MOVEMENTS OF LINGCOD (*OPHIODON ELONGATUS*)

TAGGED IN CARMEL BAY, CA

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by
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ABSTRACT

MOVEMENTS OF LINGCOD (*OPHIODON ELONGATUS*)
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Movements of 30 lingcod (*Ophiodon elongatus*) tagged with acoustic transmitters were monitored over one year using an array of acoustic receivers in Carmel Bay, CA. For all tagged lingcod, residence times in the array varied from 3.8 to 100% of their respective days at liberty. On average, lingcod spent 42.5 d ± 17.9 (SE) consecutive days in and 8.1 d ± 1.5 (SE) consecutive days out of the array. Residency significantly decreased with total length for female lingcod while a significant relationship was not exhibited for male lingcod. Large female lingcod, at lengths > 90% maturity, spent the least amount of time in the array but were present during the fall spawning season and briefly during the spring. There was an observed decline in residency in April for males and small female lingcod, the timing of which coincided with the post nest-guarding dispersal period for males and also with the return of large females into the array. Large female lingcod were recorded at significantly greater depths within the array compared to male and small female lingcod. Lingcod exhibited strong site fidelity, with tagged fish recorded on 1 receiver for an average of 76.8 % (± 3.7 SE) of all 1-hour time bins containing signals and on 2 adjacent receivers for 91.0 % (± 4.3 SE) of all 1-hour time bins. There was no significant difference in site fidelity among sexes and size classes of tagged lingcod, and patterns of movements were not found to be different among lingcod released in high, medium, and low relief habitats.

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INTRODUCTION

Movement of organisms in time and space is a key process governing population dynamics and community structure (Morales & Ellner 2002, Turchin 1998). Movements are important to determine, not only to better understand the ecological and biological roles of species within the environment, but also to improve how exploited species are managed and conserved. For marine organisms, resource managers are tasked with applying appropriate scales of management that best incorporate the population biology and dispersal capabilities of targeted species (Palumbi 2004). In recent years, traditional management strategies used over large geographic distances have been augmented with smaller-scale ecosystem-based approaches such as marine protected areas (MPAs) (Allison et al. 1998, Lubchenco et al. 2003). The influx of MPAs into management schemes has further generated a need for information on species movements, as the amount of protection provided by MPAs greatly depends on whether or not the activities of individual species are contained within reserve boundaries (Rowley 1994, Kramer & Chapman 1999).

Under the 1999 California Marine Life Protection Act (MLPA), California is currently developing a network of MPAs throughout its state waters (Weber & Henneman 2000). To ensure that the MLPA implementation process was based on scientific principals, a Master Plan Science Advisory Team (SAT) was created to provide guidelines for the sizing and spacing of MPAs within states waters (CDFG 2007). The SAT used many criteria for its guidelines, including estimates of larval dispersal for spacing between MPAs and characterizations of bottom habitat for MPA placement. For

MPA sizing, the SAT used available information on adult movement patterns for a suite of species to recommend minimum (5 – 10 km alongshore) and preferable (10 – 20 km alongshore) MPA size guidelines (CDFG 2008).

The lingcod (*Ophiodon elongatus*) was a key species identified by the SAT as likely to benefit from the implementation of MPAs (CDFG 2008). Lingcod are found primarily in nearshore waters in of 10 to 100m (McFarlane & King 2001) and are heavily targeted by commercial and recreational fisheries throughout their distribution along the west coast of North America (Jagielo & Wallace 2005). Although there have been numerous studies on their movements, activity patterns of lingcod have yet to be completely understood. These uncertainties have created complications for MPA placement and sizing. Lingcod, for example, are primarily characterized as residential (Cass et al. 1990), yet some scientists have argued that MPAs would need to be relatively large to afford lingcod complete protection from fishing (Martell et al. 2000, Walters et al. 2007). This apparent contradiction largely stems from inconsistencies in the literature, as various tag recapture studies on lingcod have either documented limited movement (Hart 1943, Davis 1986, Cass et al. 1986) or more widespread migratory behavior (Mathews and LaRiviere 1986, Smith et al. 1990, Jagielo 1995).

To clarify existing ambiguities concerning the movements of lingcod, I designed an acoustic tracking study in central California with three main objectives: 1) to determine the residence time of lingcod tagged with acoustic transmitters in the nearshore environment in Carmel Bay during a 1-year period; 2) to compare movements among sexes and sizes of lingcod; and 3) to determine if movements vary with time of day, season, physical factors, or habitat relief. This research will help resolve discrepancies regarding lingcod movements in California, and will provide resource managers and scientists with information directly applicable to the design and assessment of marine protected areas. This study will also contribute to an overall understanding of the life history and ecology of a heavily fished species.

Lingcod range from the Shumagin Islands in Alaska to Punta Banda, Baja California, with the center of their abundance in British Columbia (Cass et al. 1990). Lingcod are the largest member of the family Hexagrammidae and are sexually dimorphic in that females attain bigger sizes, grow faster, and live longer than males (Jagielo 1999). Maximum age for lingcod, determined and validated from cross sections of dorsal fin rays, is 20 years for females and 14 years for males (Beamish & Chilton 1977, McFarlane & King 2001). Aside from occupying the epipelagic zone during larval stages, lingcod are benthic fish that prey on other fishes and cephalopods (Miller & Geibel 1973). Juvenile lingcod ranging in size from 20 to 40 cm total length (TL) typically inhabit flat sandy areas before moving to rocky habitats at age two (Miller & Geibel 1973, Cass et al. 1990).

Since the 1950s, lingcod populations have declined dramatically, leading the Pacific Fisheries Management Council to declare them overfished in 2000. Lingcod populations were later declared rebuilt in 2005, although southern stocks (south of Cape Blanco, Oregon) have recovered more slowly than northern stocks (north of Cape Blanco) (Jagielo & Wallace 2005). This difference in recovery rates, along with recent genetic evidence that lingcod exhibit limited connectivity at relatively small (100 kms) spatial scales, illustrates that smaller-scale approaches to management may be more appropriate for lingcod stocks (Marko et al. 2008). However, matching appropriate scales of management for lingcod is greatly dependent on information regarding adult movement patterns.

Most of the information regarding lingcod movements has been gathered from tag-recapture studies. Although relatively inexpensive to conduct, these studies are heavily dependent on spatial and temporal patterns in fishing effort and provide information only on the net movements of fishes. As fishes are not continuously monitored in tag-recapture studies, the spatial resolution of the data is minimal and often difficult to interpret. These limitations likely explain why researchers using tag-recapture methodologies have reported conflicting results for lingcod. For example, tag-recapture studies in Washington and British Columbia characterized lingcod as residential, with 95% of recaptured fish caught within 10 km of the release site (Hart 1943, Davis 1986, Cass et al. 1986, Cass et al. 1990). Mathews and LaRiviere (1986), however, reported migratory behavior for lingcod in Canada, with 9 % of the tagged fish recaptured at distances greater than 50 km.

The apparent discrepancies of these tag-recapture studies on lingcod were later clarified with acoustic tracking techniques, which allow for continual monitoring of tagged fishes and thus provide information with greater spatial and temporal resolution. Using acoustic transmitters, Starr et al. (2005) found that lingcod tagged on an offshore pinnacle in Alaska spent large amounts of time on the pinnacle, but frequently left for 2-3 days at a time before returning. Their results explained why some tag-recapture studies indicated limited movement for lingcod whereas others reported greater dispersal distances, with the distance of movements greatly dependent on whether or not a lingcod was caught during a foray from its primary area of occupancy.

Lingcod exhibit sexual segregation in their spatial distributions, whereby adult females occupy deeper waters than male conspecifics (Jagielo 1990, Gordon 1994). In late fall, females temporarily migrate to nearshore waters to lay eggs, where males have already established territories (Cass et al. 1990). After eggs have been laid, males remain nearshore to guard nests for the following 5 to 7 weeks (Low & Beamish 1978). Off California, nest guarding occurs from October through January (Miller & Geibel 1973). Site fidelity of male lingcod is thought to decrease after nest-guarding season, however it has yet to be determined how far and to what depths they disperse. There is some evidence from tag-recapture data that males move to deeper, offshore waters (Jagielo 1995) following the reproductive season. However, nearshore catches are dominated by males year-around (Miller & Geibel 1973), indicating that at least some males remain nearshore for the duration of the year.

In Alaska, male lingcod moved to deeper waters during post-reproductive months while females concurrently moved to shallower depths (Starr et al. 2005). The authors proposed that the larger, female lingcod may have been competitively displacing male lingcod for food resources. It is unclear whether or not the male lingcod in that study moved to deeper waters because of the time of the year, the presence of females, or a combination of both. It is also uncertain if the observed depth distributions for lingcod on the offshore pinnacle in Alaska are typical of nearshore populations in California.

Although it is not clear whether male lingcod remain or disperse from the nesting area, genetic studies have indicated that males exhibit strong inter-annual fidelity to nesting locations, with some males reusing the same nesting site between years (King & Withler 2005). Interestingly, female lingcod in their study only spawned once in the study site during two years of sampling. The authors proposed that the difference in nesting site fidelity between males and females was a reproductive strategy to attain polygamy and maximize genetic diversity in progeny.

Juvenile lingcod disperse over greater distances than adults (Cass et al. 1990) and exhibit limited site fidelity compared to mature fish (Yamanka & Richards 1993). The differences in movement patterns between juveniles and adults may be habitat related, as juveniles occupy flat sandy areas until approximately 20-40 cm TL, when they move to rocky habitats (Miller & Geibel 1973). For larger lingcod in rocky areas, a size-related difference in movement patterns has yet to be thoroughly examined. Matthews (1992) provided indirect evidence for a relationship between size and movements by tracking the homing capabilities of five displaced lingcod. All but the smallest of the displaced fish demonstrated homing, leading the author to hypothesize that this fish was sexually immature and lacked homing ability. Lesser sample size and an inability to externally determine the sexual condition of the fishes in that study prevented the author from making any definite conclusions.

Although adult lingcod occupy rocky habitats (Miller & Geibel 1973, Cass et al. 1990, Gordon 1994), site fidelity and movements in relation to habitat relief have yet to be quantified for lingcod. For marine fishes, it has been proposed that sizes of home ranges is inversely related to habitat complexity (Lowe & Bray 2006). Matthews (1990) demonstrated such a relationship for two species of rockfishes in Puget Sound, whereby fishes occupying high relief habitats had smaller home ranges and stronger site fidelity than fishes in low relief habitats. The underlying basis for these patterns is that habitat quality, measured by the availability of shelter sites and prey, increases with substrate relief (Allen 1985). Thus, if habitat relief is a consistent measure of habitat quality, and habitat quality influences movements of fishes, then the site fidelity of lingcod also would be expected to increase with increasing habitat relief.

Most studies of lingcod movements were in Oregon, Washington, Canada, or Alaska (Barss & Demory 1989, Cass et al. 1990, Jagielo 1990, Smith et al. 1990, Matthews 1992, Jagielo 1995, Starr et al. 2004). Lingcod attain larger sizes at the northern range of their distribution (Karpov et al. 1995), but whether there is a geographical difference in movement patterns remains undetermined. To date, the only published tagging studies of lingcod in California have used tag-recapture techniques (Miller & Geibel 1973, Lea et al. 1999), which only indicate net movements.

Acoustic tracking techniques have advantages over traditional tag-recapture methodologies in that continuous movement data can be collected over multiple temporal and spatial scales. For relatively long-term (e.g., 1 yr) tracking studies, many researchers have successfully used automated acoustic monitoring receivers (Arendt et al. 2001, Vogeli et al. 2001, Lowe et al. 2003, Starr et al. 2002, Starr et al. 2004, Topping et al. 2006, Lindholm et al. 2007). In those studies, acoustic receivers were moored underwater and continuously recorded signals from fish tagged with individually coded transmitters. Although the spatial resolution of those studies was limited to presence or absence within the omnidirectional range of each receiver, tracking with acoustic monitors is advantageous for several reasons: 1) movements of animals can be tracked for long (>1 yr) periods of time, 2) receiver arrays allow for relatively large areas to be monitored, 3) more than one animal can be tracked simultaneously, 4) less time and effort on boats is required than active tracking with hydrophones, and 5) fishes can be tracked for 24 hours a day (Heupel et al. 2004, Simpfendorfer et al. 2002).

MATERIALS AND METHODS

Study site. Carmel Bay is located along the central California coast, on the south-western side of the Monterey Peninsula in central California (Fig. 1).

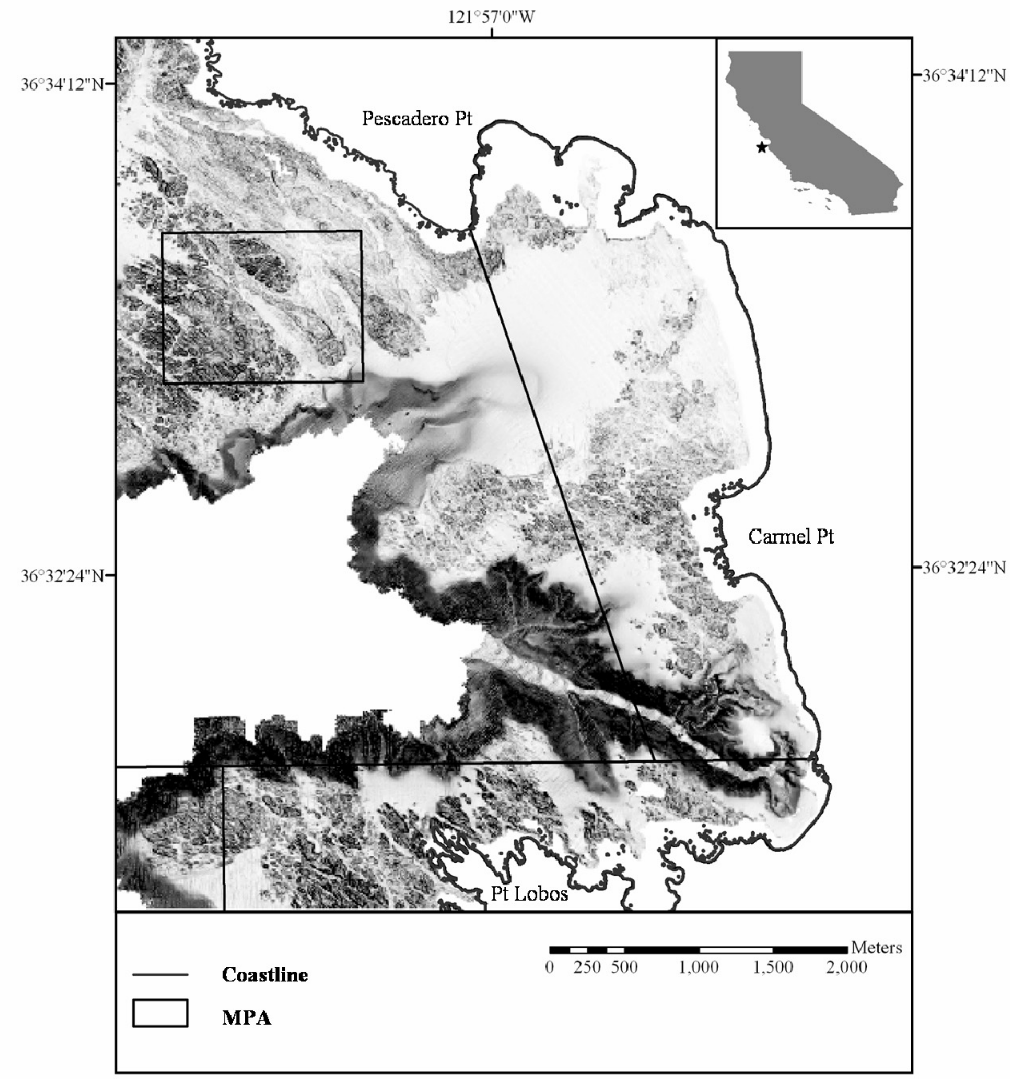


Fig. 1. Multibeam bathymetry imagery of Carmel Bay with an overlay of MPA locations. SMCA denotes State Marine Conservation Area and SMR denotes State Marine Reserve.

From Pescadero Point to Point Lobos, the bay is approximately 4 km long and 2 km wide. Carmel Bay is bisected by Carmel Canyon, one of five major canyons comprising the Monterey Canyon System (Greene et al. 2002). Due to the presence of the canyon, the continental shelf in Carmel Bay is relatively narrow. The area monitored in this study was located north of the Carmel Canyon head, from Carmel Point to approximately 1 km northwest of Pescadero Pt. (Fig. 1). Several distinct bottom habitats occur in the area, including contiguous high-relief granite outcrops, patchy areas of low-relief bedrock, and sand bottom. Nearshore areas in Carmel Bay also are characterized by the occurrence of giant kelp (*Macrocystis pyrifera*), which peaks in biomass and density during spring and summer (Reed & Foster 1984).

Four separate marine protected areas are located within or in close proximity of Carmel Bay: Point Lobos State Marine Conservation Area (SMCA), Point Lobos State Marine Reserve (SMR), Carmel Bay SMCA, and the Carmel Pinnacles SMR (Fig. 1). Point Lobos SMR, established in 1973, and Carmel Bay SMCA, in 1974, are the oldest of the MPAs in Carmel Bay (McArdle 1997). The Carmel Pinnacles SMR and the Point Lobos SMCA were established during the time of this study, with regulations implemented in September 2007 under the MLPA. Only two of the MPAs, Carmel Bay SMCA and the Carmel Pinnacles SMR, are encompassed within the area of this study. Carmel Bay SMCA only precludes commercial fishing and the Carmel Pinnacles SMR prohibits all take of fishes, invertebrates, and algae.

Fishing and tagging. In 2005, lingcod were captured on chartered commercial fishing vessels using handlines and rebar with baited hooks, known as Portuguese sticks. Fishing in 2006 took place aboard small research vessels, using rod and reel rigged with plastic jigs. Once a lingcod was captured, the overall condition of the fish was examined; only lingcod appearing healthy, with no visible damage, were selected for tagging. Lingcod were anesthetized in a 10 % seawater solution containing methylethyl sulfate (MS 222). When a fish displayed signs of disorientation, it was transferred to a tagging board for surgery. Transmitters sterilized in iodine were implanted into the peritoneal cavity through a small incision on the ventral side, and the incisions were closed using staple sutures as described in Mortensen (1990). To allow for visual identification, an external t-bar anchor tag also was implanted into the dorsal musculature of the fish. These external tags were printed with a unique identification number for the fish and the phone number of Moss Landing Marine Laboratories, should the lingcod be recaptured by other fishers after release. Similar tagging procedures have been successful in previous tagging studies involving lingcod and rockfishes (Starr et al. 2000, Starr et al. 2004).

The transmitters used in this study (Vemco V13P-1H-S256) were 44 mm long and weighed approximately 6.6 g in water. To extend battery life and reduce the possibility of signal collision among tags, the transmitters were programmed to ping randomly at intervals between 90 and 270 seconds. Expected battery life for the transmitters was approximately a year, although some tags were detected for >700 d. Each tag produced a unique identification code to allow for recognition of individual fish and also relayed depth information.

Thirty lingcod were tagged in the late summer and early fall of 2005 and 2006. Male and female lingcod in two size classes were targeted, with sex assessed from the presence or absence of a small conical papilla behind the anal vent. To increase confidence in determining sex externally, 10 lingcod were sacrificed before acoustic tagging. Sexes for all of the sacrificed fish were correctly identified, as validated by an internal inspection of their gonads. The two size classes of lingcod selected for the study were fish at lengths between 50 and 90 percent maturity, and fish at lengths greater than or equal to 90 percent maturity. As a non-lethal assessment of maturity was not possible, I acknowledged that some fish in the smaller size class could be mature and also that some lingcod grouped into the larger size class could be immature. Therefore, I could not state positively that fish in the small size class were immature and vice versa for the large size class. However, size classes were useful in the study design as they enabled me to tag lingcod over a range of sizes. Lengths at 50 percent maturity (males 47 cm TL; females 57 cm TL) and 90 percent maturity (males 61 cm TL; females 67 cm TL) were based on calculations by Silberberg et al. (2001) for lingcod in central California, using a formula to convert fork length to total length by Laidig et al. (1997). Lingcod at lengths less than 10 percent maturity (males 39 cm TL; females 46 cm TL) were not targeted because they were not caught in the study area during previous sampling efforts in 2005.

Acoustic monitoring. I used an array of thirty Vemco, Inc. VR-2 single-channel acoustic receivers to monitor movements of lingcod tagged in Carmel Bay (Fig. 1, Fig.2).

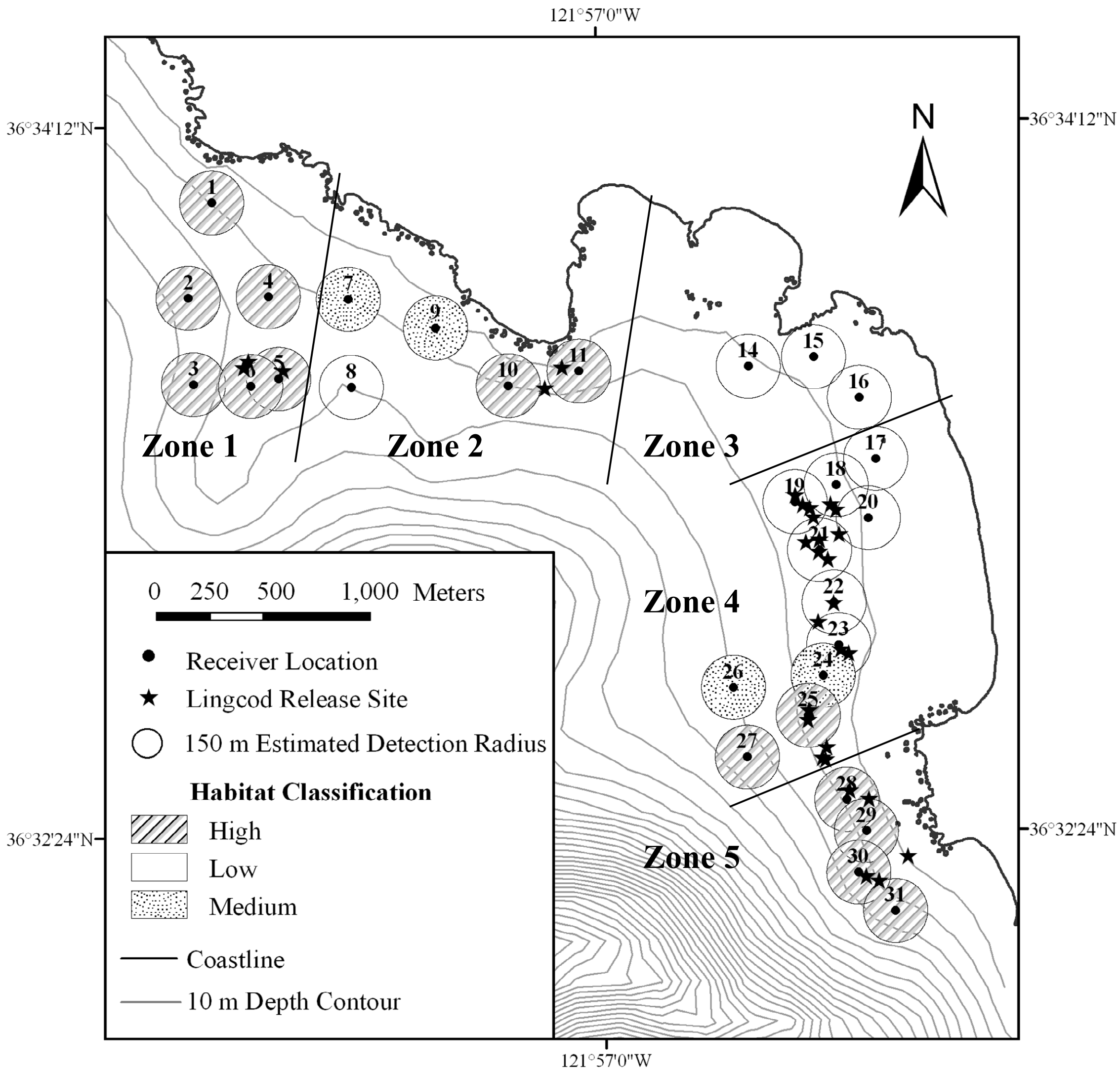


Fig 2. Configuration of VR2 receiver array with estimated 150 m detection ranges and zone delineation. Dots indicate receiver locations and stars are release locations of tagged fish. Circles indicate estimated detection zones and are shaded to reflect relief classification of the seafloor within the detection zone.

The receivers record 69 kHz signals emitted from acoustic transmitters implanted in lingcod. Along with the time and date at which the signals were received, the VR2s recorded the transmitter ID and depth of tagged fish swimming within the receiver's detection range.

From bottom to top, the moorings used to deploy the receivers consisted of a 35 kg cement block, 1 m of galvanized chain, a galvanized swivel, 1.5 cm diameter nylon line, and a subsurface float. The floats, with approximately 5 kg of lift, kept the receivers erect in the water column. Most of the moorings in the array extended 6 m from the bottom, with the receiver affixed to the line at approximately 5 m from the seafloor. In areas greater than 30 m depth, the receivers were suspended farther from the seafloor to limit SCUBA diving depths during retrieval. Approximately every 6 months, SCUBA divers retrieved receivers and replaced them with VR2s with new batteries. Data from retrieved receivers were downloaded in the laboratory, converted to text files, and transferred to a Microsoft Access database. Occasionally, during storm events, a receiver washed up on a local beach. In those cases, the receiver was retrieved and redeployed as soon as possible.

In 2005, 19 receivers comprised the array, which extended from Pescadero Point to Carmel Point (location 11 to location 31). This original receiver configuration allowed for the monitoring of lingcod movements within part of the Carmel Bay SMCA. In fall 2006, 11 receivers were added north and west of Pescadero Point (locations 1 to 10). This final configuration of receivers extended along approximately 5 km of coastline, with individual receivers moored at depths ranging from 7 to 40 m (Fig. 2). The purpose of the

2006 array extension was to include the Carmel Pinnacles, which had been designated as a state marine reserve earlier that year. The majority of fish tagging was conducted within the original confines of the 2005 array, although three lingcod were tagged on the Pinnacles in 2006.

The VR2 array used in this study was designed to maximize monitoring coverage of the entire nearshore area. Maximizing coverage area, however, diminishes the spatial resolution of data as receivers are not necessarily placed in positions with overlapping detection zones (Domeier 2005). To increase the monitoring resolution within a confined area in the array, 8 VR2 receivers were temporarily moored to form a ring around 4 permanent VR2 receivers in the array (Fig. 3). These additional 8 receivers were deployed for one month in August 2007.

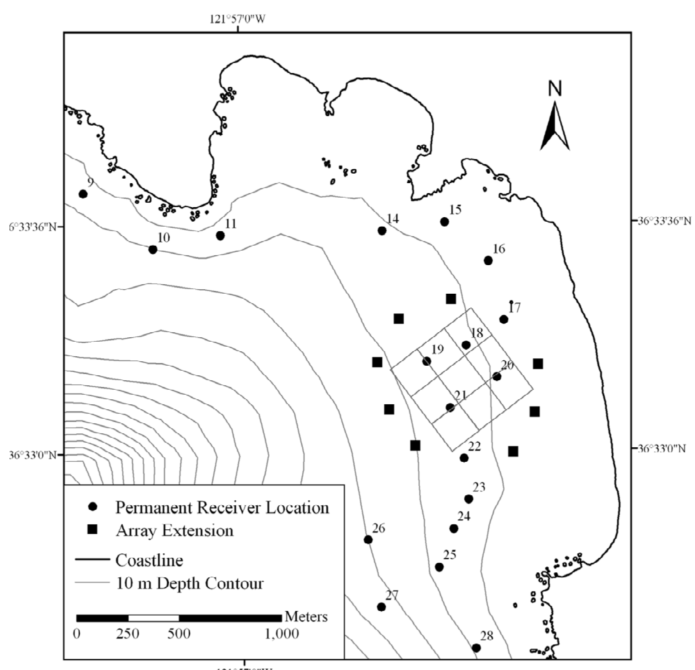


Fig. 3. Location of the temporary (1 month) receiver array extension and grid for VR100 surveys. Solid black squares indicate location of temporary VR2 receivers.

Using VR2 receivers to monitor fish movements has limitations. One of the greatest challenges with VR2s is that it is difficult to delineate whether an absence of detections is caused from an actual fish departure or from a blocked signal caused by bottom topography or vegetation. To address this problem, in August 2007 a 500 m by 500 m grid within the array was intensively surveyed with a multi-channel Vemco VR100 directional hydrophone (Fig. 3). As the VR100 was mounted to a boat at the surface, the hydrophone was mobile and able to detect acoustic signals at a higher spatial resolution in comparison with the moored acoustic receivers. For the VR100 surveys, a 500 m by 500 m grid within the array was divided into 9 cells of equivalent dimensions (approximately 170 m by 170 m). Six cells were sampled during a survey and all surveys were repeated on 4 separate days and 4 separate nights, for a total of 8 surveys. In each cell sampled, a location was randomly selected to "listen" for tag signals for 30 min. The 30-min sampling time was based on published information from Vemco regarding the time necessary to ensure the detection of a tag given its signal transmission properties and the number of other tags in the area. Data from the VR100 surveys were later compared with VR2 data from receivers within the survey area to determine if tagged fish were present in the survey area but undetected by the VR2 receivers.

Range testing. Detection ranges of VR2 receivers are affected by sea state, biological and anthropogenic noise, bottom topography, and submerged vegetation (Simpfendorfer et al. 2002). In 2005, before the receiver array was deployed, range testing was conducted to estimate detection capabilities of VR2 receivers in the study area. To gain a conservative estimate of detection ranges, the testing was conducted in kelp beds in late summer, when kelp densities were great. For the range tests, a V13 transmitter was attached to a weighted line and deployed at 50 m intervals from receivers deployed throughout the kelp bed. The transmitter was suspended 1 m from the bottom and was held at each station for 15 minutes. The receivers were then collected and downloaded. Preliminary results from these tests indicated detection ranges of 150 m for the receivers. Based on these range estimates, receivers were moored throughout the array at approximately 300 m intervals, where overlapping of detection ranges was estimated to be minimal. Range testing also was conducted in late winter, to determine whether detection ranges improved when seasonal kelp densities were low from storm activities.

Variation in detection ranges over a relatively long time scale was examined by mooring a reference transmitter (V13-1H-R04K) 1 m off the seafloor at a fixed location. This type of transmitter was programmed to relay a unique identification code but did not relay depth information. The transmitter was placed equidistant (140 m) from two VR2 acoustic receivers (at locations #22 and #23) in an area representative of seasonal kelp densities throughout the array. Data from the reference transmitter were analyzed at multiple time scales and also compared with physical parameters such as tide, time of day, wave height, mean wave direction, and windspeed. Physical oceanographic data for Carmel Bay were collected from NOAA's National Data Buoy Center for station # 46042, and tidal data were accessed from data archives from NOAA station #9413450.

Habitat classification. Equal numbers of fish were tagged and released in greater and lesser relief areas of the array. To classify habitat relief within the study area, GIS software (ArcGIS version 9) was used in combination with multibeam bathymetry data provided by the Seafloor Mapping Lab at the California State University of Monterey Bay (CSUMB). A Digital Elevation Model of bottom slope was downloaded from the CSUMB online data archives and imported into GIS. Using the Hawth's Analysis Tools Extension in ArcGIS, zonal statistics were calculated on the bottom slope raster to determine the average slope of habitat within the estimated 150 m detection zone (determined from range testing) of a receiver. Receiver zones were then assigned a high, medium, or low relief classification based on the average slope values from the zonal statistics (Fig. 2). These classifications were validated qualitatively by divers using SCUBA.

Physical parameters. To determine if physical conditions in the environment affected lingcod movements, acoustic data for tagged lingcod were compared with data of temperature, tide, and time of day. Temperatures throughout the receiver array were monitored using Onset Stow-away Tidbit temperature loggers. The loggers were deployed on receivers 14, 19, 26 and 28 at depths ranging from 10-31 m. When possible, loggers were placed at similar depths at multiple receiver locations. Tide data for the study period were collected from NOAA station #9413450 in Monterey, California. Data for day length were collected from the US Naval Observatory historical archives for Carmel, California.

Data analysis. Residence time of lingcod was estimated by calculating the proportion of days detected relative to the number of days at liberty (up until the last day a fish was detected) or until one year from the date of tagging. Due to the possibility of false signals from electronic noise, a fish was only considered present when two or more detections were recorded in a 24-hr period (Starr et al. 2000; Starr et al. 2005). Conversely, lingcod were considered to have departed from the array if ≤ 1 detection was received for the fish during a 24-hr period. For each day a fish was determined present in the array, signals were grouped into 1 hr time bins according to the time at which the signals were received (Starr et al. 2002; Lindholm et al. 2007). For example, signals detected between 14:00:00 hr and 14:59:59 hr were assigned to Bin 14. A fish was determined to be present for the hour regardless of the total number of detections received, as long as one signal was recorded during the hour. This data filter was used because the number of detections from a stationary transmitter was highly variable and thus an unreliable indicator of fish activity.

A regression analysis was used to test if overall time of residence was related to total length of tagged lingcod. Regressions were performed for each sex and residence times between sexes and size classes were examined with a 2-way ANOVA (Zar 1990). Presence through time was examined at a monthly scale using the proportion of days a fish was detected in the array relative to the number of days in a month. To account for the effect of time at liberty on the estimate of presence over time, a line of best fit was calculated from the daily count of individual lingcod detected in the array, and the residuals from this line were averaged by month. A two-sample Kolmogorov-Smirnov

(KS) test was used to test if the daily residuals from the month with the greatest average departure from the line were significantly different than the daily residual frequencies for the rest of the year.

Average monthly depth per individual fish was calculated and combined with like sexes and size classes to generate a group mean for monthly depths. Data for fish tagged in 2005 and 2006 were pooled according to month. Mean monthly depth distributions were compared among sex and size classes using a two-sample KS test.

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. Every hour bin with one or more recorded signals for a tagged fish was assigned a location within the array based on the location of the receiver(s) where the signals were recorded for that hour. Occasionally, signals from a fish were recorded on more than one receiver during an hour. In these cases, an hour bin was assigned separately to each receiver with recorded signals. By comparing the total sum of hour bins recorded on all receivers to the actual number of possible hour bins (24 per day), I was able to generate an index measuring the proportion of hour bins with signals within overlapping detection areas of the receivers.

To examine movements within the array through time, the study area was divided into zones of approximately equal size (Fig. 2). The zones were numbered from north to south, and an average of the zone numbers was used to identify the primary receiving zone that a fish occupied during a week (Starr et al. 2002). This approach was useful for quantifying relatively large movements, as smaller scale movements among adjacent receivers were grouped together within the same zone. Every hour bin with detections from a tagged fish was assigned a zone based on the location of the receivers at which the fish was detected for that hour. For example, a lingcod detected on receivers in zone 4 during an hour were assigned a zone value of 4 for that hour bin. When receivers in more than one zone were recorded during an hour, the average of the zones for that hour was calculated. Thus, if a lingcod was detected on receivers in zone 3 and zone 4 within the same hour, a 3.5 zone value was assigned for that particular hour bin. A weekly zone value was then calculated from the average of the hourly zone values for that week. For each fish, weekly rankings were compared for statistical differences using a two-sample KS test. For this analysis, the average ranking for week 2 was used as the expected zone ranking. Week 2 was selected to avoid bias caused by behavioral changes from the tagging process. A significant difference in the average zone number among weeks indicated the fish had moved between zones, and the value of the average number indicated the directionality of the movement.

Using bottom slope classifications developed in GIS (as described above), movements of lingcod were examined in relation to high, medium, and low relief habitats. Lingcod were assumed to occupy the type of habitat in which they were caught throughout the study period. This assumption was validated by examining the habitat classification of the receiver locations in which signals from tagged lingcod were recorded throughout the year. Overall presence, as calculated by the percentage of days a fish was detected in a year, was compared among lingcod released in high, medium, and low habitats with a one-way ANOVA. To compare site fidelity among habitats, the receiver with the greatest proportion of 1 hr time bins with signals in relation to possible

1 hr bins was selected for each fish. This proportion was then compared among lingcod released in different habitats using a Kruskal-Wallis test. A Kruskal-Wallis test also was used to compare the average duration (hr) of departures and the average number of departures for lingcod released in different habitats. For all analyses, non-parametric statistics were used when assumptions of normality were not met.

Seasonal temperature changes in Carmel Bay were determined by calculating the deviation of mean monthly temperatures from the annual mean. For this analysis, temperature measurements were pooled for all logger depths and locations. Lingcod presence in relation to temperature was compared to average monthly temperatures recorded throughout the array. Temperature stratification in the water column, signified by ΔT, was determined by calculating the daily differences in average temperatures recorded at loggers in shallow (14 m) and deep (31 m) water. These data for ΔT were then compared with the daily count of tagged lingcod detected in the array. To examine the possible physical effects of temperature stratification on sound attenuation, daily ΔT was also compared with the number of signals detected for the stationary reference transmitter.

Fish movements in relation to tide were examined by calculating the time difference between each signal detection and lower low water (LLW) for the day. These time differences were grouped into hourly bins ranging from 0-12 hr before or after the day's lower low water. The distributions of detections relative to time at LLW were pooled for all lingcod and tested for homogeneity using a one-sample KS test. The same analysis for tide also was conducted with data from the stationary reference transmitter.

Diel movements were analyzed by calculating the proportion of hour bins a fish was recorded during the day in relation to the total possible number of daylight hour bins throughout the fish's time at liberty. This proportion of possible hours was also calculated for night hour bins. To account for changing daylength throughout the year, the number of possible day and night hour bins was calculated for each day based on time of sunrise and sunset. Movements occurring during crepuscular times were excluded from this analysis by eliminating detections within ± 1 hr of sunrise and sunset.

RESULTS

Fishing

Thirty lingcod were captured and tagged with acoustic transmitters during two tagging periods in early fall of 2005 and 2006. Average catch per unit effort (CPUE) aboard the commercial vessel in 2005 was 0.05 ± 0.01 (SE) lingcod /hr for Portuguese sticks and 0.35 ± 0.10 (SE) lingcod/hr for handlines. In 2006, average CPUE using rod and reel was 0.38 ± 0.07 (SE) lingcod/hr.

The mean length of 10 female lingcod (70.7 cm ± 4.9 (SE)) tagged in the study was significantly greater than the mean length of 17 male lingcod (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 small size class ($t = 1.584$, $p = 1.42$). However, for lingcod in the large size class, females were significantly larger than males ($t = 7.611$, $p<0.001$).

In 2005, seven lingcod were tagged and released, of which sex was not identified for three fish. These three fish were classified into the smaller (< 90 % maturity) size class based on their total lengths. In 2006, 23 lingcod were tagged and released. In total, 16 lingcod (5 females, 8 males, and 3 of unknown sex) at lengths <90 % maturity and 14 lingcod (5 females, 9 males) at lengths >90 % maturity were tagged.

Two lingcod tagged in 2005 were never detected after release. No complications occurred during the surgical procedures for these two lingcod, and both fish were observed swimming upon release. Presence of potential predators, such as sea lions (*Zalophus californianus*) or harbor seals (*Phoca vitulina*), was not observed at the time of release. If these lingcod had died, I would have expected the fish to sink to the bottom while still transmitting signals from the acoustic tag. Similarly, given the delay of the transmitters, I would have expected to record at least one or two signal detections from these fish even if they had immediately fled the monitoring area. For these reasons, I suspect that the transmitters may have failed. Due to the lack of data, these two fish were excluded from the majority of the analysis.

Another lingcod (#226) tagged in 2005 was initially suspected of dying because it was detected almost exclusively on one receiver for 747 d. To assess whether this fish was alive or dead, an assumption was made that a transmitter resting on the bottom of the seafloor would exhibit depth variations corresponding to known tidal ranges for the area. Depths recorded for transmitter #226, however, ranged from 6-24 m, which exceeded the depths explained by changes in tidal heights. The range in depth signals for #226 was also comparable with other lingcod tagged in the study. For these reasons, lingcod #226 was considered alive and included in the analysis.

Two lingcod tagged in the study were confirmed fishing mortalities. The first mortality, tag #66, was a 62 cm (TL) male. This lingcod was killed by a spear fisherman within close proximity of the fish's site of release after 246 d at liberty. The second fishing mortality, tag #71, occurred on August 25, 2008. At 94 cm (TL), this female was the largest lingcod tagged in the study. Exact coordinates of the site of recapture were not available from the fisherman, but from his description the lingcod was caught in the same area where it was originally tagged, near Pescadero Point. This fish was killed 702 d after it was originally tagged, and 371 d since it was last detected in the array.

Receiver array

During the time of study between August 2005 and September 2007, three VR2 receivers broke free from their moorings but were recovered on the beach, and six VR2 receivers were permanently lost. The three receivers found on the beach were still operational. Data recorded in each of these receivers were recovered and the receivers were redeployed in less than 2 weeks after the time that the receivers broke free. Four of the lost receivers, at locations 12, 18, 20, and 23, were deployed in areas in which low numbers of signals were recorded for lingcod. However, the receivers lost at the top of Carmel Pinnacles, at locations 5 and 6, were in an area containing tagged lingcod. Data for locations 5 and 6 were missing from November and December, 2006, respectively, until June, 2007. The loss of these receivers affected monitoring coverage in relatively shallow (approximately 15 m deep) areas on the Carmel Pinnacles. For days in which data were available for these locations, five lingcod (tag numbers 39, 71, 73, 74, and 75) were detected. Three of the five lingcod were detected at either location 5 or 6 for < 2 d. Tag # 73 and #74, however, were detected on receivers on the pinnacle for 10 d and 50 d, respectively. The loss of data at these locations likely resulted in an underestimate of the residency times for these two fish. However, tag # 73 and # 74 were detected on receivers adjacent to the lost receivers throughout the year.

The loss of the receiver at location 23 affected range testing results, as this receiver was one of two deployed near the stationary reference transmitter. To account for the loss of this receiver, comparisons for the reference transmitter between locations were only made when data were available for both receivers. The loss of receiver 23 also affected my calculation of detections ranges in low kelp presence. In early March 2006, when kelp densities were lesser from winter storm activities, I deployed a transmitter at 50 m intervals between location 22 and 23. I was hoping to achieve replication for 50 m distance bins between the two receivers, but the loss of receiver 23 only permitted me to retrieve data from location 22.

For one month in August 2006, 8 temporary receivers were moored alongside the permanent array (Fig. 3). During this month, 6 lingcod were detected on the temporary receivers and not on the permanent array for one or more days. The number of additional days these 6 fish were recorded was <5 days for the month, with the exception of lingcod #118, which was detected on temporary receivers for an additional 17 days. The eight surveys with the VR100 confirmed the presence of 5 lingcod that would have otherwise gone undetected by the permanent VR2 array for one or more days. The VR100 detected 3 of the 5 fish for one additional day, and the other two fish were detected for an additional 2 and 3 days.

Range testing

Range testing results throughout the array were highly variable. For the transmitter deployed at 50 m intervals from receivers, the coefficient of variation for the number of signals received per hour increased approximately ten-fold after 50 m. Although transmissions as great as 500 m were detected on receivers in deeper waters, the average number of hourly detections throughout the array was <5 detections/hr when the distance was greater than 150 m (Fig. 4). In the presence of dense kelp, the average number of hourly detections was greatly reduced, yet transmissions as far as 250 m were still received (Fig. 5). Although there was considerable variation in the range testing results, we used a conservative estimate of 150 m for receiver detection ranges in this study.

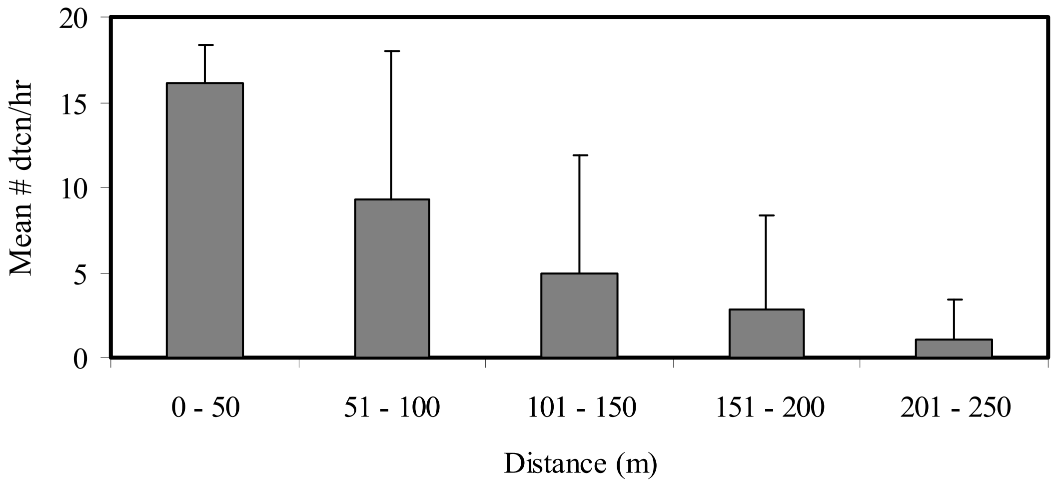


Fig. 4. Mean number (± SD) of hourly tag detections (dtcn/hr) recorded versus distance from receivers for transmitters deployed during range testing.

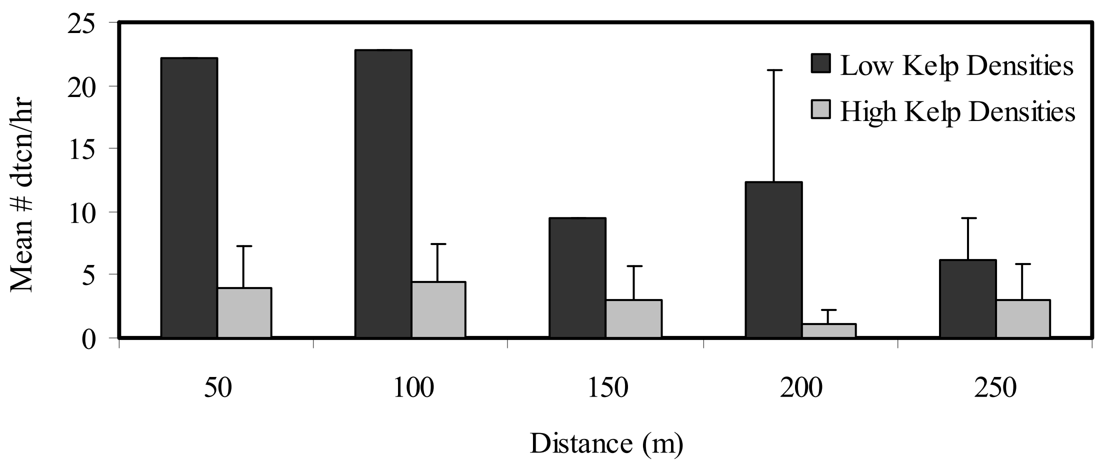


Fig. 5. Mean number (± SE) of hourly tag detections (dtcns/hr) recorded from the reference transmitter on one day in late winter (Low Kelp Densities) and on one day in late summer, at peak kelp densities (High Kelp Densities).

The reference transmitter, placed 140 m from two receivers, was detected for 100% of the days it was deployed and for 92 % of all possible hour bins. The number of daily detections was highly variable, ranging from 7-401, with a daily mean of 178.2 ±101.9 detections per day (Fig. 6).

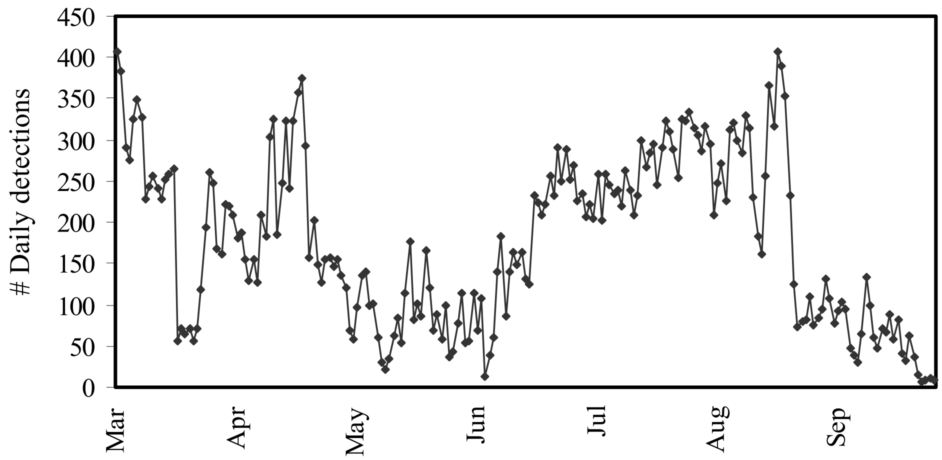


Fig. 6. Number of daily signal detections recorded in 2007 from the stationary reference transmitter by all VR2 receivers in the array.

Detection capabilities varied throughout time; the number of hours in which signals were detected was greatest for the month of July (99 % of all possible hours) and lowest for the month of September (65 % of possible hours) (Fig.7).

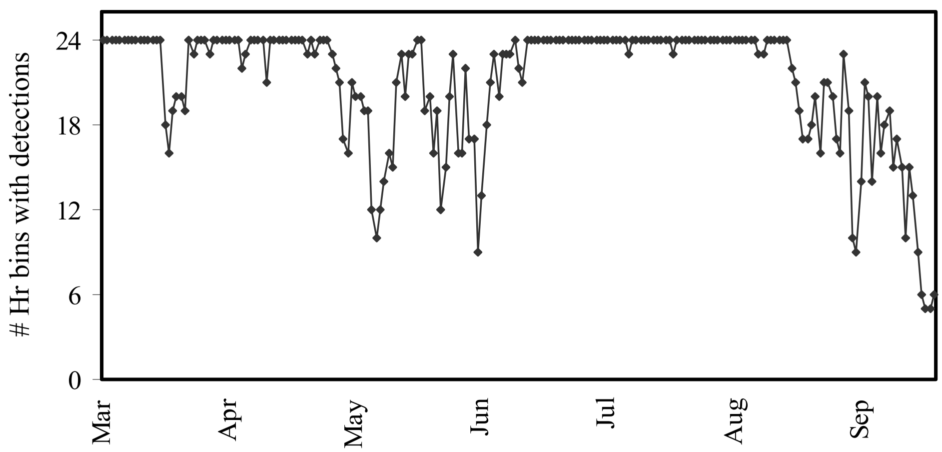


Fig. 7. Daily count of hour bins with tag signals recorded from the stationary reference transmitter in 2007. A daily count of 24 indicates that the transmitter was detected in all possible hour bins in a day.

A directional component in ranges also was observed. Receiver #22, located to the north-east of the stationary transmitter, recorded signals from the reference transmitter in 74 % of all possible hour bins, while Receiver #23, located East-south-east of the transmitter, only recorded signals from the reference transmitter for 29 % of all possible hour bins (Fig. 8). Note that receiver # 23 was lost for part of the time that the transmitter was deployed and that these percentages were calculated only for the time period when receivers # 22 and # 23 were present.

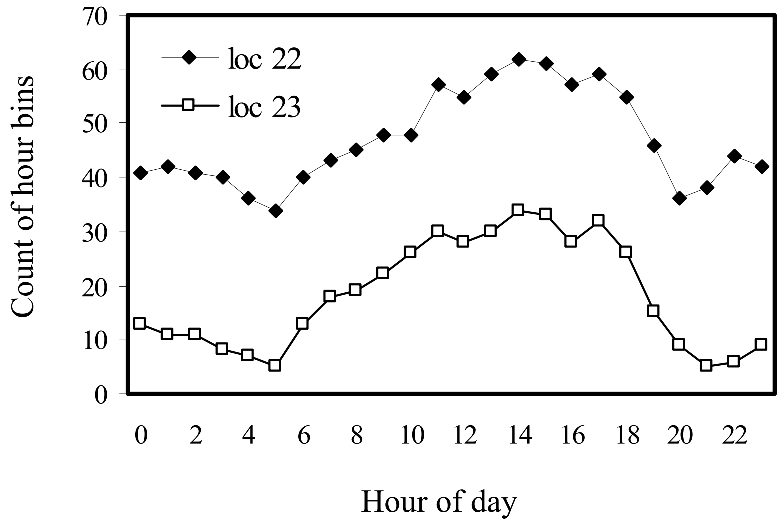


Fig. 8. Directional and diel components in detection ranges of receivers. Shown are the distributions of the total count of hour bins with recorded signals in relation to time of day for the reference transmitter on receivers 22 and 23. Receiver 22, located to the northeast of the reference transmitter, consistently received more detections than receiver 23, located to the southeast of the transmitter. Both receivers were placed equidistant (140 m) from the stationary transmitter.

The number of detections recorded from the stationary reference transmitter was greater during daylight hours than during the night, and this pattern was consistent among the two receivers moored closest to the transmitter (Fig. 8). The mean number of detections recorded during an hour was 9.28 ± 5.9 during the day and 6.11 ± 4.3 during the night. The percentage of 1 hr time bins in which signals were detected, relative to the total number of possible 1 hr time bins, was also greater during the day (91 %) than during the night (78 %).

Of the physical variables considered, thermal stratification in the water column accounted for the most variation in signals received for the reference transmitter. There was not a direct relationship between the average hourly temperature measured throughout the array and the number of hourly detections recorded for the reference transmitter. However, there was a correlation between the number of hour bins without recorded signals and ΔT, when the temperature differential between 14 m and 31 m was > 1º C (Fig. 9).

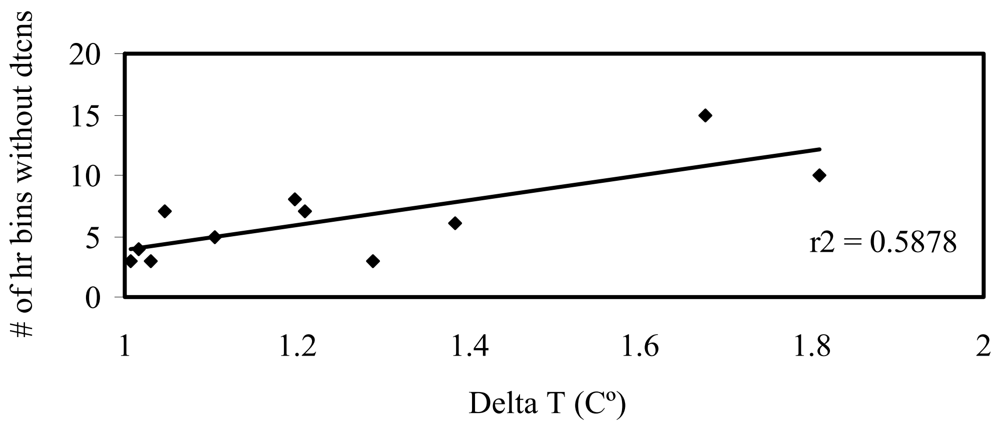


Fig. 9. Number of daily hour bins in which no signals were detected from the reference transmitter in relation to the absolute value of the difference in temperature observed between 14 m and 31 m for the corresponding day.

Tide, temperature, wave height, mean wave direction, and wind speed were not found to have a significant effect on the number of detections recorded for the reference transmitter. There was no significant difference in the number of detections in relation to time at LLW for the reference transmitter (one sample KS test, $p = 0.688$), although qualitatively the number of detections increased after LLW (Fig. 10).

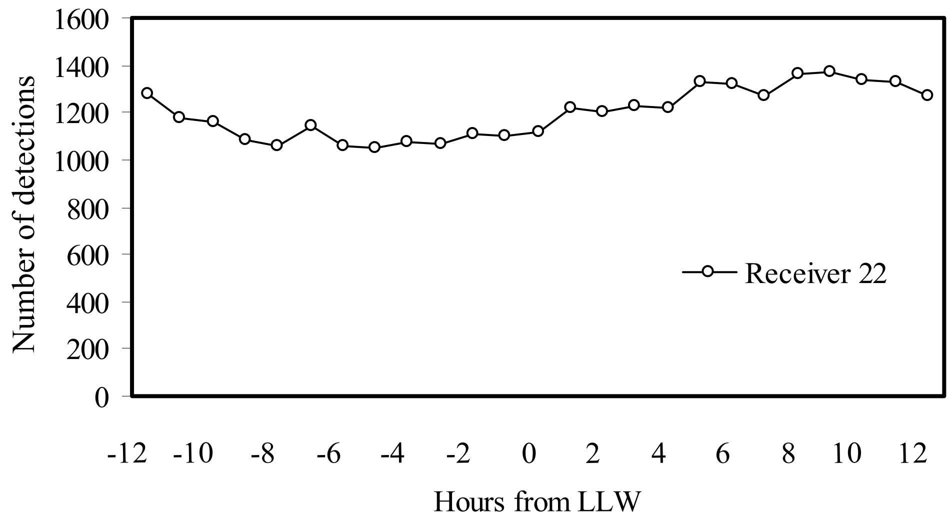


Fig. 10. Distribution of tag detections from the reference transmitter relative to time from lower-low water (LLW) for each day.

Residence times

Lingcod were detected for 3.8-100 % of their respective days at liberty, which ranged from 75-747 d (Table 1). For the days when a fish was considered present in the array (minimum of 2 signals detected during a 24 hr period), the percentage of 1 hr bins containing signals from tagged lingcod, relative to the number of possible 1 hr bins summed for each fish's time at liberty, ranged from 0.5-64.1 % (Table 1).

Table 1. Summary of 30 lingcod tagged in Carmel Bay. Class refers to fish at lengths >90 % maturity and between 50-90 % maturity. Presence 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 (% hr), and the percentage of days relative to one year from the tagging date (% 1 yr).

Tag ID	TL (cm)	Sex	Class	Date Released (mm/dd/yy)	Time at lib (d)	Presence (% d)	Presence (% hr)	Presence (% 1 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

Residency over a year, as measured by the percentage of days detected over a year, ranged from 2.2-100 %. Lingcod in the smaller size class were detected a greater percentage of days at liberty than fish in the larger size class (Fig. 11).

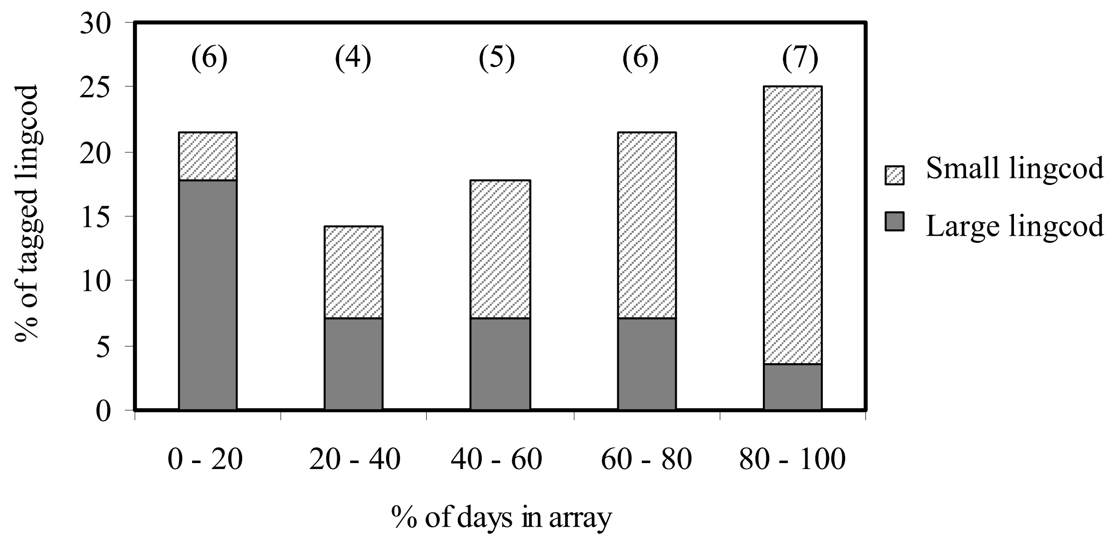
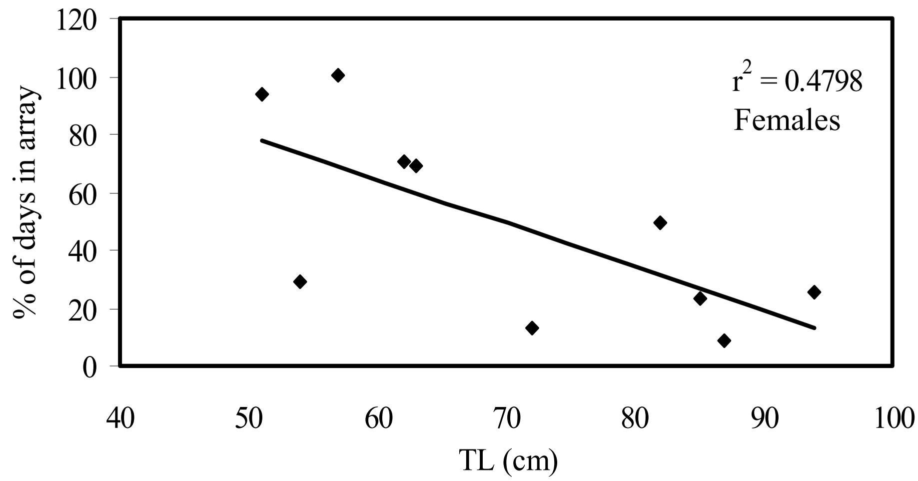


Fig. 11. Percentage of days at liberty recorded in the array for 28 tagged lingcod. Numbers in parenthesis indicate the total number of lingcod pertaining to each time category. Two lingcod were excluded from the analysis due to tag failure.

This pattern of presence was driven by females, for which the proportion of days at liberty spent in the array was significantly dependent on total length (Fig. 12; $r^2 = 0.483$, $p = 0.011$), whereas for males it was not (Fig. 12; $r^2 = 0.016$, $p = 0.650$).



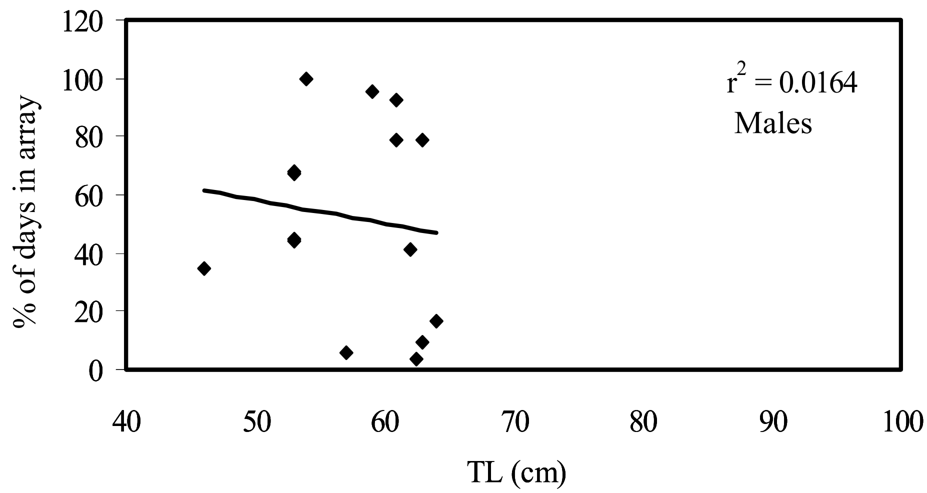


Fig. 12. Regression of percentage of days at liberty recorded in the array versus total length (cm) of lingcod for females (top) and males (bottom). A significant relationship was found for females ($p = 0.011$) but not for males ($p = 0.650$).

Mean residence time in the array, as measured by the average of consecutive days spent in the array for individual lingcod, was 42.5 d ± 17.9 (SE). The average number of consecutive days spent out of the array was less than in the array (8.1 d ± 1.5). Approximately half (43 %) of the tagged lingcod spent an average of 1 to 5 consecutive days in the array before departing (Fig. 13). Similarly, 54 % of lingcod spent on average

1 to 5 consecutive days away from the array (Fig. 13). Average residence time was > 25 consecutive days for 29 % of tagged fish. The majority of lingcod (78 %) were gone for an average of 10 consecutive days or less.

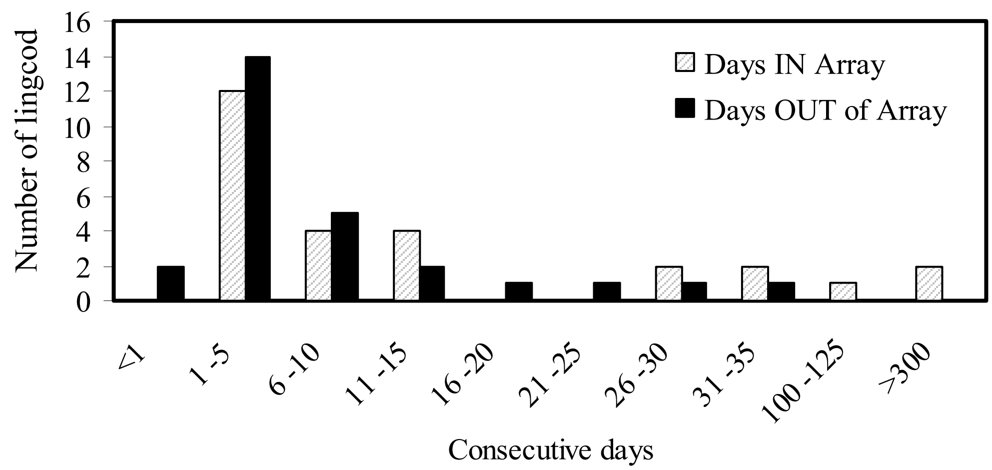


Fig. 13. Average number of consecutive days tagged lingcod spent in and out of the array.

The daily number of lingcod detected in the array decreased linearly throughout time for all sexes and size classes combined (Fig. 14). In April, however, the mean monthly proportion of days recorded in the array was less than the expected linear trend for all of the males and females in the small size class (Fig. 15). The frequency distribution of daily residuals from the expected linear trend was not found to be significantly for the month of April in comparison with the residuals from the rest of the year (two sample KS, $p = 0.16$). Although the KS test results were not significant ($p = 0.16$), qualitatively, residuals in April appeared to be more negative than the yearly residuals (Fig. 16).

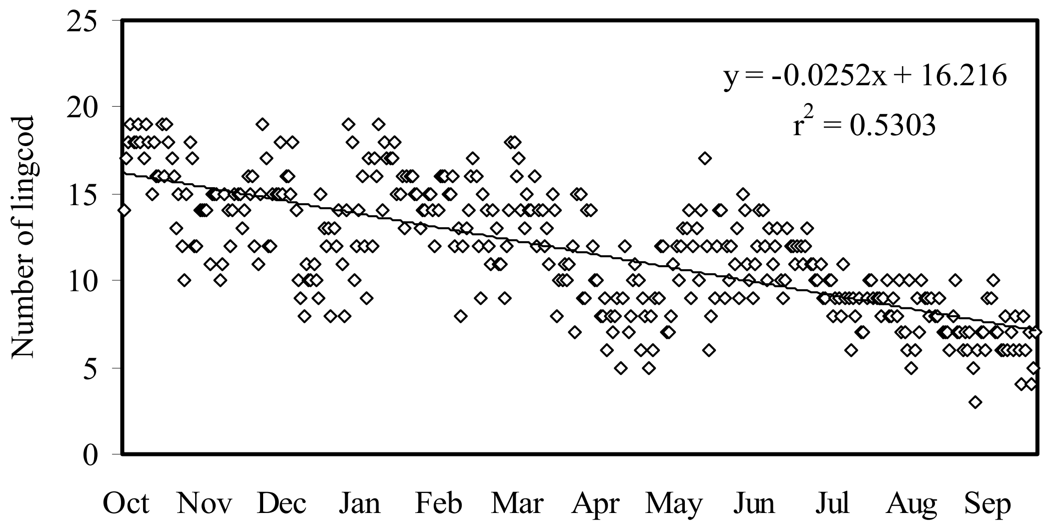


Fig. 14. The number of lingcod detected in the array for each day of the study period from Oct 2006 to Sep 2007. Shown is a linear line of best fit, which was used to compare the distribution of residuals for the month of April to the distribution of residuals for the entire year (see Fig. 16).

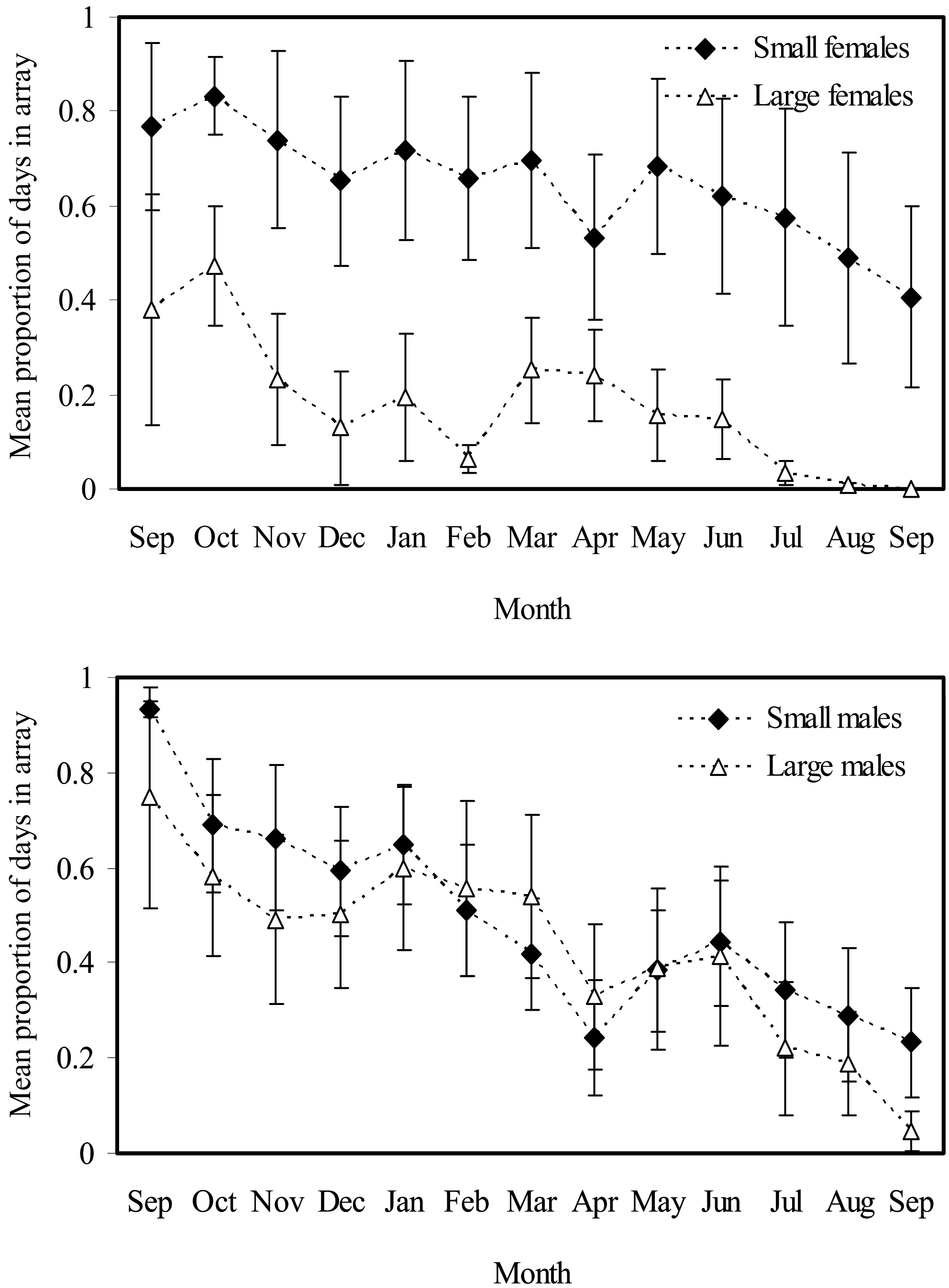


Fig. 15. Mean monthly proportion of days (± SE) detected in the array for tagged female (top) and male (bottom) lingcod.

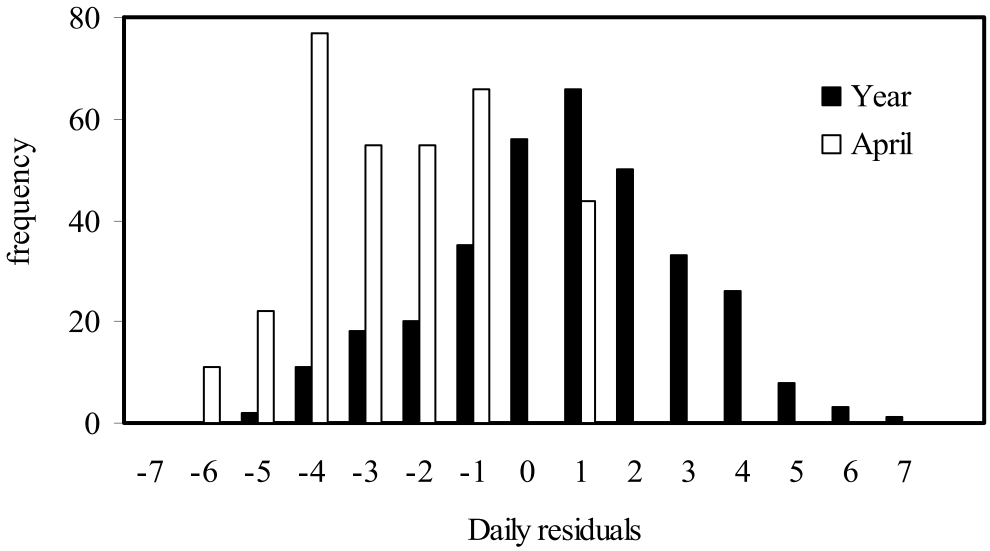


Fig. 16. Distribution of daily residuals for the month of April versus the other months in the year (pooled). Residuals were calculated from a line of best fit for the daily count of lingcod in the array (Fig. 14). Frequencies of residuals for the month of April were increased proportionally for comparison with the rest of the year. A two-sample Kolmogorov-Smirnov test indicated the distributions were not significantly different ($p = 0.16$).

The proportion of days that tagged lingcod were detected in the array each month can be described by 5 patterns: 1) proportion of days detected each month remained relatively constant throughout the year, 2) proportion of days detected each month decreased after tagging and remained relatively low (<10 % of possible days present in a month), 3) proportions of days detected each month increased throughout the year, 4) proportions of days detected each month decreased after April, 5) proportions of days detected each month decreased in April but increased in the following months.

Depth distribution

Mean monthly depths of tagged lingcod ranged from 15.5-20.1 m (Fig. 17) and were fairly consistent throughout the year for males and females in the small size class.

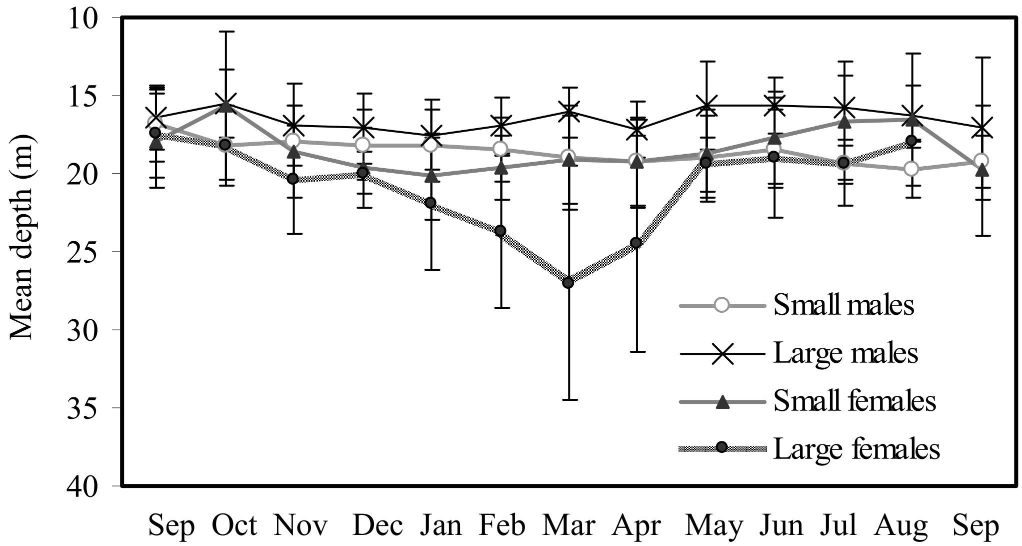


Fig. 17. Mean monthly depth distributions (± SD) of tagged lingcod, separated by sex and size class, pooled by month.

The mean monthly depths of large females, however, encompassed a greater depth range (17.5-27.0 m) throughout the year, with the deepest monthly averages occurring from February to April. The mean monthly depth distribution for large females was significantly different than that for combined males and small females (two sample KS, $p = 0.001$). The observed pattern for adult females, however, was largely driven by female lingcod #73, which was detected in deeper areas in the array during winter when the other large females were notably absent (Fig. 18).

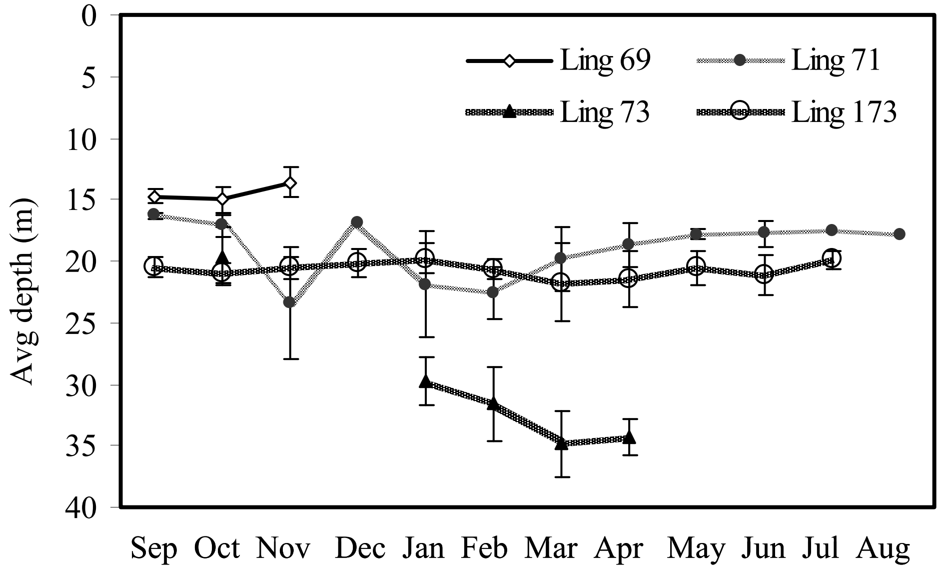


Fig. 18. Mean monthly depth distribution (± SD) of four adult female lingcod.

Recorded depths for tagged lingcod were consistently near the bottom, as determined by comparing the depth of the signals in relation to the depths of the receivers upon which the lingcod were recorded. Approximately half (48 %) of the lingcod were detected at depths < 3 m, indicating minimal vertical movements into the water column. These shallow detections were infrequent, however, comprising <1 % of the total detections recorded for each fish.

Site fidelity

Tagged lingcod exhibited limited movement within the array (Appendix A-D). Lingcod were detected by 1 receiver for 76.8 % (± 3.7 SE) of all 1 hr time bins containing signals and on 2 adjacent receivers for 91.0 % (± 3.1 SE) of 1 hr time bins (Fig. 19).

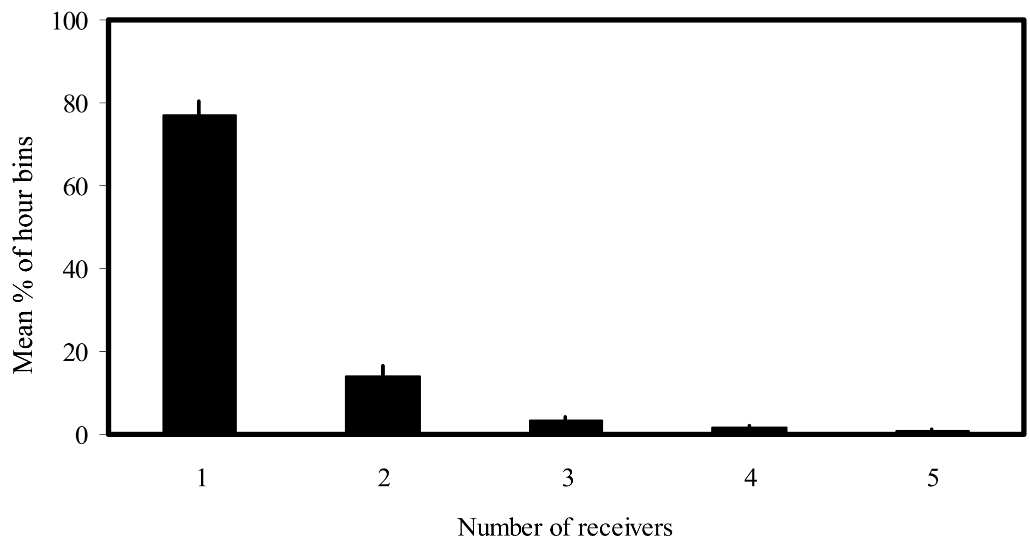


Fig. 19. Spatial movements of tagged lingcod as determined by patterns of signal detections at moored receivers. This graph depicts the mean percentage of total hour bins in which a fish was detected in relation to the number of receivers where detections were recorded. Shown are the average (± SE) percentages of total hour bins for all tagged lingcod.

Lingcod returned to the same receiver on which they were last detected for an average of 75 % (± 4.27 SE) of all departures. There was no significant difference in the maximum percentage of hour bins containing signals that were detected on one receiver among the four groups of lingcod tagged: small males, large males, small females, and large females (ANOVA: $F = 0.696$; $p = 0.565$) (Fig. 20). Nor was there a significant difference in the number of receivers with > 5 % of the total hour bins containing signals among the four groups of lingcod tagged (ANOVA: $F = 1.385$; $p = 0.275$).

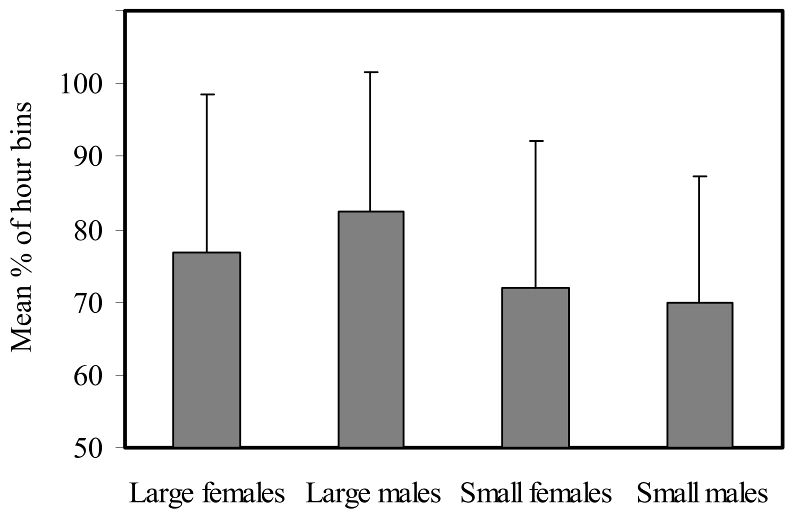


Fig. 20. Mean percentage (± SE) of total hour bins with signals recorded on one primary receiver. Lingcod at lengths >90 % maturity were grouped into the large size class and lingcod at lengths between 50–90 % maturity were categorized as small.

Only a small proportion of tagged lingcod exhibited movements between zones within the array. Two-sample KS tests comparing the expected zone value derived from week two with the observed weekly zone values were significant for 5 (18 %) lingcod. The majority of fish (82 %) monitored did not move from their primary zone of occupancy throughout the year. For the fish that moved, there was no apparent directionality of movements.

Despite exhibiting strong site fidelity, lingcod made frequent departures that usually extended beyond the area of receiver coverage. However, there were a few occasions when larger scale movements were detected within the array. Lingcod #174, for example, displayed highly directional movement from receiver # 25 near Carmel Point through to the southern extension of the array near Carmel Canyon (Fig. 21).

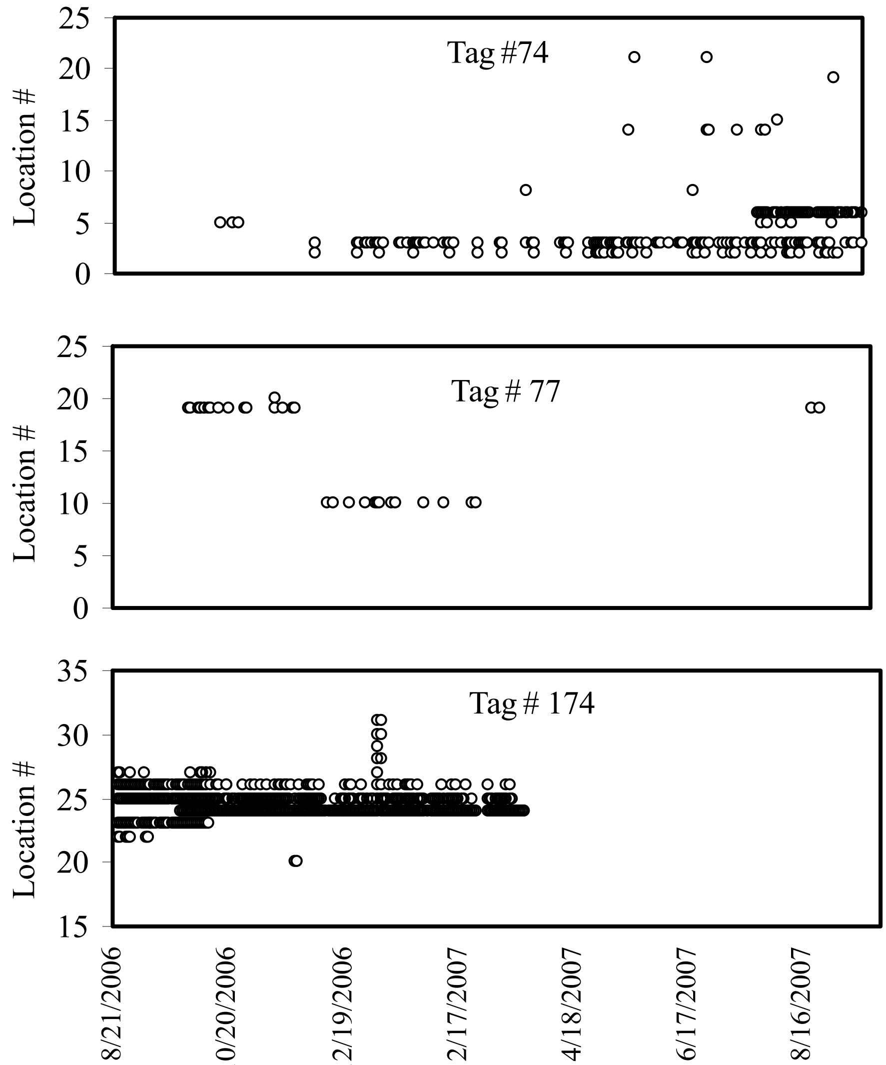


Fig. 21. Days in which different receivers recorded signals from tagged lingcod displaying movements > 1 km. Each circle represents a day in which a receiver detected a tagged fish.

During this trip, #174 swam in a southerly direction through five receivers before leaving 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/hr on the trip out and 0.46 km/h on the way back.

Lingcod #74 (male, 46 cm TL) was tagged and released on the Pinnacles, where it was detected for 95 % of the total hour bins with signals. On 8 separate occasions, this fish was detected approximately 2.5 km away on receivers within the vicinity of Arrowhead Point (Fig. 21). Time between distant receivers ranged from 13 minutes to 4 hr.

Lingcod #77 was not present in the array as consistently as #174, but displayed an interesting pattern of site fidelity at two different receiver locations (Fig. 21). This fish was detected intermittently on receiver # 19 near Carmel Beach until December, 2006, when it relocated 1.3 km to Pescadero Point. In March the fish left the array completely, only to be detected 5 months later back at its original site near receiver #19.

Habitat relief

All but one tagged lingcod primarily occupied the area where they were originally captured and released. For the other lingcod (n = 27), there was no difference in the overall percentage of days detected for lingcod released among the different habitats (ANOVA, $F = 0.951$, $p = 0.400$). Site fidelity, as determined by comparing the maximum proportion of hour bins containing signals from tagged lingcod at one receiver, was not significantly different for lingcod in different habitats (Kruskal-Wallis, $H_2 = 1.468$, $p = 0.480$). Additionally, the average duration (h) of departures was not significantly different (Kruskal-Wallis, $H_2 = 1.018$, $p = 0.601$) nor was the average number of departures significantly different (Kruskal-Wallis, $H_2 = 0.606$, $p = 0.739$) for lingcod occupying different habitats. Lingcod #77 was excluded from the habitat analysis as it departed from its release location in low relief habitat and moved to an area of high relief, thus making it difficult to characterize what habitat it primarily occupied.

Physical parameters

Temperatures in the array were monitored from November 2006 to October 2007. Water temperatures were coldest from March to July 2007, when mean monthly temperatures fell below the average annual temperature (Fig. 22).

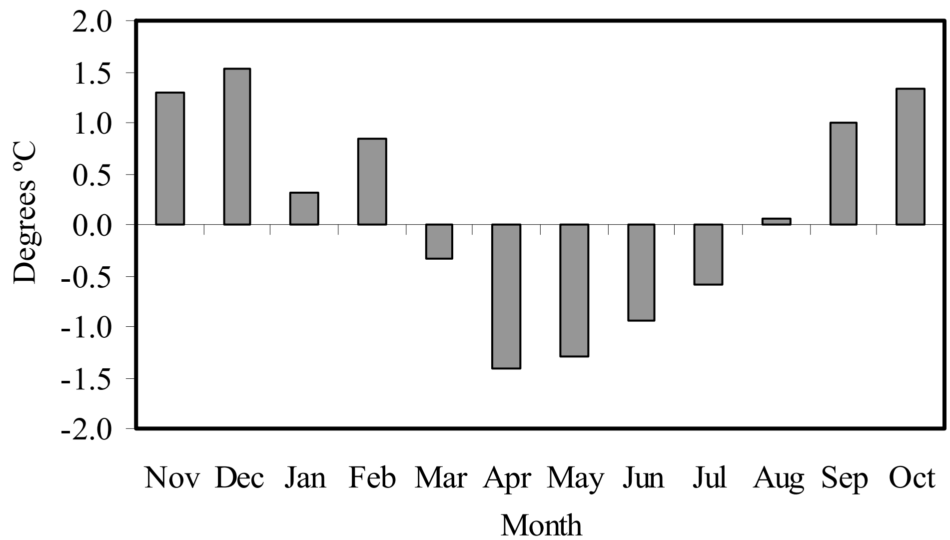


Fig. 22. Deviation of the mean monthly water temperature (ºC) from annual mean water temperature in Carmel Bay for the time period Nov 2006 – Oct 2007. Temperature was calculated from an average of measurements recorded on temperature loggers deployed throughout the VR2 array in Carmel Bay.

Mean monthly temperatures were least in April and greatest in December 2006. There was no correlation between mean monthly temperatures and the mean monthly proportion of days lingcod were recorded (Pearson correlation, p = -0.024). A decrease in the mean monthly proportion of days lingcod were detected appeared to coincide with a decrease in temperatures in April. However, lingcod presence increased in the following months when temperatures remained relatively cool. The number of lingcod recorded daily in the array was not correlated (Pearson correlation, $p = -0.369$) with daily thermal water stratification, as measured by Δ T at 14 and 31 m depth.

There was no effect of tide on detections of lingcod in the array. For all lingcod pooled, the number of detections in relation to time from LLW did not significantly differ from a uniform distribution (one-sample KS test, $p = 0.538$). No obvious tidal patterns were apparent for individual lingcod.

Tagged lingcod that were detected in the array for >10 % of the time (of possible hour bins) exhibited no diel movement patterns. For these fish that were recorded frequently, 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) (Fig. 23). Lingcod that were detected in less than <10 % of possible hour bins were primarily recorded during daylight hours.

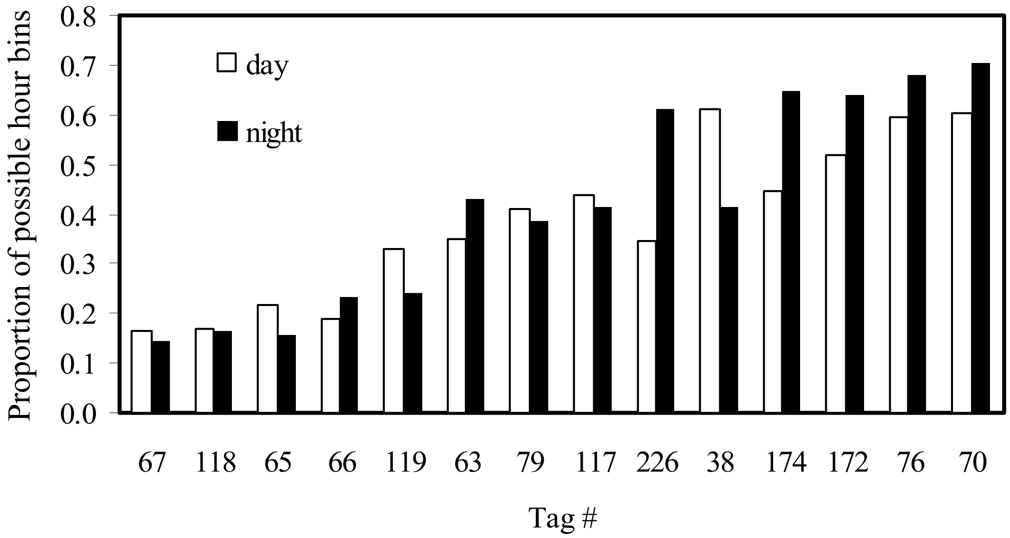


Fig. 23. Proportion of day and night hour bins containing detections of tagged lingcod in relation to the total number of possible day and night hours occurring during each fish's time at liberty. Only lingcod with recorded detections for >10 % of total possible hour bins were included in this analysis.

DISCUSSION

Fishing: CPUE and mortality

CPUE estimates for lingcod during the 2005 and 2006 sampling periods were comparable for handlines and rod and reel, whereas CPUE estimates for Portuguese sticks were relatively less. The similarities and differences in CPUE among gear types were likely attributed to how the gear was fished. Fishing techniques for handlines and rod and reel were similar in that areas were fished only as long as fish were biting; when no bites were felt on the fishing lines, the boat moved to a new fishing spot. In contrast, Portuguese sticks were deployed at fixed positions for an hour at a time, therefore less area was sampled with sticks than with handlines and rod and reel. The difference in the amount of area sampled per hour could explain why more mobile techniques such as handlines and rod and reel had greater CPUE estimates for lingcod than fixed gear.

From the descriptions provided by the fishermen that caught tagged fish, the lingcod were recaptured within close proximity of the original sites of capture. This was especially interesting for the large female (#71) that was recaptured in August, 2008, as this fish was at liberty for almost 2 years. This female was last detected on August 15, 2007, on the same receiver where she had been detected throughout the year. The fact that the fisherman caught lingcod #71 in the same area, almost a year after she was last detected and two years after tagging, demonstrated that lingcod are capable of exhibiting relatively high site fidelity for long periods of time.

Receiver array

The loss of receivers in the array was likely caused by winter storm activity in Carmel Bay. Carmel Bay is exposed to west swells and wave heights >10 m are not uncommon during major storm events. Even if moored receivers were able to withstand strong water motion, masses of giant kelp *(M. pyrifera*) uprooted from storm activities could have wrapped around mooring lines and caused receivers to break free. From the spatial patterns of receiver loss, particular areas within the array were subject to greater wave activity than other areas. Wave exposure at the Carmel Pinnacles appeared to be particularly strong, as both receivers moored at the top of the pinnacles were lost over the winter of 2006- 2007 and lost again after the lingcod study was completed, during the winter of 2007- 2008.

Based on the number of detections received for lingcod on receivers throughout the array, data loss associated with missing receivers was minimal for most of the receivers, except for those moored on top of Carmel Pinnacles. From the data that were retrieved at the pinnacles, it is likely that overall residence times were underestimated for lingcod #73 and #74. However, the underestimates of residence times were probably not severe, as both these fish were detected frequently on adjacent receivers during times when the shallow pinnacle receivers were missing. One calculation that had to be adjusted to account for the missing receivers was that for site fidelity. For most lingcod, site fidelity was determined by calculating the percentage of the total number of 1 hr bins with recorded signals from tagged fish at each receiver location. For lingcod #73 and

#74, site fidelity estimates were altered to only include dates when all pinnacle receivers were deployed and recovered. In regards to missing receivers, it is also possible that other lingcod may have ventured to the pinnacles during times without receiver coverage. However, as lingcod #73 and #74 were frequently detected on receivers adjacent to the missing receivers, it was assumed that such movements to the pinnacles by other lingcod would have been recorded by adjacent receivers with continuous data records.

During the month-long expansion of the receiver array, I determined that some lingcod were within close proximity of the study area but went undetected by receivers in the permanent array. My estimates of residence times, therefore, likely underestimate actual residence times for lingcod in Carmel Bay. Lingcod #118, for example, was detected for an additional 17 days by the temporary receivers for the month when the array was expanded. Five other lingcod also were detected on the temporary receivers on days that were not recorded for the permanent array. These lingcod were probably on the periphery of the detection zones for the permanent VR2 receivers. These results imply that lingcod absences do not necessarily indicate permanent emigration from Carmel Bay, but are caused by smaller movements beyond the detection range of the permanent receiver array.

Within the array, surveys with the VR100 hydrophone validated the presence of 6 lingcod that would have otherwise gone undetected for 24 hr. The VR100 surveys confirmed my suspicion that lingcod periodically occupy areas in acoustic shadows, where detections are blocked by bottom topography or vegetation. The implication of the

VR100 surveys is that short term absences of lingcod, at the scale of 1-2 d, may actually be caused by acoustic shadows rather than an actual departure of the fish from the study area. Therefore, I have likely underestimated the number of consecutive days that lingcod spend within the array while concurrently overestimating the number of daily absences of lingcod from the array.

Range testing

Studies using Vemco VR2 receivers have cited detection radii as great as 750 m in open water (Starr et al. 2007). In Carmel Bay, most of the receivers were moored in or near beds of giant kelp (*M. pyrifera*), where detection ranges were expected to be reduced because of obstruction of signals in the water column. Range testing in this study affirmed that detection frequencies are reduced in the presence of dense kelp. However, regardless of the season and subsequent change in kelp densities, VR2 receivers in Carmel Bay consistently detected transmissions as far as 150 m. The range estimates derived in this study are consistent with other VR2 studies conducted in kelp beds in California (Topping et al. 2006).

The observed variability in the number of daily detections for the stationary reference transmitter confirms that total detections are an unreliable indicator of movement. As the transmitter was fixed in one location, acoustic properties of the water column, rather than movement, best explain the variation in total detections received. Accurate interpretation of acoustic data greatly depends on the temporal scale at which the data are analyzed. For example, at a daily scale the reference transmitter was detected for 100 % of the days it was deployed, while presence at an hourly scale was only recorded for 92 % of possible hours. These findings emphasize the importance of selecting an appropriate scale of measurement to determine the presence of tagged fishes. From variation exhibited by the reference transmitter, utilizing the total number of daily detections can easily lead to a false interpretation of acoustic data. The scales at which data were processed in this study, on daily and hourly levels, were accurate in detecting presence. However, it is important to acknowledge that some absences of signals at an hourly level may be caused by acoustic properties of the water in the study area rather than actual fish movements. Thus, my estimates of fish presence at an hourly scale slightly underestimate actual presence.

VR2s receivers are omnidirectional (Voegeli et al. 2001), yet a highly directional component in detection capabilities was observed between the two receivers moored near the reference transmitter. It is unlikely that the observed variation was caused by functional differences in individual receivers, as multiple receivers were deployed at both locations without altering the pattern of directionality. However, the disparity in signals received at the two locations could be caused from a number of other factors, including predominate current patterns, bottom topography, or the distribution of kelp plants between the transmitter and the receivers. Directionality in ranges could significantly confound interpretations of movements at a fine scale. For example, Simfendorfer et al. (2000) used the number of signals received at multiple receivers to triangulate fish positions. This approach assumes that the number of detections received for a fish decreases with distance. If the above technique was used in the Carmel array, the position of the reference transmitter would be calculated closer to the receiver with the greater number of signals, even though the transmitter was moored at the same distance between locations.

Although environmental noise was not measured directly, the observed reduction in number of detections and percentages of hour bins recorded during night was probably caused by an increase in biological noise during the night (Love & Proudfoot 1946). The majority of the receivers were placed approximately 3-4 m from the seafloor, where benthic noises from epibenthic invertebrates could interfere with tag transmissions (Heupel et al. 2006). This was a key result of the range testing in Carmel, as a misunderstanding of the acoustics could have falsely led to the conclusion that lingcod were exhibiting diel patterns. For example, lingcod exhibiting low overall residence times (<10 % of possible hour bins with signal detections) were primarily recorded during daylight hours. However, this pattern was probably caused by increased detection capabilities of receivers during the day rather than actual fish movements.

Variation in signal detection also can be affected by thermoclines and/or picnoclines. As sound velocity increases with temperature, sound waves will bend as they pass through temperature gradients (Voegeli & Pincock 1996). For VR2 systems, water column stratification can ultimately result in loss of signal detections as tag transmissions are refracted or even reflected at density gradients. In the Carmel array, there was a positive correlation between the temperature difference in the water column and the number of daily hour bins containing no signals from the reference transmitter. This correlation provided some evidence that thermal stratification is negatively affecting the detection of signals within the Carmel array.

One factor not explored in this study was the potential effects of biological conditions on array acoustics. For example, layers of phytoplankton and zooplankton affect optical and acoustic signatures (Cheriton et al. 2007). These biological layers, known as thin layers, have been observed locally in Monterey Bay (McManus et al. 2005) and could have attributed to sound attenuation within the Carmel array.

Residence times and movement patterns

The maximum size of male lingcod caught and tagged in this study was relatively small. Lingcod in California are smaller compared to conspecifics in Alaska and Canada (Karpov et al. 1995), with the maximum length for male lingcod in California documented at 80 cm TL (Miller & Geibel 1973). The length frequencies obtained for male lingcod in this study could simply be a result of a limited sample size, especially if larger, older males are less abundant than smaller males. The size structure observed in Carmel Bay also may indicate that large males do not occupy nearshore waters, as an increase in size with depth has been documented for male and female lingcod (Jagielo 1995). Nevertheless, the timing of my fishing efforts, in September and October, overlapped with the start of spawning season when males move nearshore for nest guarding. As we were able to catch large females, it is unlikely our fishing methods were biased against catching big fish. Males that have already spawned may be more difficult to catch, however, because male lingcod may not actively feed during nest-guarding (Beaudreau & Essington 2007). Reduced feeding activity could explain our inability to catch big males, as larger lingcod spawn earlier than smaller conspecifics (Miller & Geibel 1973).

The lack of large males in our study also could be a sign that nearshore fishing pressure has removed larger, older males from the area. Although most of Carmel Bay is closed to commercial fishing, lingcod are targeted by spear-fishers and kayak-based anglers during the recreational fishing season. These fishers typically target nearshore reefs and kelp beds, where lingcod catches are dominated by males (Miller & Geibel 1973). However, more sampling is required to conclude that fishing is negatively impacting male lingcod size frequencies in Carmel Bay.

The conspicuously low presence of large females in nearshore kelp beds throughout the year was expected, given that big females reside offshore for most of the year. For the depth ranges monitored in this study, the average depth distribution for large females was significantly different than those for smaller females and males. Although it appeared that large females tagged in this study were using deeper areas of the array compared with males and smaller females, the observed monthly depth distribution for large females was explained almost entirely by female #71. Depth transmissions for female #71 were greatest in winter, when other large females were absent from the array. While speculative, the absence of the other large females in the array, during the months when #71 was monitored at deeper depths, could signify that these fish had also moved to deeper waters beyond the detection range of the array. One notable exception was lingcod #173, a female measuring 82 cm TL. Signals from this adult female were not only recorded consistently throughout the year, but indicated that the fish stayed at an average depth of 20 m.

The relationship between female residence time in the array and total length likely reflects an ontogenetic change in depth distributions. Female lingcod, at the onset of sexual maturity, move to deeper waters (Miller & Geibel 1973, Gordon 1994). Based on the literature and depth data obtained in this study, it can be assumed that the large females tagged in Carmel Bay moved to deeper waters when they left the array. The relationship between residency and total length for females was statistically determined to be linear. However, an ontogenetic shift in depth distributions may be better represented by a sharp decrease in residency in the array at the length of maturity for females.

Size was not related to presence in the array for males, perhaps as a result of the limited size range of males tagged in this study. Despite the lack of large males, the overall catch during tagging efforts was dominated by males. The observed sex ratio in this study was not surprising, as a depth-related segregation of males and female lingcod has been well documented (Miller & Geibel 1973, Gordon 1994, Jagielo 1994, Starr et al. 2005). Interestingly, the nearshore area monitored in this study proved to be an important habitat for small female lingcod. Thus, sexual segregation in lingcod may not occur until females attain larger sizes.

Segregation is common in vertebrates exhibiting sexual dimorphism in body sizes, as nutritional and energetic requirements may differ with animal size (Ruckstuhl & Neuhaus 2005). Accordingly, large female lingcod may occur in deeper habitats to access particular prey items found at depth or for metabolic benefits associated with colder water. Sexual segregation in lingcod also might be caused from differences in reproductive investment. Nesting sites, for example, are often located in nearshore areas where eggs are exposed to good water circulation (Cass et al. 1990). As nest guarders, males are thereby found in nearshore waters where conditions are optimal for egg development, at least during spawning and nesting seasons.

The overall patterns of presence and absence of tagged lingcod within the array in Carmel Bay were identical to patterns observed on an offshore pinnacle in Alaska (Starr et al. 2005). For approximately half of the lingcod tagged in Carmel Bay, the average time in the array, of 1 to 5 consecutive days, was equal to the average time spent out of the array. In Alaska, half of the fish spent 6 days or less on the pinnacle, and left for an average of 2 days at a time (Starr et al. 2005). The authors of that study concluded that lingcod spend large amounts of time in on the pinnacle but frequently move. Movement patterns for lingcod in Alaska were similar to those inhabiting nearshore coastal habitats in Carmel Bay. However, one main difference between the Alaska study and this study in Carmel Bay was the spatial scale at which lingcod were monitored. In Alaska, site fidelity was examined in relation to presence or absence on the pinnacle, whereas in Carmel Bay movements were monitored at individual receivers. The primary implication of the finer-scale monitoring in Carmel Bay is that lingcod are even more site specific than previously documented.

One important aspect to note regarding lingcod presence is the possibility of false absences caused by acoustic shadows. Lingcod reside in cracks and crevices, where acoustic transmissions may be partially or completely blocked. Accordingly, the presence of several lingcod was detected using a VR100 surface-operated hydrophone that would have otherwise been considered using only the VR2 receivers. This finding is important in relation to the estimates of presence and absence generated for lingcod in the array. Thus, lingcod residency was likely underestimated in this study and short-term absences were likely overestimated.

Directional movements within the array confirmed that lingcod do make short duration trips away from their usual area of residence (Fig. 20). The rates of movement estimated for these fish indicate that when lingcod move, they are capable of covering distances > 1 km in a relatively short amount of time (<1 hr). Starr et al. (2004) proposed that lingcod swim in the water column during forays to actively pursue prey, as some of their tagged fish were recaptured by fishermen trolling for salmon. For the lingcod tagged in Carmel Bay, there was no evidence of fish spending extended amounts of time in the water column. However, half of the lingcod were detected sporadically within 3 m of the surface. These shallow detections signify that lingcod do occasionally swim off the bottom, probably in pursuit of prey.

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, four 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. Two fish with low residence times, # 69 and #75, did not return and may have emigrated from the study site or died away from the array. A consistent result in most tag-recapture studies of lingcod is that approximately 20 % of lingcod demonstrate considerable movement (> 8.1 km) from the tagging location, with a small percentage of recaptures occurring at distances as great as

50 km (Hart 1943, Jagielo 1990, Lea et al. 1997). Lingcod thus are capable of moving great distances, however, it appears from this study and other tag recapture reports that the majority of lingcod remain within a relatively confined area.

Temporal trends in presence

As time progresses from the date of tagging, lingcod presence in the array was expected to decline due to emigration, mortality, and eventual tag failure. Even with this expected decline through time, the occurrence of lingcod in April appeared to anomalously decrease. Although a statistical difference was not detected, decreased presence in April likely was biologically relevant. For example, the timing of the decline coincided with the end of nest guarding season in California, when males likely disperse from their nesting grounds (Jagielo 1995, Miller & Geibel 1973). Studies on another member of the greenling family, *Oxylebius pictus*, indicated that males have a great energetic cost while guarding eggs (DeMartini 1987). Similarly, it has been proposed that male lingcod only opportunistically feed while nesting (Beaudreau & Essington 2007). The decrease in presence in April in this study may therefore reflect a post nest-guarding period when males actively disperse to feed and physically recover from the winter.

An uncertainty regarding lingcod behavior is whether male lingcod remain near spawning grounds throughout the entire year or leave after winter. Jagielo (1995) reported that at least a proportion of males caught nearshore disperse to deeper waters during spring and summer. Starr et al. (2005) also noted an increase in average depth for males from April to July. Nearshore catches are dominated by males throughout the year

(Miller & Geibel 1973), indicating that at least some males are shallow-water residents irrespective of reproductive season. For the males tagged in this study, three left the array in April and were not detected thereafter. Assuming that larger lingcod occupy deep waters, it is doubtful these males moved far offshore, given their relatively small sizes (53, 59, and 62 cm TL). The number of days detected for three other tagged males also was low in April, but increased in the following months. There was no relationship between size and presence of lingcod after April. My results indicate that lingcod exhibit strong fidelity throughout the year in the nearshore areas, but at least some males disperse to new locations in the spring months following nesting season.

The timing of the drop in the number of days lingcod were detected coincided with the end of nest-guarding season and also with the start of spring upwelling conditions. Upwelling, as indicated by cooler water temperatures, occurred from March to July in 2006, with the coldest temperatures recorded in April. Although overall presence was not correlated with temperature, the drop in days lingcod were detected in April could be a response to cold water conditions. Temperature response also could explain why two small female lingcod were detected less frequently in April, as these fish would not be exhibiting post nest-guarding dispersal.

Interestingly, the average monthly proportion of days spent in the array for adult female lingcod increased from March to June, coincident with strong upwelling conditions. Starr et al. (2005) reported a similar trend for females in Alaska, leading the authors to hypothesize that female lingcod were competitively displacing males to deeper waters during spring and summer months. A sexual depth segregation was not observed in Carmel Bay during spring and summer months, although this could be attributed to the limited number of fish tagged and the configuration of the array in relatively shallow waters.

It is possible that the reduction in the daily detection of lingcod in April was not indicative of fish movements but was caused by environmental conditions. To explore this possibility, range testing data from the stationary reference transmitter was examined. Signal detection for the reference transmitter was high in April, with 98 % of all possible hour bins having signals. At a daily scale, whereby at least two detections were required per 24 hr, the transmitter was detected for 100 % of the days deployed, regardless of month, water temperature, or wind. Based on the results from the reference transmitter, it is unlikely that environmental conditions caused a false interpretation of lingcod presence in the array.

Site fidelity

Lingcod exhibited strong site fidelity within the array throughout the year. For all fish, the majority of detections and hour bins were recorded on one receiver compared with multiple receivers. Although lingcod frequently made departures from the array, they typically returned to the area around the receiver following an absence. Approximately 20 % of lingcod demonstrated larger movements between zones throughout the year, but even these fish were recorded primarily by one receiver.

Most lingcod detections were recorded within one receiver's detection radius, which was estimated to be 150 m from the receiver. This was a surprising result, greater along-shore movements were anticipated from tag-recapture data. It would be interesting to examine with finer-scale tracking techniques how much space lingcod are using within a receiver's detection zone. Local spear fishermen in Carmel Bay have mentioned that lingcod are so site-specific that divers often note lingcod locations before fishing tournaments and return during competition to shoot the fish. Although anecdotal, the fishers' observations are consistent with the strong site fidelity exhibited by lingcod in this study.

Some researchers have proposed that the site fidelity of smaller, immature lingcod may not be as strong as mature fish (Mathews 1992). However, there was no obvious pattern in detections across receivers with respect to the size of lingcod tagged in this study. Whereas overall residence times in the array decreased with total length for females, large and small females demonstrated similar patterns of site fidelity and movements when detected in the array. This result is somewhat surprising, as the small females were presumed to be immature but still demonstrated high site fidelity. It also is possible that the spatial scale at which lingcod were monitored with the VR2s was not appropriate to detect differences in site fidelity in relation to fish size.

Habitat relief

Habitat suitability, as measured by relief, has been documented to influence spatial utilization patterns in fishes (Mathews 1990; Lowe & Bray 2006). In Carmel Bay, lingcod tagged and released in low relief habitats demonstrated similar site fidelity and movement patterns as lingcod tagged in high and medium relief areas. The lack of significant differences may indicate that the habitats monitored in this study were equally suitable for lingcod, regardless of relief. From qualitative observations made on scuba, low-relief areas in the array were characterized by ledges and crevices where lingcod could find shelter, and all habitats were dominated by a seasonal presence of giant kelp (*M. pyrifera*). As rockfish recruitment is strongly associated with *M. pyrifera* (Carr 1991), and juvenile rockfishes are key prey items of lingcod (Beaudreau & Essington 2007), the presence of giant kelp throughout the array could signify the availability of key prey items regardless of substrate relief.

One observation made during the temporary extension of the array in September, 2007, was that no detections were recorded for lingcod by shallow receivers in sandy habitats. Flat sandy habitats are probably not used by the size classes of lingcod tagged in this study, although one tracking study in Washington indicated that lingcod will traverse over sandy and do not necessarily follow rocky habitat contours when moving (Matthews 1992).

Physical parameters

Tides have the potential to greatly affect fish movements. For example, tides in estuaries control the amount of area available for fish to use whereas tidal changes at the mouth of bays or inland straits can create strong currents that greatly influence where and how fast fish swim. In subtidal habitats along an open coast, tides play a less dominant role in habitat composition compared with estuaries and fiords. Thus, it was not surprising that lingcod movements in Carmel Bay were not associated with tides. However, it is possible that tides could indirectly affect lingcod by influencing the abundance and distribution of their prey. Indirect influences of tides were not detected in this study because prey availability was not monitored and the scale at which monitoring occurred might have been too great to detect more subtle behavioral changes.

Lingcod that regularly occupied the array exhibited no detectable diel patterns of movement. Matthews (1992) observed that displaced lingcod homed back to their original capture location only during nocturnal hours, and she hypothesized that lingcod make bigger movements during the night to minimize predation risk. Evidence of such nocturnal behaviors in Carmel Bay was not found, but the scale at which movements were quantified with VR2 receivers may not be appropriate to delineate finer-scale movements.

Applications for management

Dispersal estimates for lingcod were at the core of the scientific debate over MPA size recommendations for the central California region. Lingcod were listed by the SAT as a species exhibiting small to moderate home ranges (5-20 km), and therefore were considered one of the key species likely to benefit from MPAs (CDFG 2008). Yet Walters et al. (2007) modeled lingcod with dispersal rates of 10 km/yr and concluded that MPAs at the scale for the SAT's recommendation of 5-10 km alongshore were too small to offer substantial protection for lingcod.

Although lingcod are undoubtedly capable of relatively large movements, the majority of lingcod tagged and monitored in this study did not disperse 10 km a year. Contrary to reports that lingcod disperse 500 m a day (Smith et al. 1990), lingcod in Carmel Bay exhibited strong site fidelity to particular areas within the array, regardless of size, sex, or habitat relief. At least half of the lingcod tagged in this study were detected for a year, with two lingcod detected within a relatively confined space for two years. These results indicate that lingcod are primarily residential and are likely to benefit from MPAs, even at the minimum MPA size guidelines of 5-10 km.

One major caveat to my conclusion, however, is that lingcod can make extended movements >1 km away from their core activity areas. These extended movements could make lingcod susceptible to fishing mortality in smaller MPAs, if the movements are not contained within reserve boundaries. Therefore, the amount of protection afforded by a MPA to an individual lingcod greatly depends on the proximity of the fish's core activity area in relation to reserve boundaries. In Alaska, Starr et al. (2005) proposed that lingcod may be foraging during these extended movements. If so, lingcod may be extra vulnerable during forays, as hungry fish may be more prone to biting fishing lures.

Low occurrence of adult females in the array implies that nearshore MPAs may not be adequately protecting large, mature, female lingcod from fishing. It is well documented that larger females typically occupy deeper, offshore waters during non-reproductive seasons (Miller & Geibel 1973, Barss & Demory 1989, Jagielo 1990, Gordon 1994). To protect these larger, presumably mature lingcod, rocky habitats in offshore waters also should be considered for MPAs. Based on the similarity of movement patterns observed for lingcod tagged in Carmel Bay and in offshore waters in Alaska (Starr et al. 2005), the sizing of these offshore MPAs would not necessarily have to be any greater than nearshore MPAs to encompass the majority of lingcod movements.

MPA classification, rather than size, may be the most critical factor determining the level of protection afforded to lingcod. For example, the majority of lingcod tagged in this study were captured and released within the Carmel Bay State Marine Conservation Area. Although this MPA prohibits all commercial fishing, lingcod in Carmel Bay are still subject to fishing pressure from recreational fishers. The intensity of recreational fishing was demonstrated in that 2 of the 30 lingcod tagged in this study, or 6.7 % of tagged lingcod, were caught by fishermen. However, not all of the lingcod tagged in this study were above the legal size limit of 61 cm (24 inches TL). When only legal-size lingcod were considered, the percentage of tagged lingcod caught and killed by fishers was 12.5 %. These estimates of fishing mortality assume that all recaptured lingcod were reported, however the actual percentage may be greater had some recaptured lingcod gone unreported.

In central California, recreational catches for lingcod have increased dramatically since 1998 (Jagielo & Wallace 2005). Currently, the recreational fishing season for lingcod is closed from December to April for boat anglers, and from December to March for divers and shore-based anglers. These closures are intended to protect lingcod during nest guarding season, although nearshore spawning and nest guarding occurs before the December closure for at least a portion of the reproductive stock.

It is important to acknowledge that this study was not intended to sample the full size distribution of lingcod. However, the fact that few males above the legal size limit were captured may be an indicator that lingcod populations are under considerable fishing pressure, despite traditional management practices and MPA designation in Carmel Bay. To determine whether the recreational fishery is affecting lingcod populations, future research is required to compare lingcod size frequencies and structure within and between the Carmel Bay SMCA and the Pt Lobos and Carmel Pinnacles State Marine Reserves.

Summary

The presence of tagged lingcod within the nearshore environment in Carmel Bay was consistent with many aspects of previous studies. Large female lingcod spent the least amount of time within the array and their presence was greatest in the fall, when spawning migrations occur off California (Miller & Geibel 1973). Large females also were recorded at deeper depths within the array compared with males and small females. From the literature, it can be assumed that these large females were residing in deeper waters when they were not detected within the array (Cass 1990, Barss & Demory 1989). The return of large females to the relatively shallow waters of the array in the spring was also observed for lingcod in Alaska (Starr et al. 2005) and may explain why residence times for males and small females decreased in April, if competitive displacement for resources is related to size for lingcod.

At least a proportion of male lingcod disperse offshore after nest-guarding season (Jagielo 1995). Seasonal dispersal may thus explain why three male lingcod permanently departed the array in April. The majority of male lingcod tagged in the study, however, remained in the study area throughout the year. Interestingly, small female lingcod also inhabited the nearshore areas in Carmel Bay throughout the year, signifying that sexual segregation in lingcod first occurs when females attain larger sizes.

Lingcod exhibited strong site fidelity within the receiver array, with the majority of detections of a tagged fish recorded on one receiver regardless of the sex and size of the lingcod tagged. The strong site-fidelity exhibited by the small, presumably immature female lingcod was somewhat surprising because small lingcod have been reported to be less site specific than larger conspecifics (Yamanaka & Richards 1993, Mathews 1992). The results from this study signify that lingcod occupy relatively small areas once they move to rocky habitats. For future comparative studies, it would be interesting to track movements of juvenile lingcod on flat, sandy habitats and large females on deep, offshore reefs. Data from the VR2 receivers indicated that lingcod made frequent departures from the array that averaged less than 5 consecutive days. However, from the VR100 surveys, I was able to confirm that some of these absences were caused by acoustic shadows rather than departures. Therefore, actual estimates of site fidelity and residence times of lingcod are likely greater than the estimates provided in this study.

Lingcod did not exhibit obvious movement patterns in relation to physical and environmental parameters. I found no evidence of diel activity patterns, nor was site fidelity and residency significantly different for lingcod occupying habitats of varying relief. The overall proportion of lingcod detected in the array decreased in April, when water temperatures concurrently decreased during spring upwelling. However, there was not a statistically significant correlation between temperature and the number of days per month that lingcod were detected throughout the year.

This study of lingcod movements in Carmel Bay has important implications for designing and evaluating marine protected areas. Although capable of movements greater than 1 km, lingcod exhibited strong site fidelity and high residence times within relatively confined areas in nearshore rocky habitats. Lingcod, therefore, are prime candidates to benefit from marine protected areas. Nearshore MPAs, however, would have a minimal effect on protecting mature female lingcod in deeper waters. Thus, future placement of MPAs also should take into account the distributions of large female lingcod.

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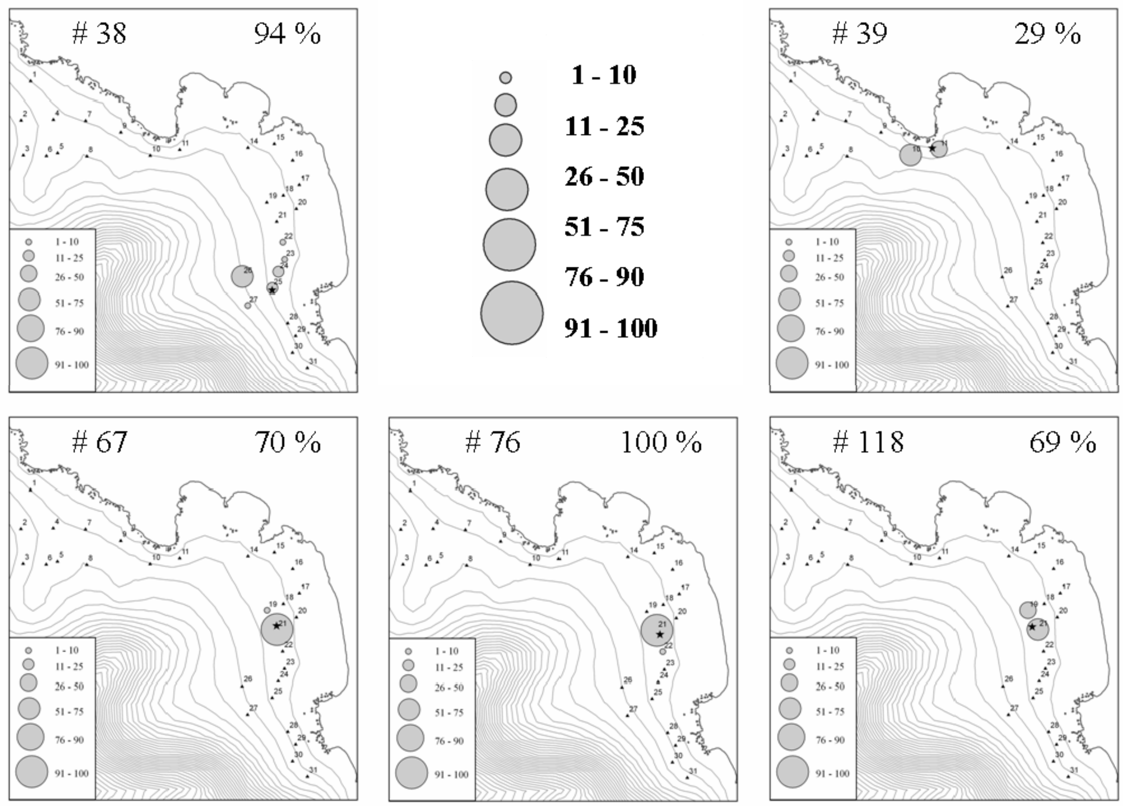
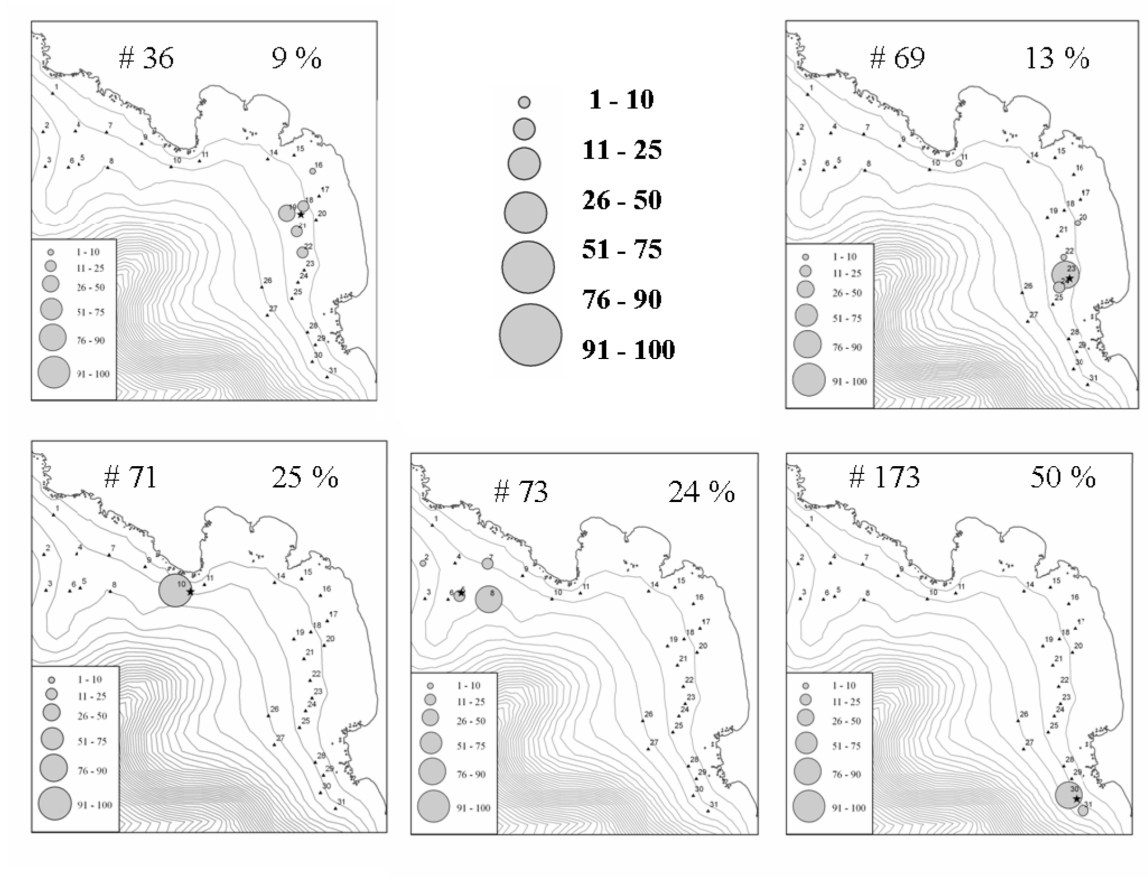
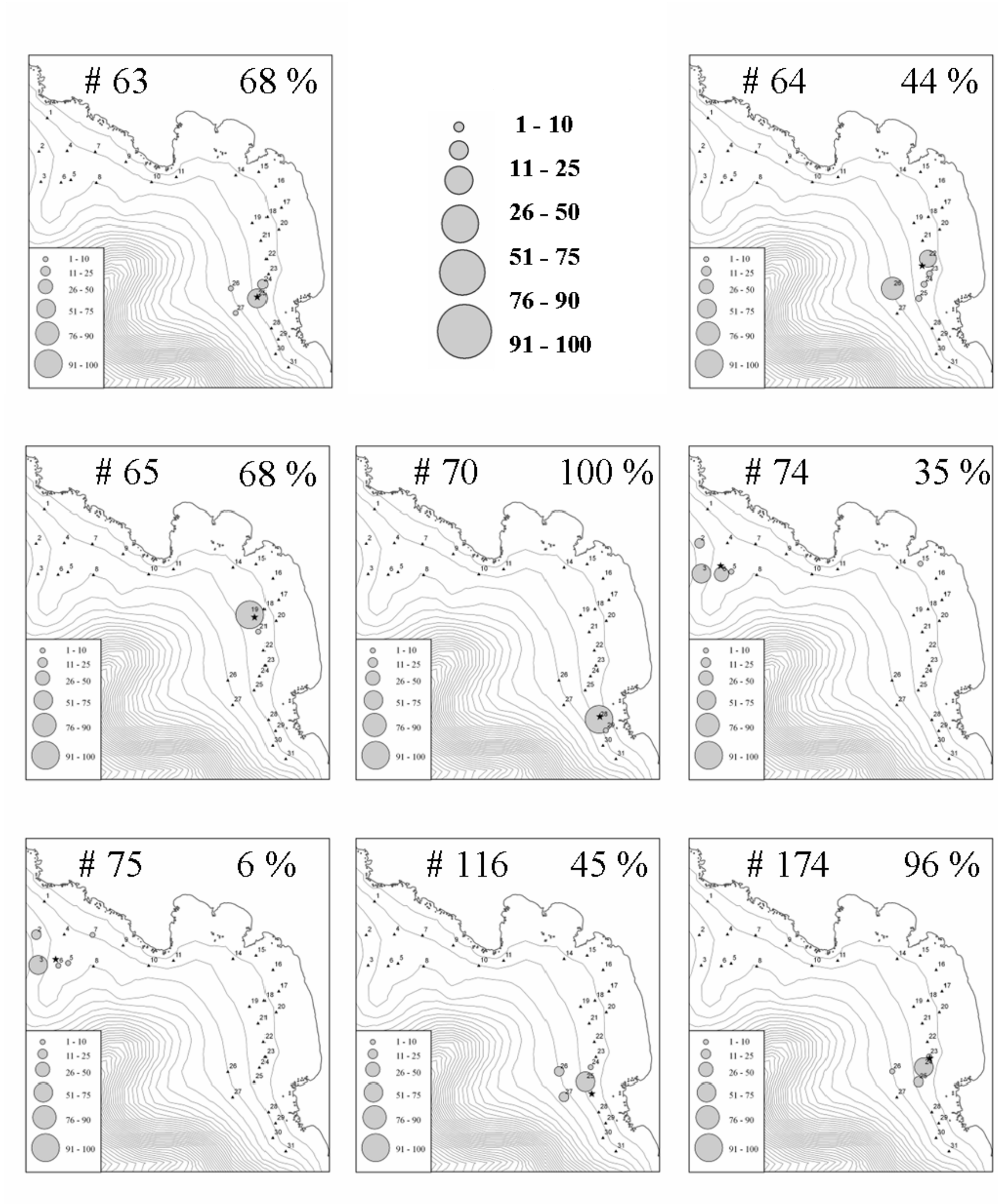


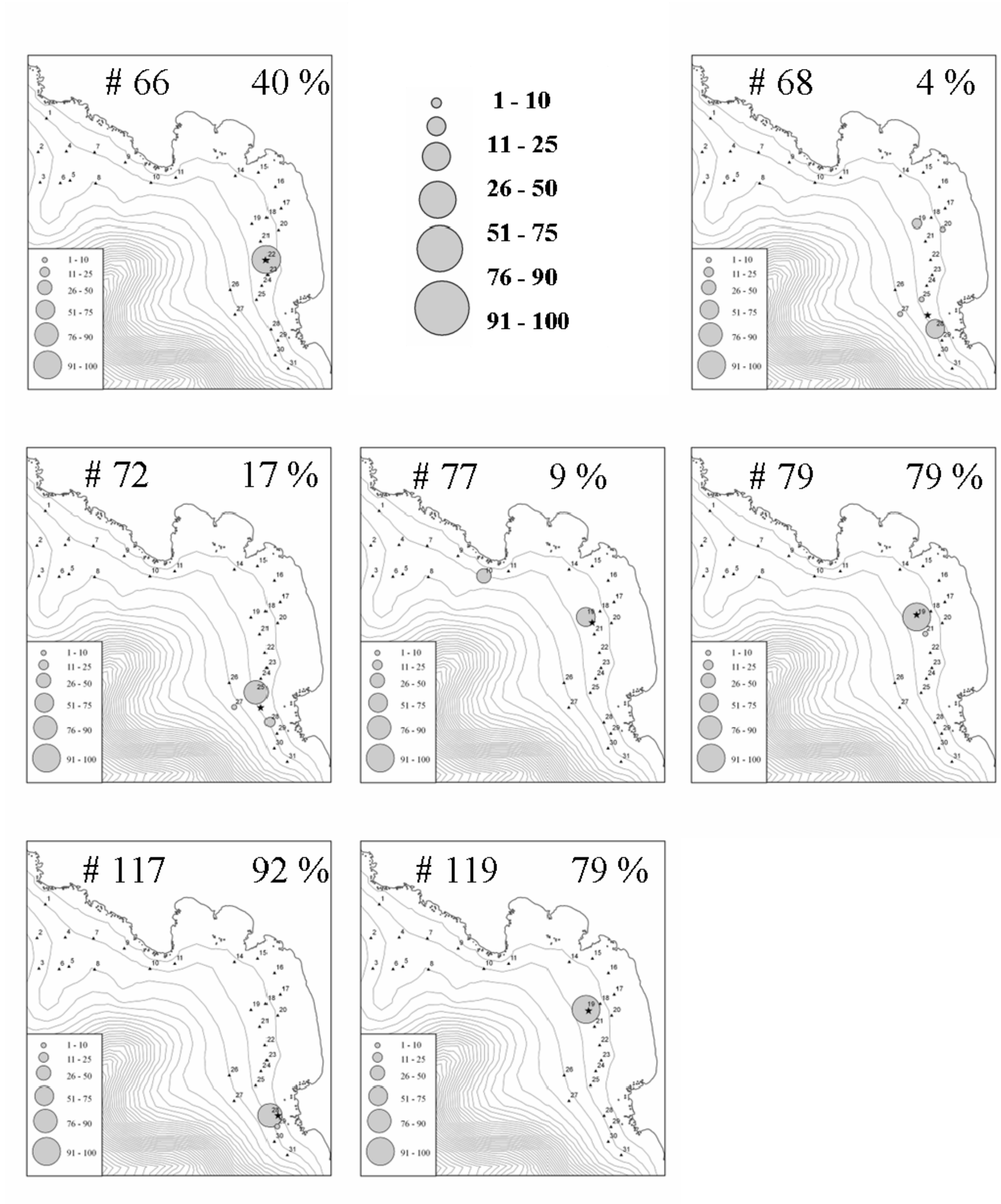
Appendix A. Proportion of hour bins with recorded signals relative to receiver locations for small female lingcod. Numbers at the top of each map correspond to the tag number of the lingcod (left) and the percentage of days at liberty detected in the array (right).



Appendix B. 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. 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. 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).