six months.

Acoustic Range Testing and Validation

Detection ranges of VR-2 receivers are affected by sea state, biological and anthropogenic noise, bottom topography, and submerged vegetation (Simpfendorfer et al. 2002). We estimated receiver detection ranges by analyzing signal transmissions from V13 transmitters suspended 1 m off the seafloor for 15 minutes, at 50 m increments away from moored receivers. We

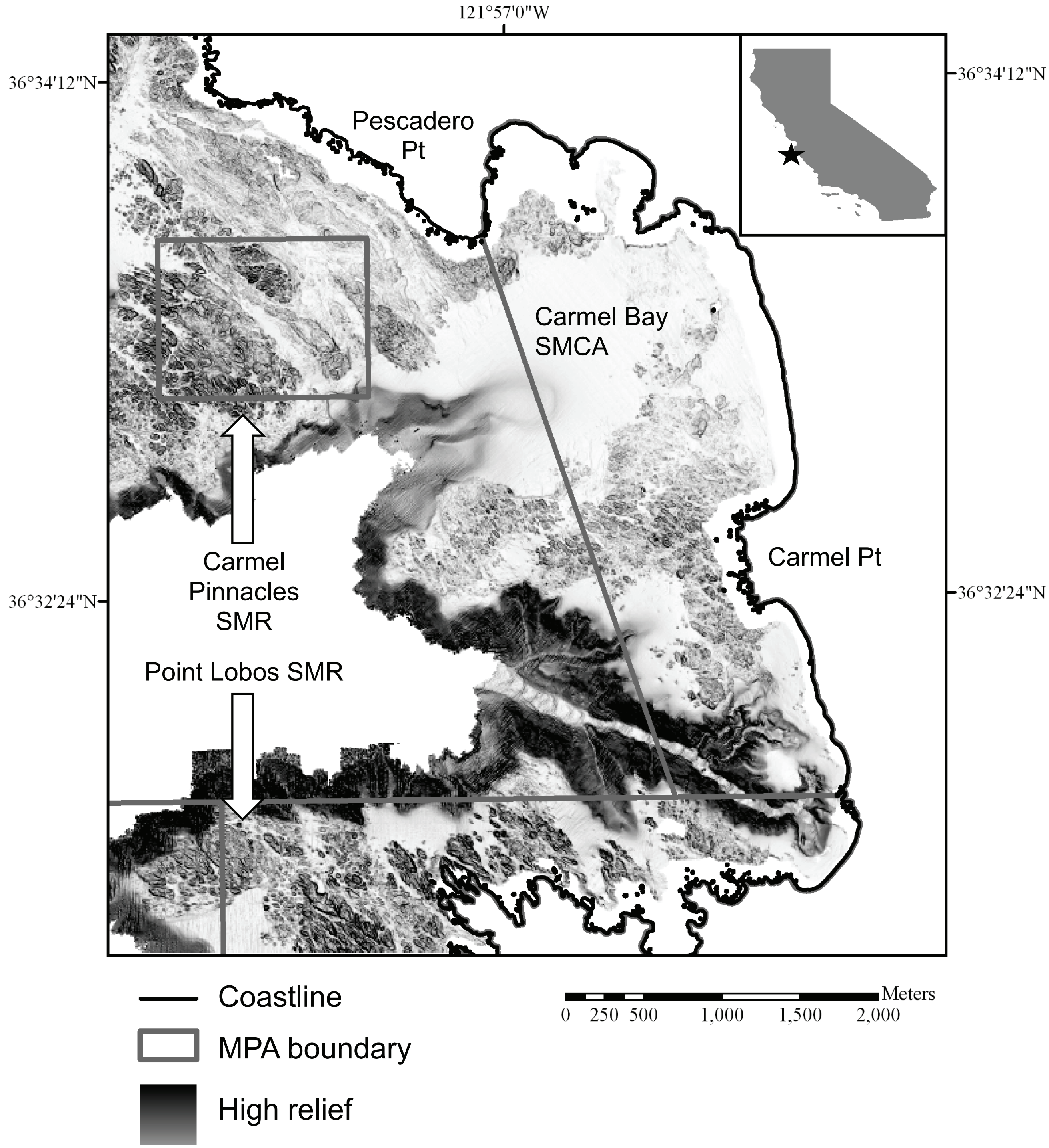


Figure 1. Multibeam bathymetry imagery of Carmel Bay with marine protected area (MPA) boundaries. SMR denotes State Marine Reserve and SMCA denotes State Marine Conservation Area (data courtesy of the Seafloor Mapping Lab of California State University Monterey Bay).

repeated range testing in winter and in late summer, when seasonal densities of giant kelp (*Macrocystis pyrifera*) were low and high, respectively. Our range testing results indicated that the mean number of detections/hr decreased with distance from a receiver; the mean of detections/hr were lower in late summer compared to winter, presumably due to higher seasonal kelp densities in late summer. For this study, we used a conservative estimate of 150 m radii for detection ranges, which was consistent with other reported VR2 receiver ranges in California kelp beds (Topping et al. 2006).

To examine how signal transmissions varied over time,

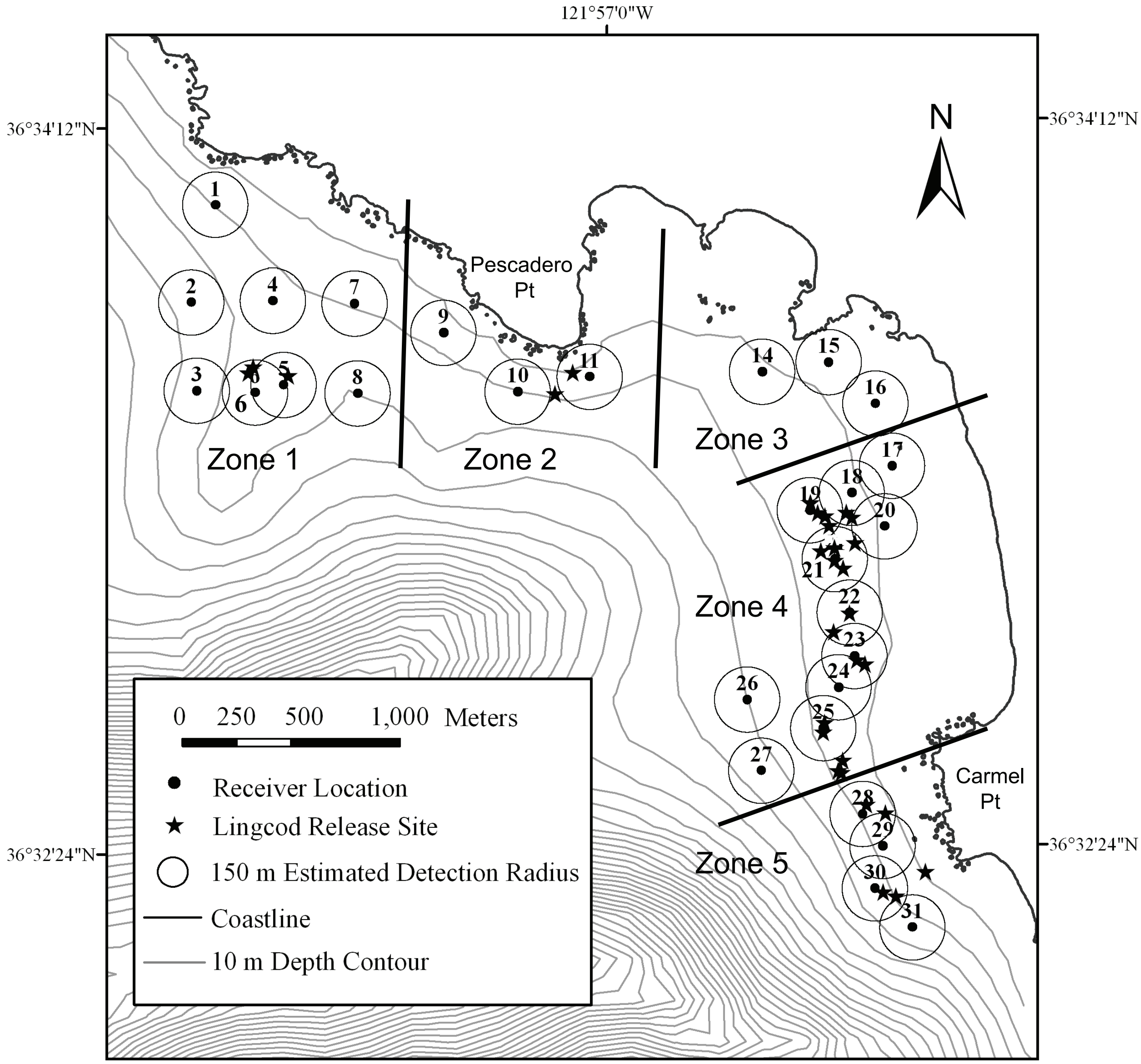


Figure 2. Configuration of VR2 receiver array with estimated 150 m detection ranges and zone delineation. Small black circles indicate receiver locations and stars are release locations of tagged lingcod.

we deployed a V13 "reference" transmitter 1 m off the seafloor and recorded and analyzed its detections over seven months. We placed the reference transmitter 140 m equidistant from two receivers, i.e., within our estimated detection range for the VR2 receivers. The total number of daily detections recorded for the stationary reference transmitter was highly variable, ranging from 7–401 detections/day, and averaging 178.2 ± 101.9 detections per day. At a daily and hourly scale, however, signals from the stationary reference transmitter were detected for 100% of the 212 days deployed and for 92% of all possible hour-bins. Due to the variability in individual transmissions, we analyzed residence times in this study by grouping signals into hour-bins and 24-hr periods (see Data Analysis, next page).

To validate the detection capabilities of the VR2 array and to account for the possibility of detection failure from acoustic shadows, we surveyed a 500 m^2 grid near receivers 18–21 (fig. 2) with a Vemco VR100 directional hydrophone that was mounted on a small boat. We conducted 30-minute VR100 surveys on four separate days and nights, for a total of eight surveys. We then compared signals of tagged fish recorded by the VR100 with those recorded by VR2 receivers 18–21 for a 24-hr period. Over the eight days we conducted surveys, the VR100 confirmed the presence of five lingcod within the range of receivers 18–21 that would have otherwise gone undetected by those receivers for 24 hrs.

Data Analysis

Residency is a term frequently used to evaluate the tendency of a species to stay in one place. We defined and analyzed residence times as the percentage of days an individual was detected within our study area in relation to total days at liberty (% days, from date of tagging until the last date of detection), as a percentage of hour-bins with detections in relation to total possible hour-bins during time at liberty (% hour), and as a percentage of days detected relative to one year from the tagging date (% year). Due to the possibility of false signals from electronic noise, a fish was only considered present when two or more detections were recorded within a 24-hour period (e.g., Starr et al. 2000). Lingcod were considered to have departed from the array if ≤1 signal was received from the tagged fish during a 24-hour period. For each day a fish was determined to be present in the array, all recorded signals were grouped into one hour time bins relative to the time of signal transmissions (Starr et al. 2002; Green and Starr 2011; Green et al. 2014). For example, signals detected between 14:00:00 hour and 14:59:59 hour were assigned to hour-bin 14.

We used a two-way ANOVA to determine if residence time (% days) was related to total length or sex of tagged lingcod. We performed a separate regression analysis for each sex to test if residence times (% yr) were related to fish length. We analyzed seasonal patterns in residency by calculating the average monthly proportion of days lingcod were detected for each sex and size class. Also, we used a generalized linear model (GLM) to identify differences in proportion of days detected within combinations of sex and size classes. An average monthly depth of each fish was calculated and sexes and size classes were pooled to generate a group mean. Mean monthly depth distributions were compared among sex and size classes using a two-sample KS test. For the depth comparisons, we used lingcod tagged in 2006 and one large female tagged in 2005 (the other 2005 fish either did not have sex assigned or the tags malfunctioned).

Spatial patterns of activity were quantified by tallying the number of days and the number of hour-bins for which a fish was detected at each receiver. Movements over time were examined by dividing the study area into zones of approximately equal size (fig. 2). Zones were numbered north to south, and an average of the zone numbers was used to identify the primary zone that a fish occupied during a week (e.g., Starr et al. 2002). Every hour-bin containing detections from a tagged fish was assigned a zone based on the location of the receivers where the fish was detected for that hour. The hourly zone values were averaged for each week and compared among other weeks using a two-sample KS test for each individual fish. To avoid potential bias caused from the tagging process, the weekly zone average for the second week after release date was selected as the expected value for the KS test. At a finer spatial and temporal scale, we calculated the percentage of time that each lingcod was detected on a particular receiver within the array by summing the total number of hour-bins recorded on a receiver and dividing by the total overall number of hour-bins with detections. We compared the percentages of hour-bins recorded on one primary receiver among sexes and size classes of tagged lingcod using an ANOVA.

Lingcod movements in relation to physical conditions in the environment were examined using cross correlation analyses to compare acoustic data with atmospheric pressure, wind, upwelling indices, wave height, water temperatures, tides, and time of day. Cross correlation analysis addresses autocorrelation of data by fitting a model to time trends and then correlating residuals using lag times in multiples of one day. Temperatures throughout the receiver array were monitored using Onset StowAway TidbiT temperature loggers deployed on receiver mooring lines and positioned at shallow (12–16 m) and deep (27–34 m) depth intervals. Oceanographic and atmospheric data were acquired from the historical data archives of the National Oceanic Atmospheric and Administration (NOAA). Wave height, wind speed, and barometric pressure were recorded from Monterey Buoy 46042, (http://www.ndbc.noaa.gov). Tidal height was recorded from Monterey tide station 9413450, (http://tidesonline.nos.noaa.gov/). Day lengths were derived from the historical archives of the US Naval Observatory from Carmel, California (http://aa.usno.navy.mil/data/). Daily and monthly upwelling indices, expressed as $m^3 s^{-1} 100 m^{-1}$ of coastline at 122°W, 36°N, were obtained from NOAA Fisheries Pacific Fisheries Environmental Laboratory (PFEL) (www.pfeg.noaa.gov/products/PFEL).

Diel movements were analyzed by calculating the proportion of hour-bins in which a fish was recorded during the day (and night) in relation to the total possible number of day (and night) hour-bins throughout the fish's time at liberty. To account for changing day length throughout the year, the number of possible day and night hour-bins was calculated for each day based on time of sunrise and sunset. Crepuscular movements were excluded from this analysis by eliminating detections within ±1 hour of sunrise and sunset.

TABLE 1
Summary of 30 lingcod tagged in Carmel Bay. Class refers to fish at lengths >90% maturity and between 50%–90% maturity. Residency was calculated as the percentage of days (% d) recorded in relation to total days at liberty (lib), the percentage of hour-bins containing signals in relation to total possible hour-bins during time at liberty (% hr), and the percentage of days relative to one year from the tagging date (% yr).

Tag ID	TL (cm)	Sex	Class	Date Released (mm/dd/yy)	Time at lib (d)	Residency (% d)	Residency (% hr)	Residency (% yr)
37	66	M	>90	08/18/05	–	–	–	–
66	62	M	>90	09/13/06	246	40.2	21.4	27.4
68	62.5	M	>90	10/07/06	210	3.8	0.6	2.2
72	64	M	>90	09/22/06	321	16.8	2.8	14.8
77	63	M	>90	10/07/06	327	9.2	1.0	8.5
79	61	M	>90	09/01/06	371	79.0	39.6	80.5
117	61	M	>90	08/29/06	360	92.2	42.6	91.2
119	63	M	>90	09/11/06	376	79.0	28.6	81.6
4049	66	M	>90	09/06/05	–	–	–	–
63	53	M	50–90	09/22/06	263	67.7	38.5	48.8
64	53	M	50–90	09/04/06	376	43.9	6.7	45.5
65	53	M	50–90	09/12/06	373	67.8	19.1	69.3
70	54	M	50–90	09/23/06	367	99.7	64.1	100
74	46	M	50–90	09/28/06	362	34.8	6.0	34.5
75	57	M	50–90	09/29/06	344	5.8	0.5	5.5
116	53	M	50–90	08/21/06	311	44.7	8.1	38.4
174	59	M	50–90	08/24/06	211	95.7	54.3	55.6
36	87	F	>90	08/18/05	92	8.7	0.5	2.2
69	72	F	>90	09/16/06	281	12.5	3.7	9.9
71	94	F	>90	09/23/06	323	25.4	4.0	22.5
73	85	F	>90	09/27/06	195	23.6	5.9	12.6
173	82	F	>90	09/07/05	325	49.8	9.0	44.4
38	51	F	50–90	09/05/06	385	94.0	50.4	99.5
39	54	F	50–90	09/14/06	75	29.3	4.9	6.0
67	62	F	50–90	08/30/06	391	70.3	15.7	75.6
76	57	F	50–90	09/29/06	361	100	62.4	99.5
118	63	F	50–90	08/29/06	327	68.8	16.9	61.9
172	59	?	50–90	09/07/05	364	100	56.7	100
225	58	?	50–90	09/08/05	747	49.3	10.7	47.7
226	58	?	50–90	09/08/05	747	99.2	47.6	100

RESULTS

Fishing

We identified the sex for 27 of the 30 lingcod we tagged (table 1). Of the lingcod with known sex, the mean length of the 10 females we tagged (70.7 cm ± 4.9 SE) was significantly greater than that for the 17 males tagged (58.6 cm ± 1.2 SE) ($t = 2.941$, $p = 0.007$). There was no significant difference in length between sexes for lingcod grouped in the smaller size class ($t = 1.584$, $p = 1.42$), but females were significantly larger than males for lingcod grouped in the larger size class ($t = 7.611$, $p < 0.001$).

Receiver Array

Between August 2005 and September 2007, three receivers broke free from their moorings but were found on Carmel Beach, and six receivers were permanently lost. The three receivers recovered on the beach were quickly redeployed so that <2 weeks of data were missing from these locations, whereas the other six receivers were replaced after several months. Four of the six locations with missing receivers were in areas with few to no recorded detections for lingcod (receiver locations 12, 18, 20, and 23). Receivers at locations 5 and 6 on the Carmel Pinnacles were missing from November and December 2006, respectively, until June 2007. The loss of data at these locations likely resulted in an underestimate of residency times for two fish (tags #73 and #74). However, tags #73 and #74 were detected on receivers adjacent to the lost receivers throughout the year, indicating the fish were near or within the study area.

Residence Times & Depth Distribution

Tagged lingcod in Carmel Bay were detected an average of 50% of days in a year, and 30% of the lingcod we tagged were detected, on average, for over 80% of days in a year (table 1). A relatively even number of tagged lingcod were detected for <20, 40, 60, 80, and 100% of their days at liberty (fig. 3). Small lingcod were detected significantly more often than large lingcod (% days) (ANOVA: $F = 11.121$; $p = 0.004$), but there was no significant difference in percentage of days detected by sex (ANOVA: $F = 0.491$, $p = 0.494$). There was no significant interaction between sex and size class ($F = 1.619$, $p = 0.221$). A regression analysis revealed that the size-

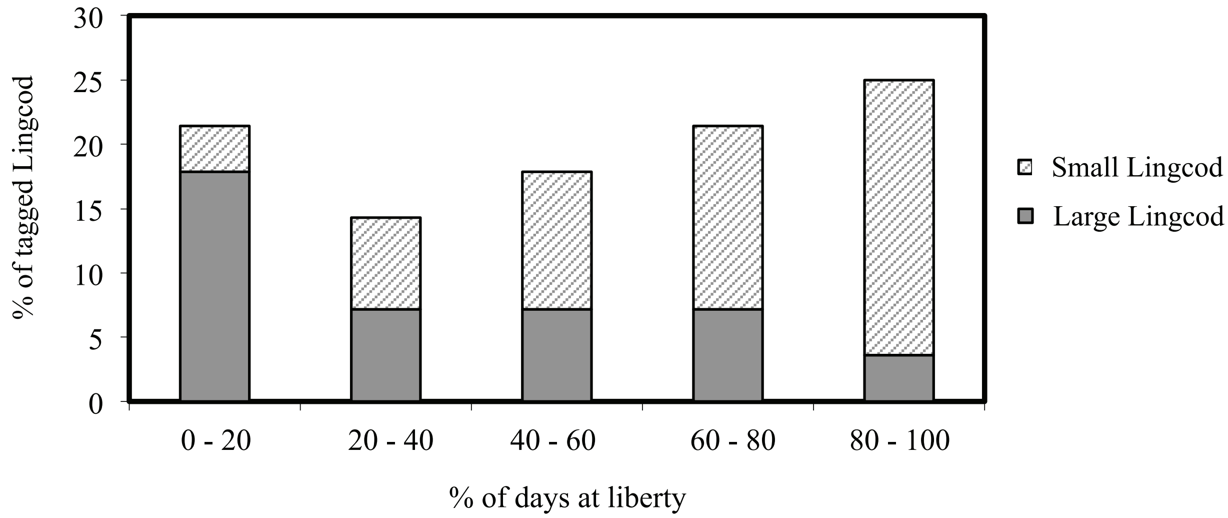


Figure 3. Percentage of days at liberty recorded in the array for 28 tagged lingcod. Two lingcod were excluded from the analysis due to tag failure.

related pattern in residence times was driven by females, for which the percentage of days at liberty (% days) spent in the array was significantly dependent on total length ($r^2 = 0.483$, $p = 0.008$), but not for males ($r^2 = 0.016$, $p = 0.650$). A GLM analysis confirmed that large females were detected significantly fewer days in the study area than other sizes and sexes of lingcod (GLM, df = 4, $p < 0.05$).

Six lingcod (20% of the tagged fish) were detected for less than 20% of the possible days at liberty. Despite the low overall percentage of days detected, two of the six fish were detected sporadically for a few days at a time throughout the year, indicating that the fish were probably near the array but just outside of detection. Three lingcod with low overall residence times, tags #69, #75, and #77, were detected sporadically for several months before leaving the array, only to be detected once again after absences of several months (fig. 4). Lingcod tag #36 departed the study area permanently after 91 days at liberty.

Mean monthly depths of large male lingcod ranged from 15.5–20.1 m (fig. 5) and were fairly consistent throughout the year for males and females in the small size classes. Large females occupied a greater depth range (7.0–17.5 m) over time, with the deepest monthly average depths occurring from February to April. The mean monthly depth distribution for large females was significantly different than for combined males and small females (two sample KS, $p = 0.001$), yet it should be noted that female #73 drove the observed depth pattern for large females. This lingcod was detected in deeper areas within the array during the winter while the other large females were primarily absent.

Seasonal Patterns in Residency

Seasonal patterns of residency within the array were notably distinct for large female lingcod, compared to males and small females (fig. 6). Residence times for large females were greatest during the fall and increased again in the spring. Of the five large females tagged, lingcod #173 was detected consistently for a year on the same two receivers whereas residency for the other four females decreased after October or November (fig. 4). Of these four females, #36 was never detected again, whereas #69 was detected seven months later in a different part of the array, approximately 2 km away. The other two large females, #71 and #73, went mostly undetected throughout the winter from November until mid-March, with the exception of a few detections in January and February. Both of these fish were detected again in mid-March, and lingcod #73 was detected on the Carmel Pinnacles for approximately one month before leaving permanently. Fish #73 primarily occupied the pinnacles, an area where receivers were lost, and therefore residency may have been higher than we were able to measure. Lingcod #71 was regularly detected near Pescadero Point through July 2007; in August 2008 it was recaptured near the same area by a recreational fisherman, 371 days after its last detection.

Patterns in residency over time were similar for both size classes of males and small females (fig. 4, fig. 6). For males, presence over time could be characterized by three patterns: 1) male lingcod consistently occupied the study area throughout the year, except for a brief period of absence (≤2 weeks) in late March/April ($n = 8$ fish), 2) male lingcod were not detected in the array ($n = 1$) or were detected only sporadically ($n = 2$) after April; and 3) male lingcod exhibited low overall residence times (detected on <10% of possible days) but were detected intermittently throughout the year of monitoring ($n = 4$). Three of the four male lingcod with low overall residence times (pattern 3) were males in the large size class. Small female lingcod exhibited the

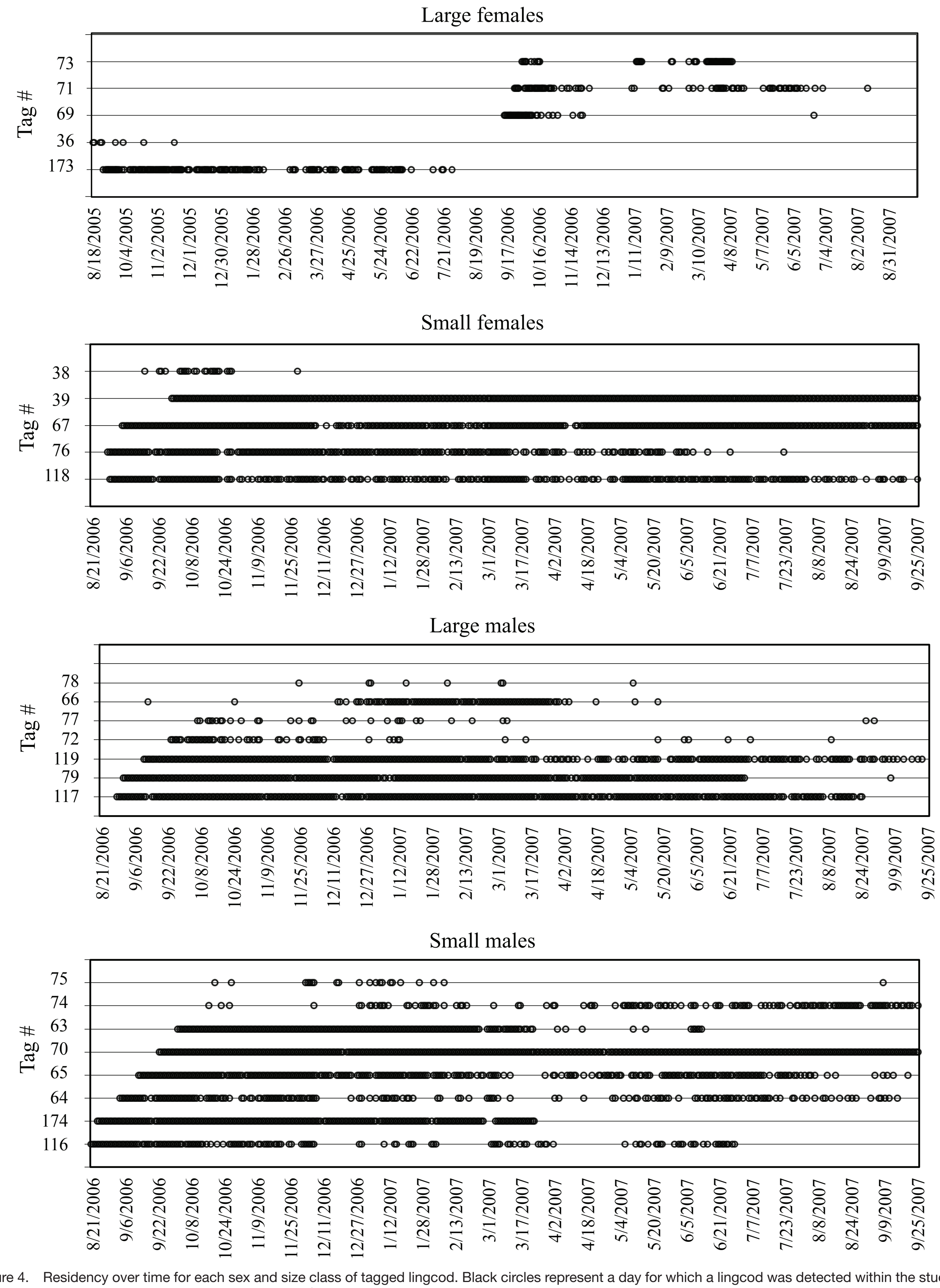


Figure 4. Residency over time for each sex and size class of tagged lingcod. Black circles represent a day for which a lingcod was detected within the study area (with a minimum of two detections per 24 hour period).

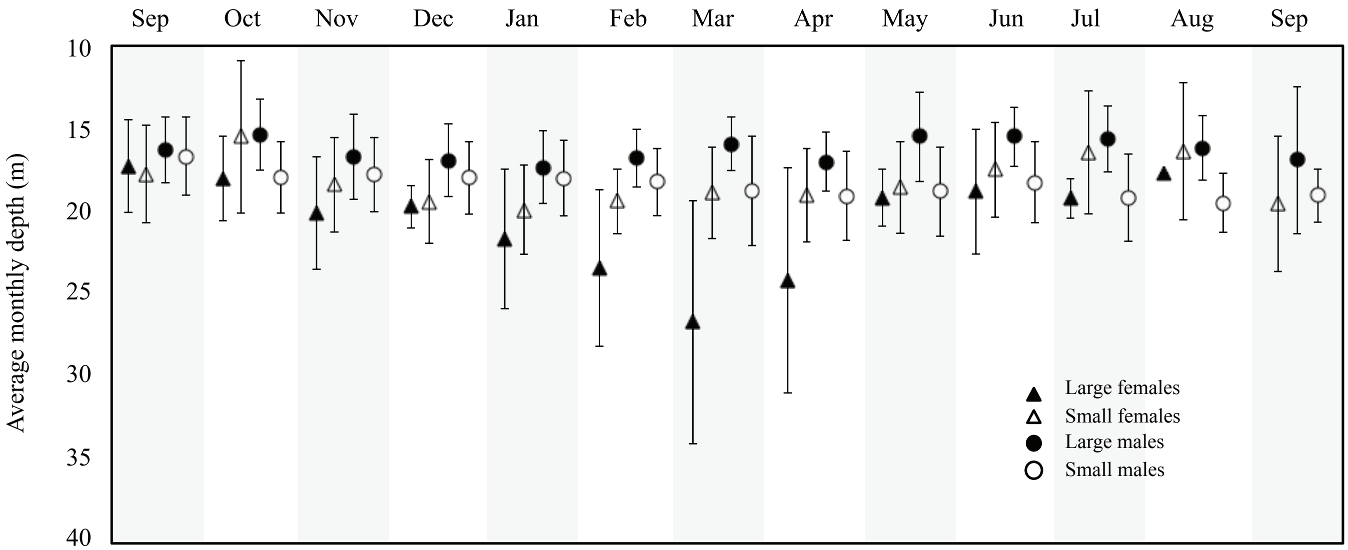


Figure 5. Mean monthly depth distributions (± SD) of tagged lingcod, separated by sex and size class, pooled by month.

highest residency of tagged lingcod. Similar to males, residency decreased in April when two of the tagged small females were absent for several days. Two other small females were detected consistently throughout the year and one was only detected for approximately one month after tagging in September 2006.

Spatial Patterns in Movements

Tagged lingcod exhibited limited movement within the array, and the majority (82%) of tagged lingcod rarely left their primary zone of occupancy during their time at liberty. Two-sample KS tests comparing the expected zone value derived from week two with the observed weekly zone values were only significant for five lingcod (18%) (tag #39, $p = 0.049$; tag #71, $p = 0.000$; tag #72, $p = 0.008$; tag #77, $p = 0.023$; tag #79, $p = 0.000$). At a finer spatial scale, 12 lingcod (42% of males and females in both size classes) were detected on one primary receiver for greater than 90% of hour-bins with detections; of these fish, six lingcod were detected on one receiver for >97% of hour-bins (Appendices A–D). For all lingcod combined, 76.8% (± 3.7 SE) of all hour-bins with detections were recorded on 1 receiver, and 14.1% (±2.5 SE) of all hour-bins were recorded on two adjacent receivers. Percentages of hour-bins with signals recorded for a given lingcod on one primary receiver were not significantly different among the four groups of tagged lingcod: small males, small females, large males, large females (ANOVA: $F = 0.696$; $p = 0.565$).

Although the majority of lingcod movement patterns were constrained to one or two adjacent receivers, some longer distance forays were captured within the 5 km of coastline we monitored (fig. 7). For example, lingcod #74 (male, 46 cm TL) was tagged and released on the Pinnacles (receivers #2–8), where it was detected for 95% of the total hour-bins containing recorded signals. On seven separate occasions, #74 was detected approximately 2.5 km away on receivers #14, 15, and 21 (fig. 7). The time that signals were recorded between distant receivers ranged from 13 minutes (from receiver #3 to #14) to 17 hours (from receiver #14 to #6). Lingcod #77 (male, 63 cm) also displayed an interesting pattern of residency at two separate locations within the array (fig. 7). This fish was detected intermittently on receiver #19 near Carmel Beach for two months before departing in early December. Sixteen days later, it was detected 1.3 km away on receiver #10 near Pescadero Point, where it was again recorded intermittently until March 6. After an absence of five months from the array, this lingcod was detected again on the original receiver (#19) in late August. Lingcod #174 (male, 59 cm) displayed highly directional movement from receiver #25 near Carmel Point through to the southern extension of the array near Carmel Canyon (fig. 7). During this trip, #174 swam in a southerly direction past five receivers (#27–31) before going undetected for 52 hours. The fish then utilized a similar route for the return trip back to its primary receiver, where it remained for the rest of its days at liberty. The overall distance from primary receiver location #25 to the last receiver of detection was approximately 1 km, with the lingcod swimming at an estimate rate of 0.72 km/hour on the trip out and 0.46 km/hour on the way back.

Physical Parameters

Water temperatures were coldest from March to July 2007, when mean monthly temperatures fell below the average annual temperature recorded during our study.

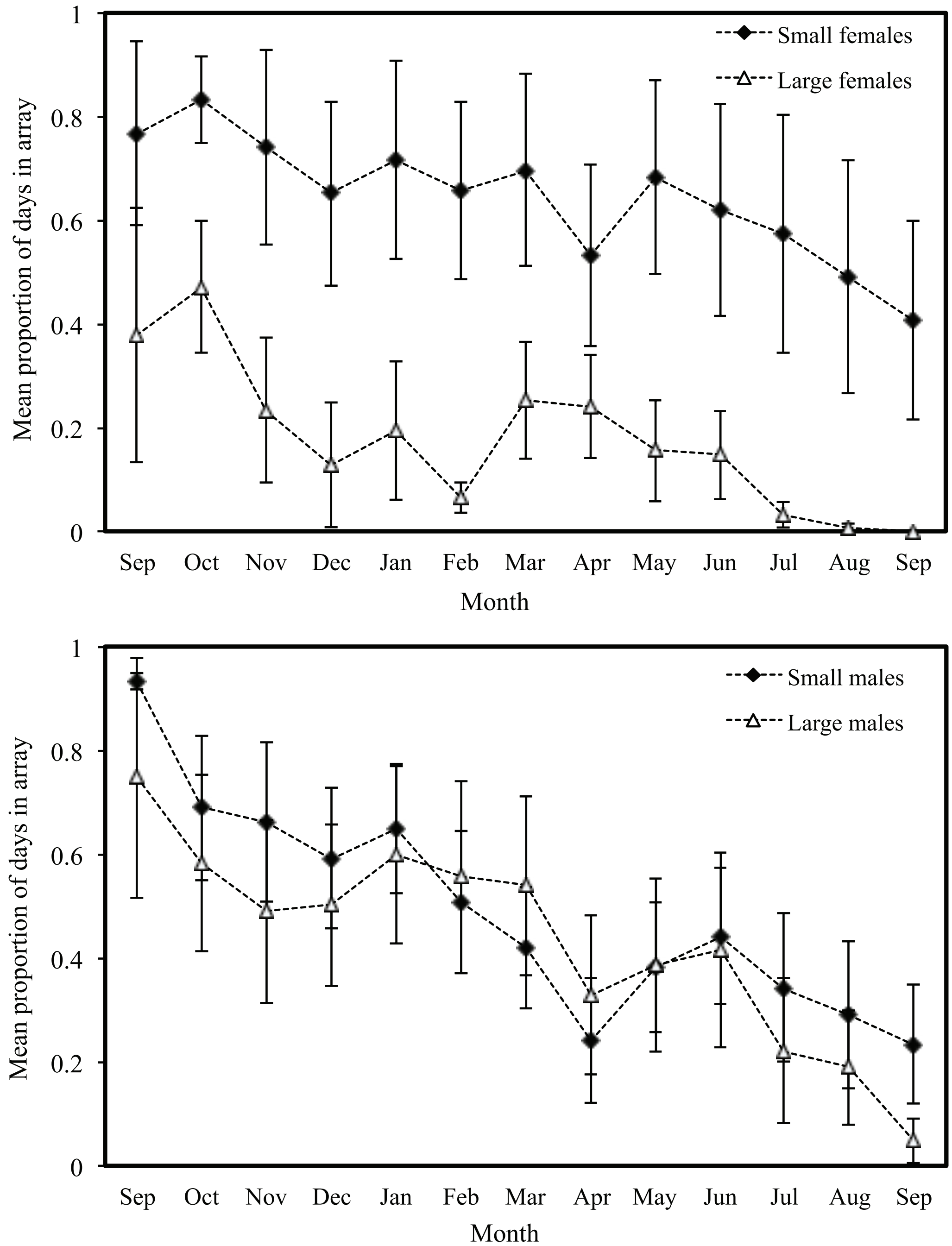


Figure 6. Mean monthly proportion of days (± SE) detected in the array for tagged female (top) and male (bottom) lingcod.

The cold water coincided with strong upwelling conditions. Cross correlation analyses indicated significant relationships between the number of lingcod detected in the array and environmental variables associated with upwelling conditions, such as wind speed, water temperature, and upwelling indices (table 2). The number of lingcod detected in the array increased as wind and the upwelling index increased and water temperatures decreased. Also, more lingcod were detected as the wave energy increased. Lag times for these significant relationships were all 2 days after the onset of upwelling.

Tagged lingcod that were detected in the array for >10% of possible hour-bins did not show a diel pattern in detection, i.e., day and night presence in the array was similar. For example, for the subset of fish we analyzed, the mean proportion of possible hour-bins in which signals were recorded during the day (0.39) was comparable with that for the night (0.42). Twelve lingcod were

TABLE 2
Lag in days, correlation coefficients (r), and p values associated with cross correlations among selected environmental variables and the number of tagged lingcod detected during the time period from 10 November 2005 to 27 September 2007.

Variable	Lag time (d)	Correlation	p
Upwelling index	2	0.279	<0.001
Atmospheric pressure	1	0.240	<0.001
Wind speed	2	0.133	0.018
Wave height (squared)	2	0.258	<0.001
Sea surface temperature	1	–0.180	0.001
Temperature at 14 m deep	1	–0.137	0.014
Temperature at 31 m deep	1	–0.224	<0.001
Temperature difference 14-31 m deep	1	0.130	0.019

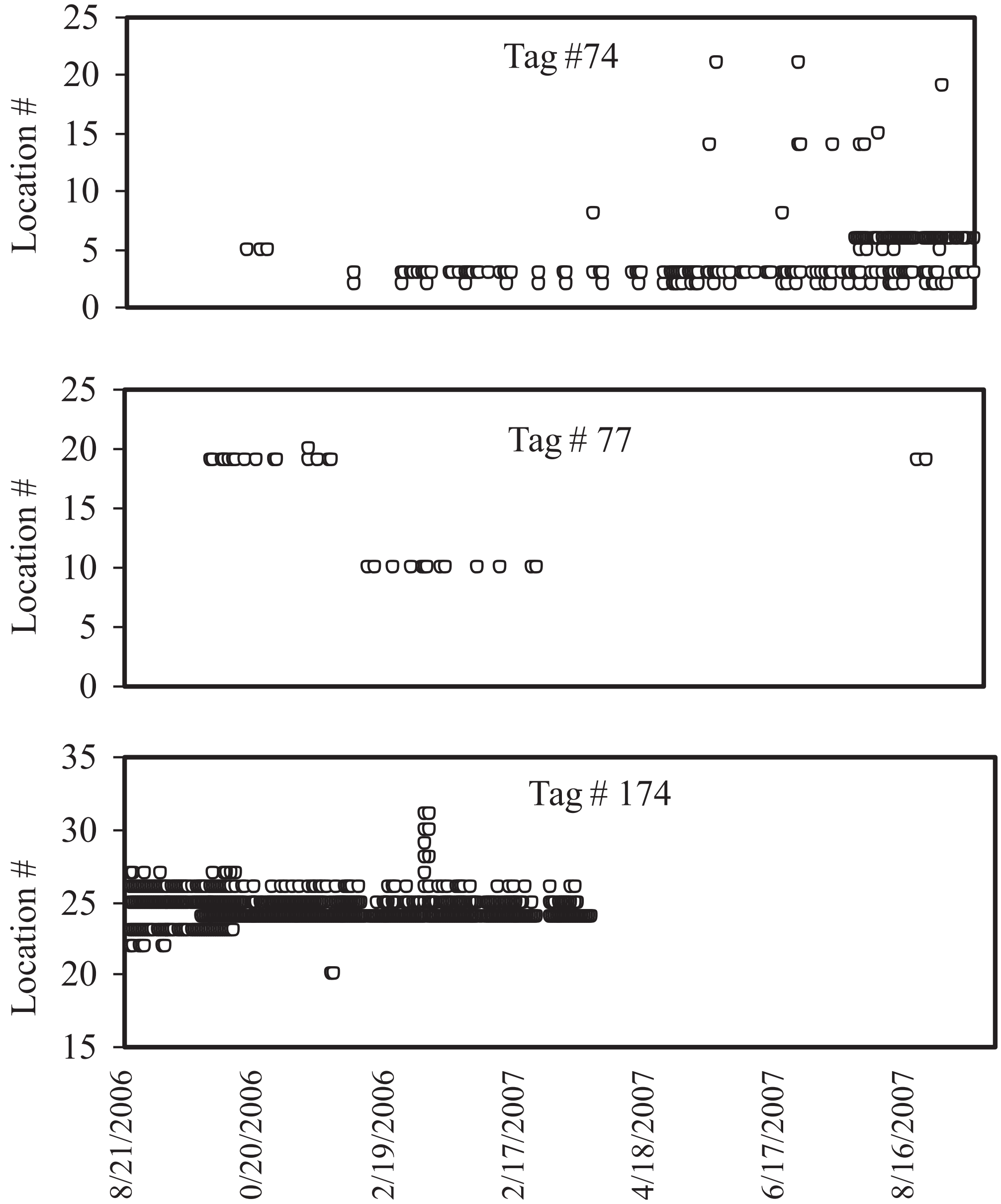


Figure 7. Spatial utilization patterns for tagged lingcod demonstrating movements >1 km. Each circle represents a day in which a receiver detected a tagged fish.

detected for less than <10% of possible hour-bins. Of these fish, ten were primarily recorded during daylight hours and two were detected more during the night.

DISCUSSION

Lingcod Movements and MPA Management

MPAs are often designed with two seemingly contradicting purposes: to protect marine organisms from fishing and to benefit fisheries via spillover of adults beyond reserve boundaries. From the movement patterns we observed, it appears that lingcod are suited to serve both MPA purposes. Over the course of a year, tagged lingcod demonstrated relatively high residency. On average, half of the lingcod we tagged remained within the 5 km area we monitored for at least 50% of days in a year, and 30% of lingcod were detected for over 80% of days in a year. These patterns in residency indicate that lingcod, over the course of a year, are likely to remain within the boundaries of a typical California MPA (~5 km long x 3 km wide), as evident by the higher densities and larger sizes of lingcod found in MPAs than nearby reference areas (Starr et al. 2015).

Our estimates of residence times should be considered conservative; we know from our validation surveys with the VR 100 receiver that some tagged fish were present but went undetected by the stationary VR-2 receivers for a 24 hour period. Given that lingcod are demersal fish that sometimes occupy cracks and crevices, these false absences were likely caused by acoustic shadows. We conducted VR100 surveys over eight days, of which fish with false absences went undetected by the VR-2 receivers for one or two days at the most. This indicates that our estimates of residency were affected over short time scales of a few days, while longer-term absences were likely caused by true departures from the monitored area.

In general, lingcod movements in Carmel Bay were highly constrained, with the majority of lingcod detections recorded at one or two adjacent receiver locations (Appendix A–D). This pattern in spatial utilization did not differ among sexes and size classes of lingcod, and thus we found no evidence that smaller, presumably immature, lingcod were no more or less site-specific than larger fish, at least at the spatial scales we measured. Our observations of restricted movements for lingcod in Carmel Bay are consistent with acoustic tagging studies conducted at finer spatial scales, whereby lingcod also exhibited relatively confined home ranges of 2000–3000 m^2 (Tolimieri et al. 2009) and 21,000 m^2 (Beaudreau and Essington 2011).

Of the larger scale movements we captured, lingcod demonstrated the capacity to travel multiple kilometers in under an hour, as well as the ability to home back to the same receiver location within our study area. Previous displacement experiments on lingcod have shown their ability to home (Matthews 1992) and to travel relatively large distances over short periods of time (Anthony et al. 2012). Two lingcod tagged in our study would, on occasion, leave their primary receiver location and move 1–2 km to another set of receivers. The duration of time between these multiple centers of activity varied by fish, but the general patterns in movements are analogous to the use of multiple core areas described by Tolimieri et al. (2009). The ability of lingcod to travel multiple kilometers, either during a foray or due to an occasional shift in a core area of activity, could result in fishery benefits should the movements span across MPA boundaries.

The residential behavior of lingcod, combined with their ability to travel multiple kilometers, helps explain why previous tag and recapture studies either documented limited lingcod movement or more widespread migratory behavior (Mathews and LaRiviere 1986; Smith et al. 1990; Jagielo 1995). In the present study, 20% of the lingcod we tagged were detected for <20% of days at liberty, and the majority of those fish permanently left the 5 km of coastline in the study area. Although we don't know how far these fish moved, tag and recapture studies conducted over multiple years have reported similar percentages of lingcod emigration, with 20% of tagged lingcod exhibiting movements >8.1 km, and in some cases, as great as 50 km (Hart 1943; Jagielo 1990; Lea et al. 1997). Of importance to MPA managers is that the mean monthly percentage of days tagged lingcod were detected in Carmel Bay declined with time. This indicates that lingcod may exhibit a slow but constant rate of dispersion out a specific MPA with time.

Movements Related to Lingcod Size and Sex

Lingcod tagged in Carmel Bay demonstrated distinct patterns in residency and depth distributions based on sex, size class, and reproductive season. Lingcod are known to migrate to deeper waters at the onset of maturity (Jagielo 1999; Miller and Geibel 1973), and the patterns we observed for females in this study captured this ontogenetic separation. In the relatively shallow (7–40 m) depths we monitored, large female lingcod were present during fall spawning months but exhibited lower overall residence times and occupied deeper depths, compared to males and small females, for the rest of the year. Similarly, Starr et al. (2005) documented that adult lingcod segregate by sex for much of the year in Alaska. In the present study, it appears that this difference in sexual segregation occurs after the onset of maturity, as the small female lingcod tagged in Carmel Bay occupied similar depths and receiver locations as the males. Unlike females, male lingcod did not demonstrate a size-related difference in depth distributions or residence times, although this could be attributed to the relatively small size range of males tagged in this study.

Movements Related to Season and Physical Factors

The notable presence of large females in the receiver array during the fall directly coincides with their seasonal migration to shallow waters for reproduction (Miller and Geibel 1973). Four of the five large females tagged in this study were detected for several months on a receiver, went undetected for several months, and then were ultimately detected again on the same receivers throughout the year. The largest female we tagged (#71) was recaptured by a fisherman within 300 m of its original tagging location after 702 d at liberty. While we can only speculate on their movements outside of the array, the eventual return of these large females to the study area suggests these fish are not dispersing great distances outside of the reproductive season.

Similar to females, large male lingcod occupy deeper waters than their smaller counterparts for the majority of the year, but migrate to shallower waters to spawn and guard nests in fall and winter months (Cass et al. 1990, Jagielo 1995). Although not statistically significant, three of the four male lingcod exhibiting low overall residence times in this study were categorized in the larger size class and thus may have primarily resided in deeper waters beyond the areas we monitored. Male lingcod only feed opportunistically while guarding nests (Beaudreau & Essington 2007), then disperse in the spring (Low & Beamish 1978; Jagielo 1995; Starr et al. 2005; Bishop et al. 2010). In our study, there was an observed decrease in the mean monthly percentage of days that male lingcod were detected in April, which directly coincided with the end of nest guarding season and the start of spring upwelling conditions. However, the cross correlation analyses revealed an increase in daily detections of tagged lingcod during upwelling. We believe that these results, while seemingly contradictory, support the idea that lingcod in Carmel Bay are more actively foraging in the spring. Because the fish are more active, greater movement rates during spring upwelling conditions increased the likelihood of lingcod being detected by the receivers, even though monthly residency dropped as lingcod expanded their movements beyond the area we monitored. Starr et al. (2005) reported a similar springtime expansion of horizontal and vertical activity spaces for lingcod tagged in Alaska.

Interestingly, six of the seven male lingcod exhibiting low residence times in the spring were detected later in the year in the same area within the array. Thus, whereas male lingcod in Carmel Bay may be more active in the spring, they may not be dispersing far from their winter grounds. King and Withler (2005) used genetic sampling to show that individual male lingcod will return to specific nesting sites over multiple winter spawning seasons. Our results indicate that at least some male lingcod remain in the same general area throughout the rest of the year as well.

The number of lingcod detected was positively correlated with increased atmospheric pressure, wind speed, and upwelling indices and with decreased water temperatures, which are all associated with spring upwelling conditions. As stated earlier, we believe the increased number of detections is related to increased foraging activity, which is caused by an increased in the productivity of coastal waters caused by upwelling and the associated settlement of many juvenile fishes (Caselle et al. 2010). Also, the number of lingcod detected was positively correlated with wave energy. We believe this is related to lingcod coming off the bottom to avoid effects of the increased surge on the seafloor that is associated with wave orbitals.

CONCLUSIONS

Our observations of lingcod movements in Carmel Bay indicate that MPAs can be an effective management tool for conserving lingcod and for providing fishing benefits via adult spillover. Our study documented relatively restricted movements and long residence times for lingcod and supports other studies showing that this species can benefit from spatial closures to fishing (Starr et al. 2004, 2015). Although MPAs may provide a refuge from exploitation, our study reinforced conclusions of other research that suggests lingcod are also capable of moving multiple kilometers while foraging or during seasonal transitions (Jagielo 1990; Starr et al. 2004; Bishop et al. 2010). To this end, fishing grounds adjacent to MPAs are likely to be enhanced when these larger scale movements extend past a reserve boundary. In terms of conservation and fisheries benefits, MPA managers should expect that MPAs the size of California marine reserves (~15 km^2) will protect lingcod for long periods of time in a year, while supplementing fisheries outside the MPAs as a small subset of the lingcod in the MPA move out from time to time.

ACKNOWLEDGMENTS

We would like to thank John "J. D." Douglas, from MLML Marine Operations, and Diana Steller, from the MLML Research Diving Program, for supporting the many field logistics associated with this project. We thank two anonymous reviewers for providing suggested changes to the manuscript. Funding for this project was graciously provided by the UC Sea Grant Extension Program, the Dr. Earl H. Myers and Ethel M.

Myers Marine Biology Trust, the David and Lucile Packard Foundation, the PADI Foundation, and Otter Bay Wetsuits. The Seafloor Mapping Lab at California State University of Monterey Bay provided the multibeam imagery of Carmel Bay. Tagging procedures were conducted under SJSU IACUC permit #814.

LITERATURE CITED

Anthony, K. M., M. S. Love, and C. G. Lowe. 2012. Translocation, homing behavior and habitat use of groundfishes associated with oil platforms in the East Santa Barbara Channel, California. Bull. S. Calif. Acad. Sci., 111(2), pp. 101–118.

Beaudreau, A. H., and T. E. Essington. 2007. Spatial, temporal, and ontogenetic patterns of predation on rockfishes by lingcod. Trans. Am. Fish. Soc. 136:1438–1452.

Beaudreau, A. H., and T. E. Essington. 2011. Use of pelagic prey subsidies by demersal predators in rocky reefs: insight from movement patterns of lingcod. Mar. Biol. 158.2: 471–483.

Bishop, M. A., B. F. Reynolds, and S. P. Powers. 2010. An in Situ, individual-based approach to quantify connectivity of marine fish: ontogenetic movements and residency of lingcod. PLoS ONE 5:12: e14267.

Caselle, J. E., J. R. Wilson, M.H. Carr, D.P. Malone, and D. E. Wendt. 2010. Can we predict interannual and regional variation in delivery of pelagic juveniles to nearshore populations of rockfishes (genus sebastes) using simple proxies of ocean conditions? CalCOFI Rep 51:91–105.

Caselle, J. E., A. Rassweiler, S. L. Hamilton, and R. R. Warner. 2015. Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. Sci. Rep. 5: 14102.

Cass, A. J., R. J. Beamish, and G. A. McFarlane. 1990. Lingcod (*Ophiodon elongatus*). Can. Spec. Pub. Fish. Aquat. Sci. 109:1–44.

Gordon, D. A. 1994. Lingcod fishery and fishery monitoring in southeast Alaska. Alaska Fish Res Bull 1:140–152.

Green, K. M., and R. M. Starr. 2011. Movements of small adult black rockfish: implications for the design of MPAs. Mar Ecol Prog Ser. 436:219–230.

Green, K. M., A. P. Greenley, and R. M. Starr. 2014. Movements of blue rockfish (*Sebastes mystinus*) off central California with comparisons to similar species. PLoS ONE 9:6: e98976.

Hamel, O. S., S. A. Sethi, and T. F. Wadsworth. 2009. Status and future prospects for lingcod in waters off Washington, Oregon, and California as assessed in 2009. Status of the Pacific coast groundfish fishery through 2009. Stock Assessments and Fishery Evaluation. Pacific Fishery Management Council, Portland, OR.

Jagielo, T. H. 1990. Movement of tagged lingcod (*Ophiodon elongatus)* at Neah Bay, Washington. Fish. Bull. 88:815–820.

Jagielo, T. H. 1995. Abundance and survival of lingcod at Cape Flattery, Washington. Trans. Am. Fish. Soc. 124:170–183.

Jagielo, T. H. 1999. Movement, mortality, and size selectivity of sport- and trawl-caught lingcod off Washington. Trans. Am. Fish. Soc. 128:31–48.

Jagielo, T. H., D. Wilson-Vandenberg, J. Sneva, S. Rosenfeld, and F. Wallace. 2000. Assessment of lingcod (*Ophiodon elongatus*) for the Pacific Fishery Management Council in 2000. Pacific Fishery Management Council, Portland, OR.

Jagielo, T. H., and F. R. Wallace. 2005. Assessment of lingcod (*Ophiodon elongatus*) for the Pacific Fishery Management Council. Pacific Fishery Management Council, Portland, OR.

King, J. R., and R. E. Withler. 2005. Male nest site fidelity and female serial polyandry in lingcod (*Ophiodon elongatus*, Hexagrammidae). Mol. Ecol. 14:653–660.

Kramer, D. L., and M. R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. Environ. Biol. Fish. 55:65–79.

Laidig, T. E., P. B. Adams, K. R. Silberberg, and H. E. Fish. 1997. Conversions between total, fork, and standard lengths for lingcod, *Ophiodon elongatus*. Calif. Dep. Fish. Game, Fish Bull. 83(3):128–129.

Lea, R. N., R. D. McAllister, and D. A. Van Tresca. 1999. Biological aspects of nearshore rockfishes of the genus *Sebastes* from central California. Calif. Dep. Fish. Game, Fish Bull. 177:1–109.

Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. Ruttenberg, S. D. Gaines, S. Airamé, and R. R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384:33–46.

Low, C. J., and R. J. Beamish. 1978. A study of the nesting behavior of lingcod (*Ophiodon elongatus*) in the strait of Georgia, British Columbia. Can. Fish. Mar. Serv. Tech. Rep. 843.

Lowe, C. G., K. M. Anthony, E. T. Jarvis, L. F. Bellquist, and M. S. Love. 2009. Site fidelity and movement patterns of groundfish associated with offshore petroleum platforms in the Santa Barbara Channel. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science. 1:71–89.

Mathews, S. B., and M. LaRiviere. 1987. Movement of tagged lingcod, *Ophiodon elongatus*, in the Pacific Northwest. Fish. Bull, 85:153–159.

Matthews, K. R. 1992. A telemetric study of the home ranges and homing routes of lingcod, *Ophiodon elongatus,* on shallow rocky reefs off Vancouver Island, British Columbia. Fish. Bull. 90:784–790.

Miller, D. J., and J. J. Geibel. 1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera,* experiments in Monterey Bay, California. Calif. Dept. Fish and Game, Fish. Bull. 158.

Molloy P. P., I. B. McLean, and I. M. Coté. 2009. Effects of marine reserve age on fish populations: a global meta-analysis. J. Appl. Ecol. 46:743–751.

Silberberg, K. R., T. E. Laidig, P. B. Adams, and D. Albin. 2001. Analysis of maturity in lingcod, *Ophiodon elongatus*. Calif. Fish. Game 87:139–152.

Simpfendorfer, C. A., M. R. Heupel, and R. E Hueter. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can. J. Fish. and Aquat. Sci, 59(1), pp. 23–32.

Smith, B. D., G. A. McFarlane, and A. J. Cass 1990. Movements and mortality of tagged male and female lingcod in the Strait of Georgia, British Columbia. Trans. Am. Fish. Soc. 119:813–824.

Starr, R. M., J. N. Heine, and K. A. Johnson. 2000. Techniques for tagging and tracking deepwater rockfishes. North Am. J. Fish. Manage. 20:597–609.

Starr, R. M., J. N. Heine, J. M. Felton, and G. M. Cailliet. 2002. Movements of bocaccio (*Sebastes paucispinis*) and greenspotted (*S. chlorostictus*) rockfishes in a Monterey submarine canyon: implications for the design of marine reserves. Fish. Bull. 100:324–337.

Starr, R. M., V. O'Connell, and S. Ralston. 2004. Movements of lingcod (*Ophiodon elongatus*) in southeast Alaska: potential for increased conservation and yield from marine reserves. Can. J. Fish. Aquat. Sci. 61:1083–1094.

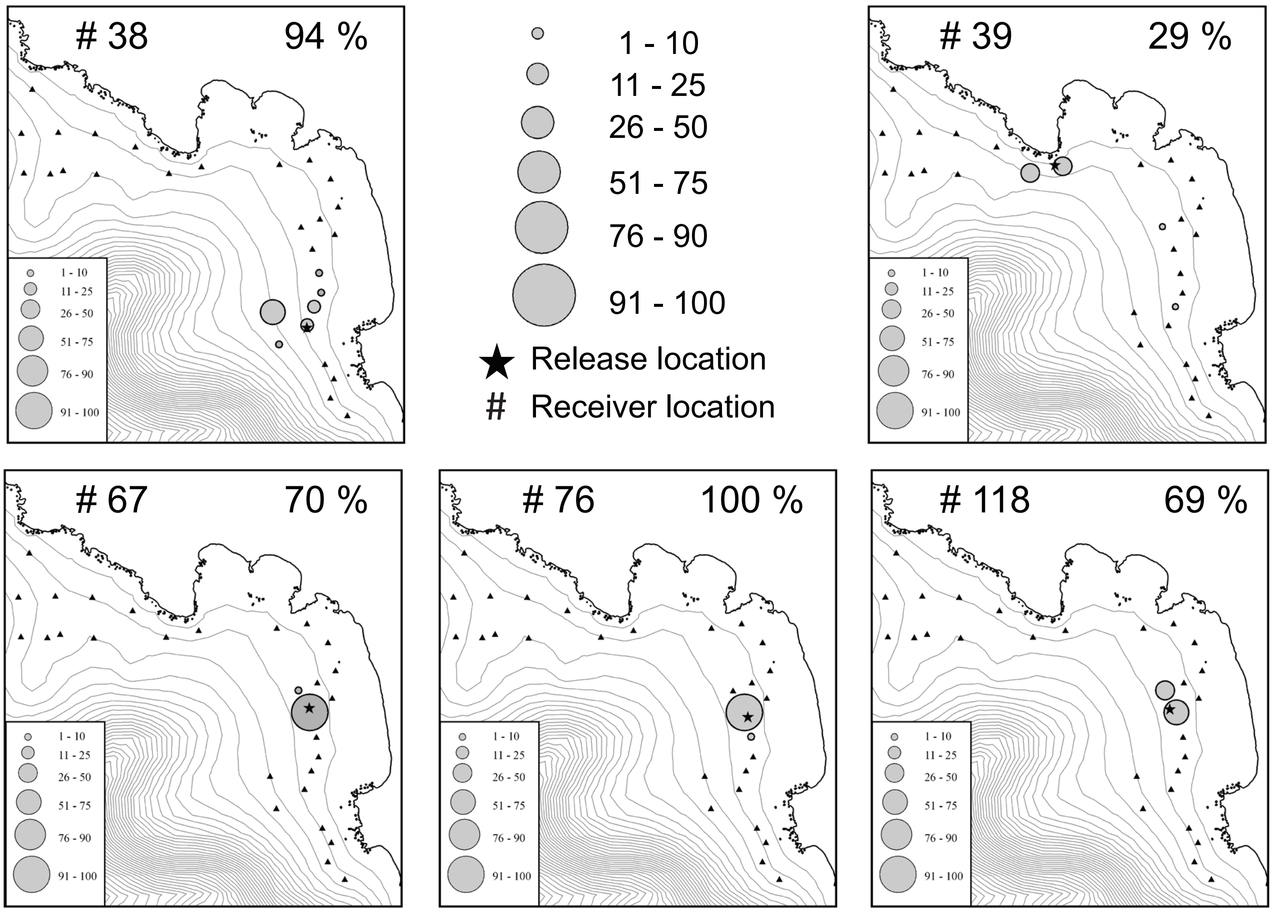
Starr, R. M., V. O'Connell, S. Ralston, and L. Breaker. 2005. Use of acoustic tags to estimate natural mortality, spillover, and movements of lingcod (*Ophiodon elongatus*) in a marine reserve. Mar. Technol. Soc. J. 39:19–30.

Starr, R. M., D. E. Wendt, C. L. Barnes, C. I. Marks, D. Malone, G. Waltz, K. T. Schmidt, J. Chiu, A. L. Launer, N. C. Hall, and N. Yochum. 2015. Variation in responses of fishes across multiple reserves within a network of marine protected areas in temperate waters. PLoS ONE 10: e0118502.

Tolimieri, N., K. Andrews, G. Williams, S. Katz, and P. S. Levin. 2009. Home range size and patterns of space use by lingcod, copper rockfish and quillback rockfish in relation to diel and tidal cycles. Mar Ecol Prog Ser, 380, pp. 229–243.

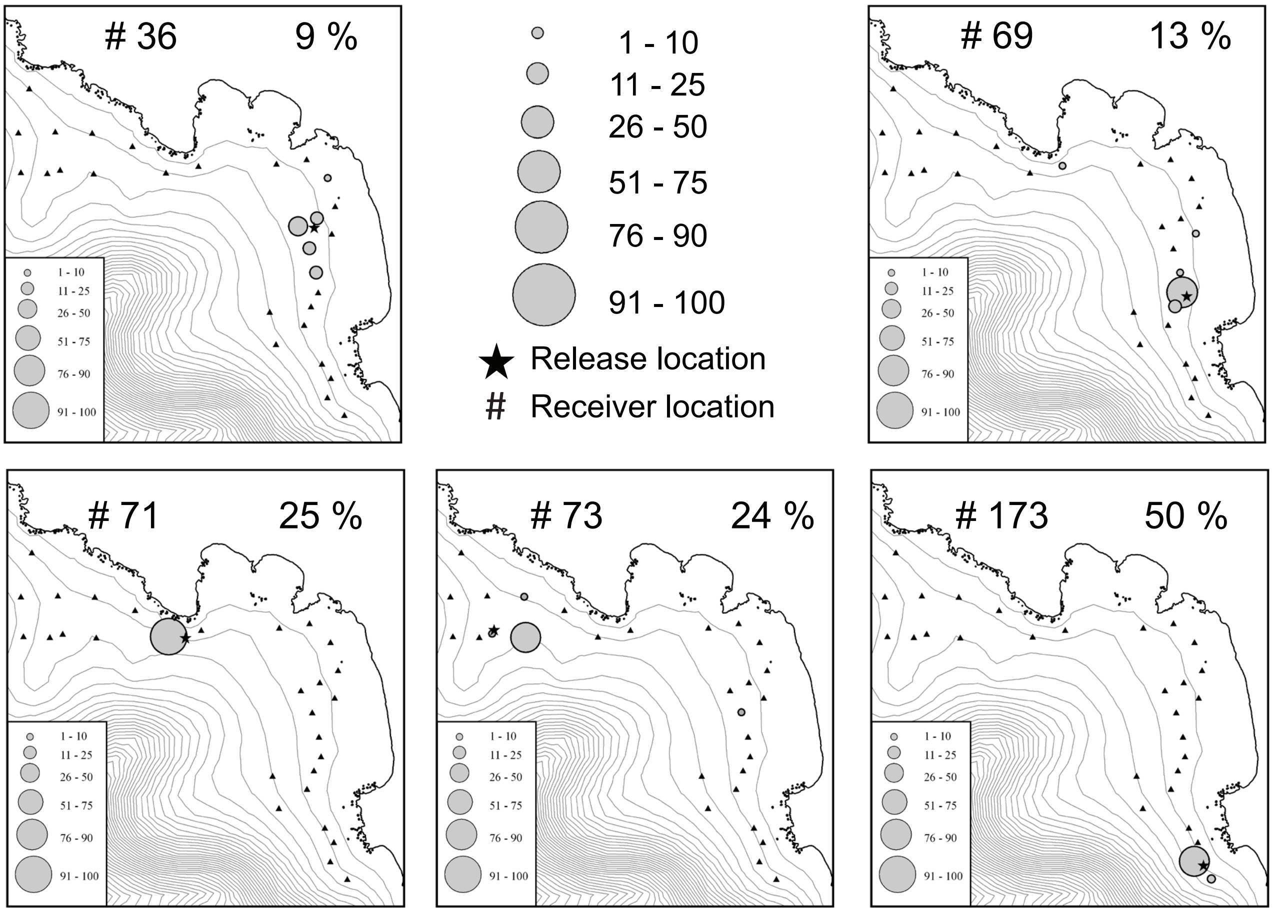
Topping, D. T., C. G. Lowe, and J. E. Caselle. 2006. Site fidelity and seasonal movement patterns of adult California sheephead *Semicossyphus pulcher* (Labridae): an acoustic monitoring study. Mar. Ecol. Prog. Ser. 326:257–267.

APPENDIX A



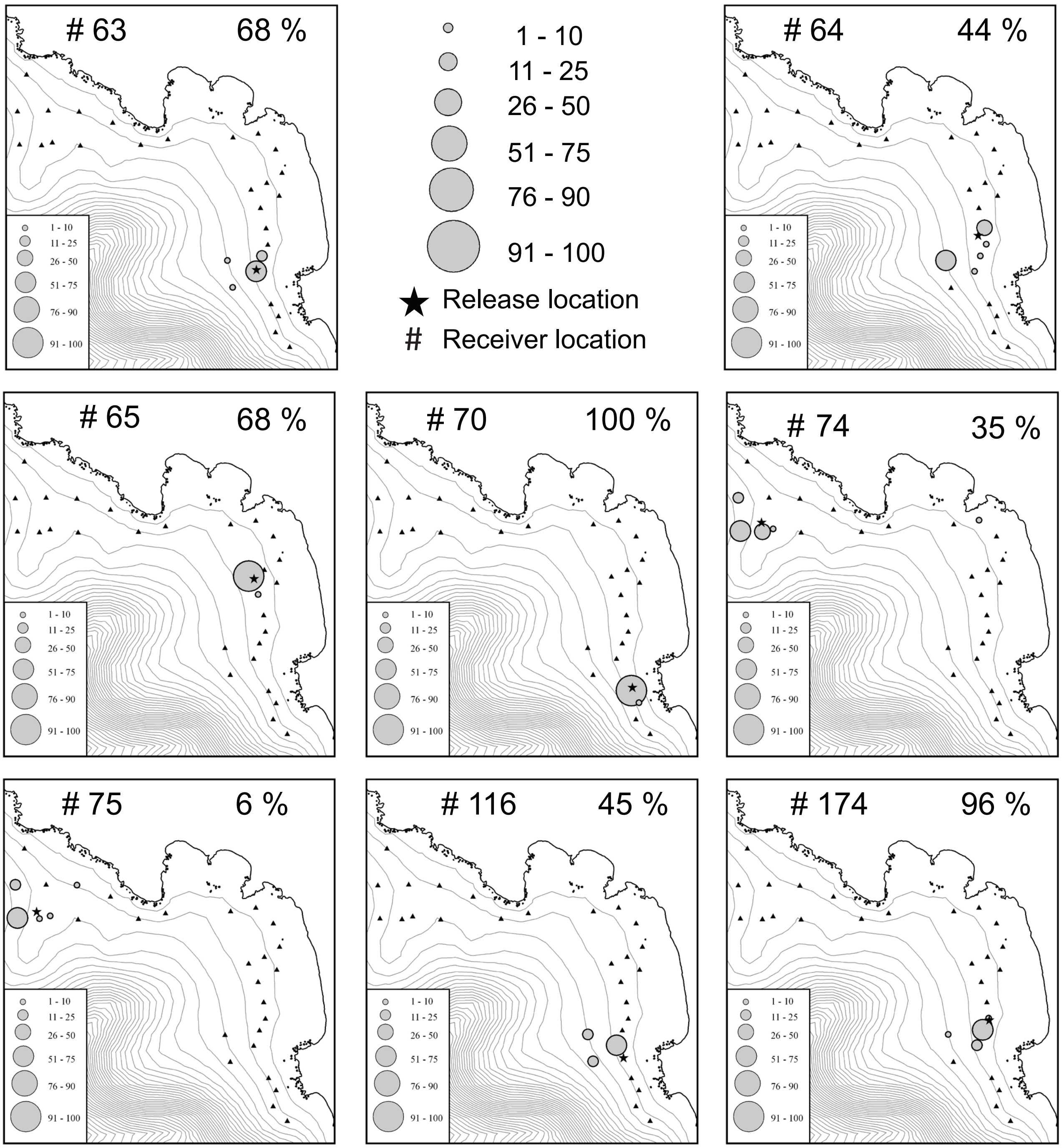
Appendix A. Proportion of hour bins with recorded signals relative to receiver locations for small female lingcod. Numbers at the top of each map correspond to the tag number of the lingcod (left) and the percentage of days at liberty detected in the array (right).

APPENDIX B



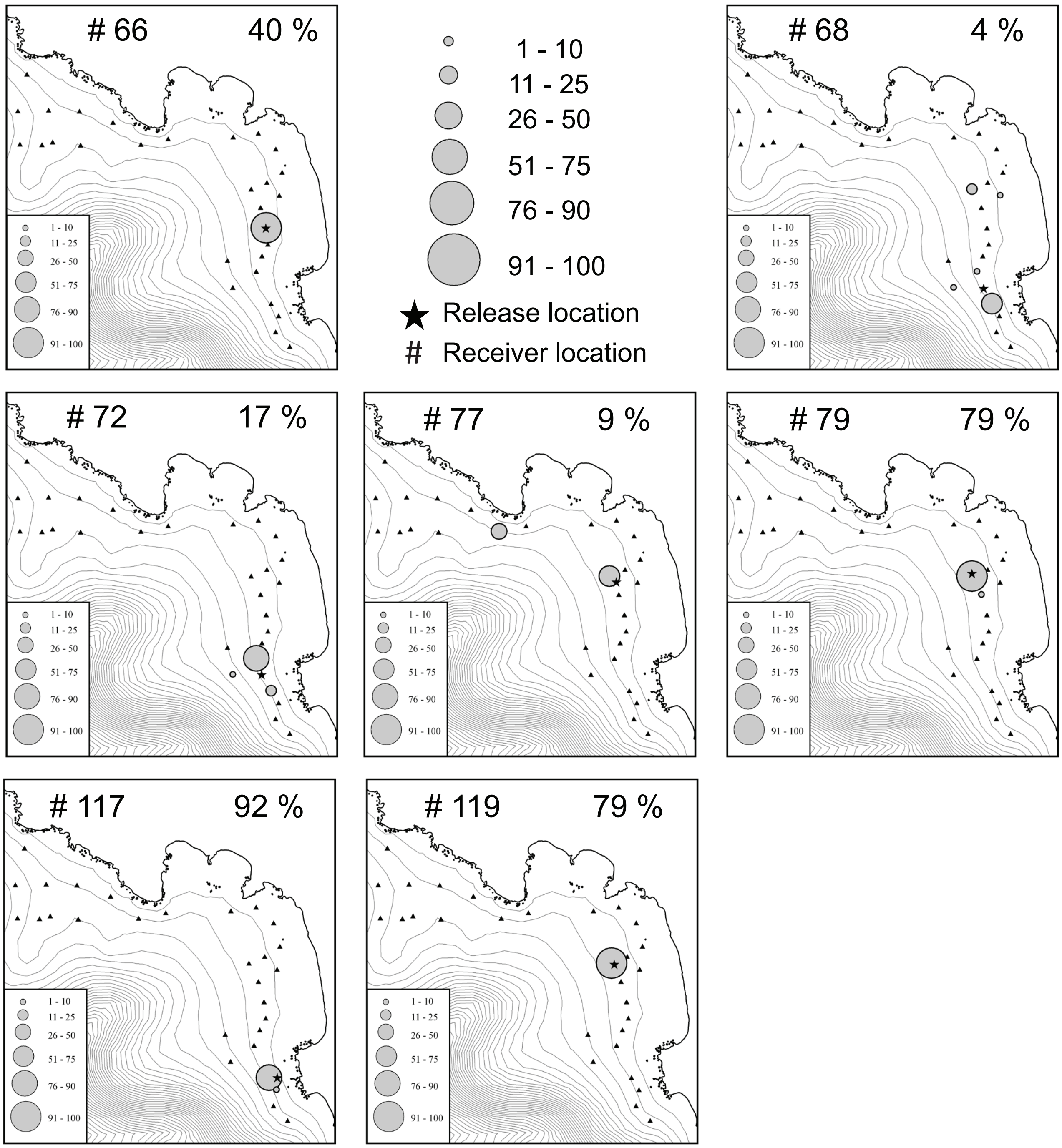
Appendix B. Proportion of hour bins with recorded signals relative to receiver locations for large female lingcod. Numbers at the top of each map correspond to the tag number of the lingcod (left) and the percentage of days at liberty detected in the array (right).

APPENDIX C



Appendix C. Proportion of hour bins with recorded signals relative to receiver locations for small male lingcod. Numbers at the top of each map correspond to the tag number of the lingcod (left) and the percentage of days at liberty detected in the array (right).

APPENDIX D



Appendix D. Proportion of hour bins with recorded signals relative to receiver locations for large male lingcod. Numbers at the top of each map correspond to the tag number of the lingcod (left) and the percentage of days at liberty detected in the array (right).