Fine-scale movement patterns, site fidelity, and habitat selection of ocean whitefish (*Caulolatilus princeps*)

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Abstract

The fishery for California groundfishes is managed using broad species complexes, although some non-groundfish species are managed similarly due to the perception of shared behavioral characteristics. This study integrates acoustic telemetry and a GIS to quantify movement patterns of one such species, the ocean whitefish (*Caulolatilus princeps*) in a marine protected area. Seventeen ocean whitefish were tagged and actively tracked over multiple 24-h periods to measure fine-scale movement patterns. Home ranges based on 95% kernel utilization distributions averaged $20,439 \pm 28,492$ ($\pm$S.D.) m^2. Fish were active during the day, foraging over sand habitat at depths averaging 21 ± 8 m, but were inactive at night, taking refuge near rocky reefs at depths averaging 15 ± 7 m. Seventeen additional fish were tagged with coded acoustic transmitters and passively tracked using automated underwater acoustic receivers for up to 1 year. Approximately 75% of these fish exhibited long-term (1 year) fidelity to home ranges in the study area. Results suggest that MPAs can be an effective means of protecting populations of ocean whitefish and based on their habitat associations, ocean whitefish can be managed separately from other reef associated groundfishes.
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1. Introduction

Recent declines in some California groundfish stocks have emphasized the importance of understanding the behavior of coastal fish species. These population declines have led to more aggressive fisheries management, including seasonal closures, area closures, and depth restrictions, which are managed in California by regions along the coast. A large portion of both the recreational and commercial fishing in California is based in the southern management region (from Point Conception to the Mexican border), yet there remain critical gaps in our knowledge of as the degree of larval dispersal, recruitment, and movement patterns of many southern California coastal fish species. The groundfishes, which primarily include rockfishes (*Sebastes* spp.), are generally managed in broad species complexes relative to their inhabited depths (e.g., nearshore, shelf, and slope). The ocean whitefish (*Caulolatilus princeps*) is included in this management regime because this species is often caught by recreational anglers while targeting rockfishes. However, combined species management has resulted in increased restrictions on the fishery for ocean whitefish primarily due to declines in some rockfish stocks.

Ocean whitefish are among the tilefish family (Branchiostegidae) and range from British Columbia to Peru, although rarely occur north of Point Conception, California. They are typically more abundant at offshore islands and banks than along the coast, and often form loose aggregations in 10–150 m depth (Leet et al., 1992). Ocean whitefish can be found in a variety of habitats, although they feed primarily on interstitial invertebrates (Elorduy-Garay and Caraveo-Patiño, 1994). Females mature at 3–4 years (39–47 cm TL) and males mature at 4–5 years (47–56 cm TL) (D. Cooksey, unpubl. data). While ocean whitefish have been found to be reproductively mature and active both in Baja California, Mexico (Elorduy-Garay and Ramirez-Luna, 1994) and in the Southern California Bight (D. Cooksey, unpubl. data), pelagic larvae have only been found off Baja California (Moser et al., 1986). This suggests that the source of larval production for this species is primarily farther south in Mexican waters. As a result, it has been hypothesized that

ocean whitefish in the Southern California Bight have migrated north from Mexico (Moser et al., 1986; Waples and Rosenblatt, 1987; Leet et al., 1992). However, coastal benthic fish trawl surveys in the Southern California Bight from 1969 to 1999 (J. Allen, unpubl. data) indicate that ocean whitefish recruitment does occur at areas along the southern California shelf, typically in the warmest years. Ocean whitefish recruits (4–8 cm total length) occur in southern California in 15–60 m depths from October to April, peaking from November to February. Thus, remaining uncertainties regarding migration and local production make knowledge of ocean whitefish movement patterns important in gaining a better understanding of their population dynamics.

The first goal of this study was to use active acoustic telemetry to describe the home range and movement patterns of adult ocean whitefish, characterize benthic habitat selection, and test for density-dependent effects on movement patterns by determining the relationship between conspecific density and home range size. Our second goal was to use passive acoustic telemetry to describe long-term (1 year) site fidelity of adult ocean whitefish (*C. princeps*) in a southern California marine reserve. Conducting this research in a marine reserve provided quantitative data on movements of ocean whitefish while controlling for effects of fishing, as well as an assessment of reserve effectiveness for this species.

2. Materials and methods

2.1. Study site

Ocean whitefish were caught and tracked within the Catalina Marine Science Center Marine Life Refuge (CMLR) (33°26.697′N, 118°29.184′W), a no-take marine reserve located near Two Harbors, Santa Catalina Island, which is approximately 40 km from the southern California coast (Fig. 1). Additional areas beyond the reserve boundary that are used in this study include Blue Caverns, Bird Rock, Isthmus Reef, Campground, and Two Harbors (Lowe et al., 2003; Topping et al., 2005, 2006) (Fig. 1).

2.2. Active tracking

Short-term (1–2 months), fine-scale movement and activity patterns of ocean whitefish were determined using active tracking techniques. Adult ocean whitefish were caught within the CMLR using hook and line. Standard surgical techniques were used (Summerfelt and Smith, 1990; Zeller, 1999; Eristhee et al., 2001; Jepsen et al., 2002; Bridger and Booth, 2003; Lowe et al., 2003; Topping et al., 2005) to implant a small (Vemco Model V8SC-1L), continuous pulse acoustic transmitters in the peritoneal cavity of 17 adult ocean whitefish between November
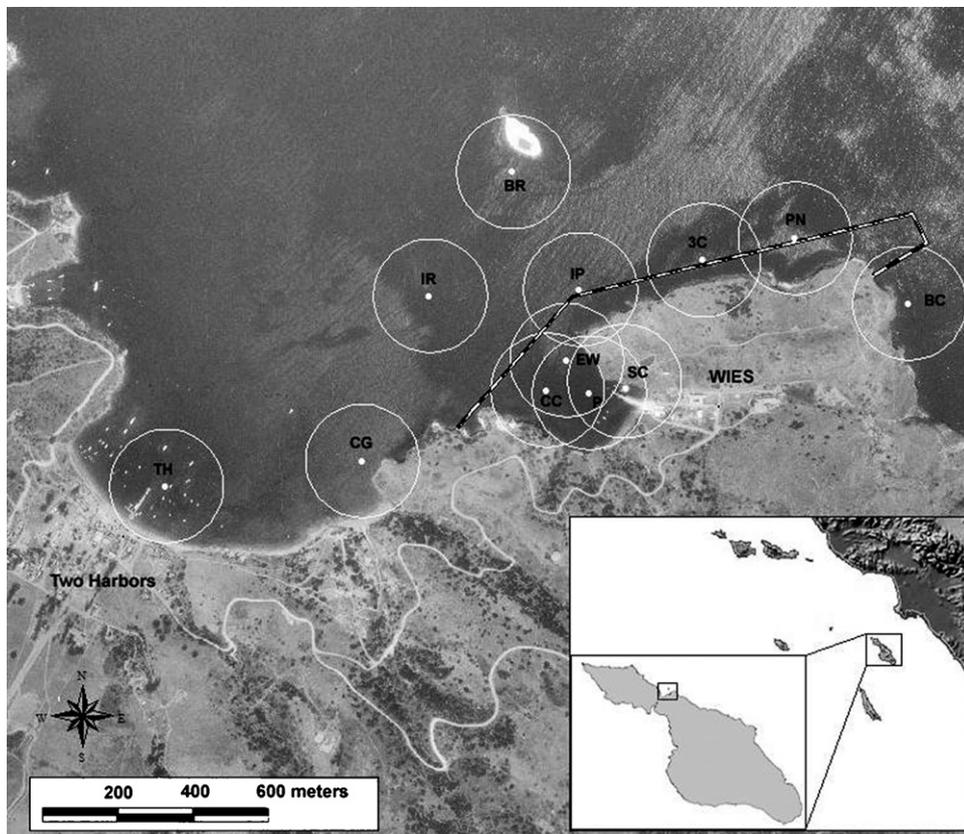

Fig. 1. Aerial photograph of the CMLR (33°26′N, 118°29′W) and town of Two Harbors. The inset shows the location of the site at Santa Catalina Island in relation to the southern California coast. White dots represent the location of 12 VR1 acoustic receivers (TH—Two Harbors, CG—Campground, IR—Isthmus Reef, BR—Bird Rock, CC—Chalk Cliffs, P—Pier, SC—Shark Cove, EW—East Wall, IP—Intake Pipes, 3C—3 Caves, PN—Pumpernickel, and BC—Blue Caverns), and white rings indicate 150 m acoustic detection radii of each receiver. The black and white hatched line represents the reserve boundary.

2003 and June 2005. These transmitters were programmed to a specific frequency within a 65–80 kHz range, with a continuous pulse interval of 1000, 1250, 1500, 1750, or 2000 ms. Following the tagging, the total length (TL) was measured and each individual was fitted with an external plastic dart tag (Hallprint Ltd.) inserted through the dorsal musculature to allow easy identification of tagged fish by divers (Lowe et al., 2003; Topping et al., 2005, 2006). Each fish was then released at the site of capture at which time active acoustic tracking commenced. Fish were tracked from a 4 m skiff with a Vemco Model V10 directional hydrophone and Model VR60 acoustic receiver (e.g., Holland et al., 1993; Lowe et al., 2003; Topping et al., 2005). The 31–61 days battery life of the transmitters allowed multiple 24 h tracks for each fish, allowing fine-scale movement measurements. To assess the effects of catch, handling, and surgery on behavior, additional control fish were fed acoustic transmitters hidden in squid by divers (Winger et al., 2002). However, these control fish were only tracked for one 24 h period each because transmitters were usually passed after 1–2 days.

Short-term movements and habitat use were analyzed using a geographic information system (GIS) with Arcview 3.2 and the Animal Movements Analyst Extension (Hooge and Eichenlaub, 2000). Activity spaces were calculated using two methods: the 95% kernel utilization distribution (KUD), the area in which an individual has a 95% chance of being found during the tracking period (Lowe et al., 2003; Topping et al., 2005); and the minimum convex polygon (MCP), a polygon created using all the outermost position fixes. Position fixes for each track were separated by day and night, defined as the periods between times of sunrise and sunset, and both the KUD and MCP were determined over each period. Once activity spaces were determined for each track, relocation positions from all tracks for each fish were pooled to create overall KUD and MCP home range estimates. Total distance traveled was calculated as the sum of the distances between successive position fixes over each 24 h period. A linearity ratio, the ratio between the distance from the first to last recorded position and the total distance traveled during the tracking period (Zeller, 1997), was calculated to measure the degree to which individuals exhibited home ranging behavior. Small linearity ratios indicate back-and-forth movements (home ranging), whereas large ratios indicate unidirectional movements (nomadic). Aspect ratios for each MCP were calculated by dividing the maximum distance across the MCP (length) and the maximum distance perpendicular to the maximum length (width). This described the shape of the MCP, with values close to 1 indicating circular activity spaces, and values close to 0 indicating more elliptical activity spaces. Linear regressions were used to measure the relationships between fish total length and various movement parameters (e.g., activity space size and aspect ratio, mean linearity ratio, and mean distance traveled).

Because effects of catch and handling-induced stress could affect post-release behavior and survivorship in fishes (Jarvis and Lowe, 2008), short-term survivorship was measured by assessing fine-scale movements of each fish during each track immediately following release. To test for behavioral effects of stress due to catching and surgical procedures, two-sample *t*-tests were used to compare daily activity space (using both the 95% KUD and MCP estimates), distance traveled, and mean linearity ratio for the first 24 h following release between fish surgically fitted with transmitters and control fish that were fed transmitters via SCUBA. Fish surgically fitted with transmitters were usually tracked multiple times over a 1–2 month period. A repeated-measures ANOVA was used to compare 24 h activity spaces, mean distance traveled, and mean linearity ratio between the first and subsequent tracks among surgically fitted fish.

Habitat selection was measured by plotting each track over geo-referenced, high-resolution bathymetry (1 m²) and benthic habitat (2 m²) maps (derived by the California State University Monterey Bay Seafloor Mapping Lab). The ratio of the proportion of each habitat used to the proportion of the habitat available yielded individual habitat selection (Manly et al., 2002). Available habitat was defined using Arcview GIS as the proportion of area of each habitat type within the MCP for each individual tracked. With this method, a value greater than 1 would indicate habitat selection. A Chi-square Goodness of Fit test was used to measure significance of habitat selection (Manly et al., 2002). All statistical tests with active tracking data were performed with the significance level $\alpha = 0.05$.

2.3. Passive tracking

Long-term (1 year) movement patterns and site fidelity of ocean whitefish were determined using passive acoustic telemetry. We used random pulse coded transmitters (Vemco Model V8SC-2L-R256), which emitted a pulse series containing a specific code unique to each tag at a 69 kHz frequency at random intervals between 40 and 120 s. This yielded a battery life of approximately 1 year.

Seventeen additional tagged individuals were monitored by an array of 12 omni-directional underwater automated acoustic receivers (Vemco Model VR1), which were attached to fixed subsurface moorings inside and outside the marine reserve approximately 10 m below the surface (Topping et al., 2006; Hight and Lowe, 2007). Each VR1 receiver had an effective detection range of approximately 150 m (Topping et al., 2006), thus creating a detection area that encompassed virtually the entire reserve (Fig. 1). The receivers recorded the date and time each tagged fish was detected over the 1-year period. Passive tracking data were analyzed to quantify survivorship, diel periodicity, and monthly site fidelity to the CMLR over a 1-year period. Survivorship was assessed using temporal changes in the detection rate or diel periodicity in both the number of detections and the monitors frequented by individuals. Site fidelity was measured as detection frequency per functional day to control for temporal gaps in VR1 coverage at a particular location. The mean proportion of days fish were detected per month, as well as mean daily number of detections each month were calculated to assess site fidelity and analyzed using a one-way ANOVA and Tukey's pair-wise comparisons. Expansion or contraction of area use was measured by creating MCPs around the effective detection ranges of all receivers frequented each month. This approach was used rather than simply the number of receivers frequented because the receivers were not arranged

in a spatially uniform array. Mean monthly detection areas were analyzed using an ANOVA and Tukey's pair-wise comparisons. All statistical tests with passive tracking data were performed with the significance level $\alpha = 0.05$.

2.4. Density surveys

Visual surveys of ocean whitefish density were conducted by divers at areas where individuals were actively tracked inside the CMLR. Because the ocean whitefish is generally a demersal species, all transects were conducted solely along the bottom. The CMLR was divided into four areas (Cove, Intakes, Three Caves, and Pumpernickel; Fig. 1), each stratified by depth (15, 20, and 30 m), thus creating 12 sampling zones. Transects were 4 m wide (2 m on each side of the diver), 4 m tall, and 30 m in length. All transects were surveyed by a single experienced diver to maintain consistency in abundance estimations and transect dimensions. Density surveys were conducted periodically throughout the year, although to ensure adequate visibility transects were not conducted during low light hours.

The effect of conspecific densities on activity space size of ocean whitefish was measured to test for density-dependent effects on fish movements. It was hypothesized that increased conspecific densities would yield larger home ranges, possibly due to increased intraspecific competition. Mean ocean whitefish densities were assigned to each of the 12 depth zones by pooling all transects conducted in each zone. Position fixes for each active track were then layered over the zones in a GIS, and the proportion of fixes in each zone during each track was used to calculate the mean proportion of time spent by a fish in each zone. A conspecific fish density value was then assigned to each fish by using the mean density in each zone weighted by the proportion of time spent in each zone. These values were then paired with the corresponding 95% KUD and MCP values for each actively tracked individual. However, sampling zones were stratified by depth, which was likely to be a covariate affecting densities. Therefore, weighted mean depths were also calculated using the same method described for conspecific density. Linear regressions were used to measure the effect of conspecific density and depth on size of activity space.

3. Results

3.1. Active tracking

Short-term survivorship for the actively tracked individuals was high (94%), with only one mortality out of 17 actively tracked fish, despite frequent signs of barotrauma (e.g., over-inflated swim bladders). Post-release survival of tagged ocean whitefish was determined based on rate, timing, and directionality of movement. There were no significant differences in activity space size using either the 95% KUD ($t = -1.22$, $p = 0.24$) or MCP ($t = -0.58$, $p = 0.57$) between ocean white fish fed or surgically fitted with acoustic transmitters. There were also no significant differences in either the mean distance traveled (two sample t-test: $t = 1.40$, $p = 0.18$) or mean linearity ratio ($t = -0.95$, $p = 0.36$) between individuals fed or surgically fit-

ted with acoustic transmitters. Individuals surgically fitted with transmitters were tracked for up to three 24 h periods per fish. The initial track was conducted immediately following release, and the second track of the same fish was conducted at least 10 days after release to allow recovery from potential stress associated with catching and surgery. There were no differences in 95% KUD sizes ($F = 2.46$, $p = 0.13$), MCP sizes ($F = 0.38$, $p = 0.70$), rates of movement ($F = 1.80$, $p = 0.21$), or linearity ratios ($F = 2.42$, $p = 0.13$) between the initial and subsequent tracks for surgically fitted fish. To further test for an initial stressed period, only the first tracks of fed and surgically fitted fish were compared. There were no significant differences in mean linearity ratio ($t = -1.51$, d.f. = 14, $p = 0.15$) or 24 h activity spaces ($t = 0.078$, d.f. = 14, $p = 0.939$). However, distance traveled during the first track of surgically fitted fish was significantly less than for the first track of fed fish ($t = 2.69$, d.f. = 14, $p = 0.02$).

Seventeen ocean whitefish (size range: 36–60 cm TL) were tagged (11 surgical implants and 6 fed) within the CMLR and actively tracked over one to three 24 h periods between November 2003 and June 2005 (Table 1). Ocean whitefish exhibited diurnal activity patterns, with repeated use of daytime and nighttime areas. Because limited movement at night resulted in a high concentration of points in a very small area, nighttime positions were omitted from the 95% KUD to avoid bias in the activity space estimate. Mean daytime activity space size using a 95% kernel utilization distribution (KUD) was $20,439 \pm 28,492 \, \mathrm{m}^2$ (±S.D.), and using a minimum convex polygon (MCP) was $35,474 \pm 50,554 \, \mathrm{m}^2$ (Table 1 and Fig. 2a–f). Data for only 16 fish are included in activity space analyses due to one assumed predation event that occurred during the initial track of fish ID #16 (Table 1). Ten of the 16 individuals had 95% KUDs that extended beyond the reserve boundary, including two fish that were tracked approximately 1 km beyond the edge of the reserve. Mean distance traveled was $3781 \pm 1215 \, \mathrm{m \, day}^{-1}$ (±S.D.), and linearity ratios averaged 0.032 ± 0.022 (Table 1).

There was no significant relationship between activity space size and fish total length (TL) using either the MCP ($F = 0.01$, $r^2 = 0.10$, $p = 0.93$) or 95% KUD ($F = 0.00$, $r^2 = 0.00$, $p = 0.97$) estimates. There was also no significant relationship between fish TL and either mean distance traveled per day ($F = 0.78$, $r^2 = 0.05$, $p = 0.39$) or mean linearity ratio ($F = 0.34$, $r^2 = 0.02$, $p = 0.57$). However, MCP aspect ratios were significantly lower for fish tracked along the narrow rocky reef wall than for those tracked inside the cove ($t = 5.46$, $p < 0.001$).

The habitat selection index indicated significant day–night differences in habitat selection (Fig. 3). During the day, ocean whitefish exhibited significant selection for sand habitat ($X^2 = 141.01$, d.f. = 15, $p < 0.001$), and no significant selection against any other habitat type. During nighttime periods, ocean whitefish exhibited significant selection for high relief bedrock slope over all other habitat types ($X^2 = 243.36$, d.f. = 8, $p < 0.001$), and were seldom found to use steep volcanic bedrock habitat ($X^2 = 7.70$, d.f. = 2, $p = 0.021$). Bottom depth utilization showed clear day–night differences with ocean whitefish at a mean depth of $21 \pm 8 \, \mathrm{m}$ (S.D.) during the day, and moving shallower at night to a mean depth of $15 \pm 7 \, \mathrm{m}$ (Fig. 4). Overall,

Table 1
Summary information for all 17 actively tracked ocean whitefish tagged within the CMLR

Fish ID	Months tracked	Number of tracks	Total length (cm)	Implant method	95% KUD (m²)	MCP (m²)	Mean distance traveled day⁻¹ (m) ± S.D.	MCP aspect ratio	Mean linearity ratio ± S.D.
1	November 2003	1	60	Fed	7,018	14,183	3818	0.761	0.014
2	April 2004	1	60	Fed	29,935	36,654	3639	0.662	0.057
3	April 2004	1	60	Fed	15,921	29,396	5572	0.672	0.022
4	June 2004	2	39	Surgical	41,186	147,346	4882 ± 2180	0.138	0.060 ± 0.051
5	June–July 2004	2	39	Surgical	1,927	4,688	1928 ± 1273	0.578	0.018 ± 0.006
6	July 2004	3	36	Surgical	117,335	177,207	6211 ± 2693	0.531	0.053 ± 0.024
7	September–October 2004	3	37	Surgical	8,899	17,026	2662 ± 603	0.382	0.006 ± 0.001
8	November–December 2004	3	42	Surgical	10,262	21,752	2493 ± 331	0.452	0.049 ± 0.050
9	January 2005	2	41	Surgical	20,510	13,911	2634 ± 115	0.151	0.062 ± 0.066
10	January–February 2005	3	42	Surgical	3,874	4,987	3846 ± 882	0.638	0.011 ± 0.009
11	March 2005	1	45	Fed	2,174	17,396	3738	0.834	0.013
12	April–June 2005	3	42	Surgical	10,880	17,565	3558 ± 743	0.485	0.011 ± 0.006
13	July 2005	1	48	Fed	5,754	10,806	5566	0.590	0.013
14	July 2005	1	40	Fed	2,722	6,808	3551	0.639	0.028
15	August 2005	3	45	Surgical	28,102	27,466	2920 ± 898	0.192	0.032 ± 0.042
16	August 2005	*	40	Surgical	*	*	*	*	*
17	August 2005	3	36	Surgical	10,526	20,392	3486 ± 830	0.283	0.071 ± 0.048

All transmitters used were Vemco model V8SC-1L. Mean values are reported (±S.D.), although individuals that were only tracked once do not have measures of dispersion. A probable predation event during the first track for fish #16 precluded adequate data collection. Hence, values are represented by asterisks (*).

ocean whitefish generally followed the rock–sand ecotone, using a variety of habitats during the day but primarily selecting for sand. At night, individuals also used a range of habitats, but selected for high relief bedrock slope, and used shallower depths than during the day.

There were significant differences in conspecific densities between sampling zones within the CMLR ($F = 3.133$, $p = 0.001$). Ocean whitefish densities were lower in the shallower (15 m) depth zones (mostly rocky habitat), and increased significantly in the deeper (20 and 30 m) zones (mostly sand habitat). There was no significant effect of ocean whitefish density or depth on either 95% KUD size ($p = 0.289$; Fig. 5) or MCP size ($p = 0.440$), although two outliers are driving this lack of a relationship. These individuals (fish # 1–3) were fed transmitters by divers, and observational evidence suggests that these three fish could have actually been the same individual. Pooling these three individuals to calculate a single home range and density value yields a significant relationship between conspecific densities and home range size ($F = 6.23$, $p = 0.034$).

3.2. Passive tracking

Of the seventeen additional ocean whitefish (35–45 cm TL) caught and surgically fitted with coded acoustic transmitters (Table 2), 12 fish were detected consistently over the study period, and 9 of those 12 were detected virtually every day excluding gaps in VR1 coverage (Fig. 6a). One individual (ID # 202) was not detected at all. Longer-term survivorship was estimated at 88% (14 out of 16—one omitted), although mortality events were presumed based on lack of diel periodicity in detections. The two fish were assumed dead because they exhibited no diel pattern in detection frequency, and disappeared shortly after release. However, the only confirmed mortality was a single individual, fish # 206, which was reported caught by a recreational

Table 2
Summary information for all 17 passively tracked ocean whitefish within and around the CMLR

ID code	Date deployed	Total length (cm)	Number of days detected	% Days detected
11	July 9, 2004	37	108	27.27
12	July 9, 2004	40	262	65.99
201	June 20, 2004	42	330	100.00
202	June 22, 2004	38	0	0.00
203	June 22, 2004	41	8	1.93
204	June 21, 2004	37	415	100.00
205	June 20, 2004	37	415	100.00
206	June 20, 2004	43	316	76.14
207	June 20, 2004	38	415	100.00
208	June 22, 2004	44	365	88.38
209	July 11, 2004	36	415	100.00
210	July 10, 2004	35	415	100.00
211	July 11, 2004	35	161	54.58
212	June 23, 2004	40	26	6.31
213	June 22, 2004	44	385	93.22
214	June 22, 2004	39	400	96.39
215	June 22, 2004	45	412	99.76

All transmitters used were Vemco model V8SC-2L-R256. Fish ID 202 was likely fitted with a faulty transmitter.
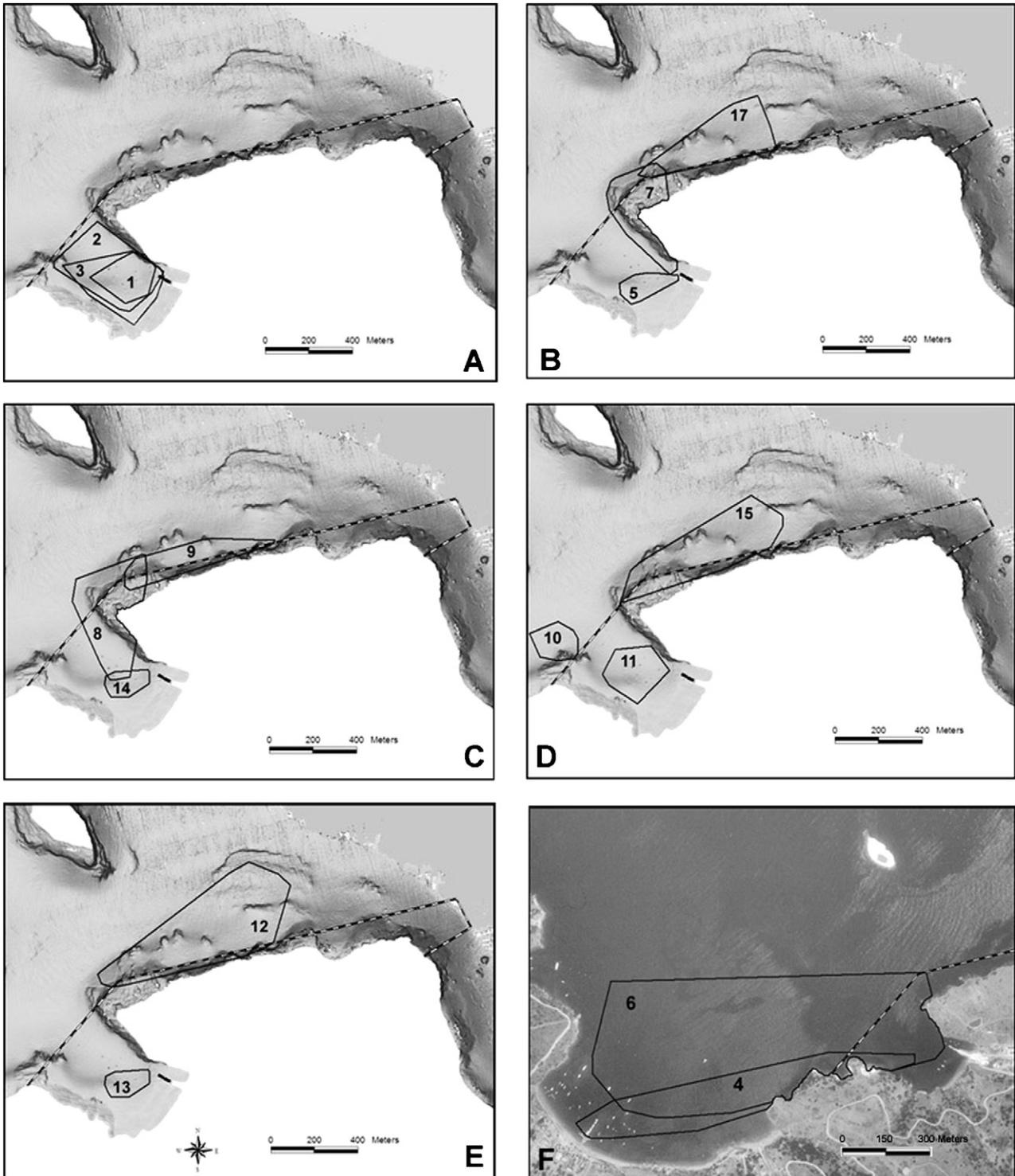
Fig. 2. High resolution shaded relief maps showing benthic topography with diel home range estimates using MCPs for fish #s (A) 1–3, (B) 5, 7, and 17, (C) 8, 9, and 14, (D) 10, 11, and 15, (E) 12 and 13 and (F) aerial photo map for fish #s 4 and 6.

fisherman in May 2005 outside the reserve near Isthmus Reef. As a result, this individual was not considered a long-term mortality associated with catch-and-release stress. The proportion of days that tagged fish were detected per month did not significantly differ between June 2004 and June 2005 when VR1 coverage was standardized to account for temporal gaps ($F = 1.51$, $p = 0.13$;

Fig. 7a). Mean monthly MCP area was significantly less in June 2004 than subsequent months ($F = 2.04$, $p = 0.03$; Fig. 7b). The mean number of detections per day was significantly less in November 2004 than in other months, after correcting for gaps in temporal VR1 coverage ($F = 2.76$, $p = 0.002$; Fig. 7c).
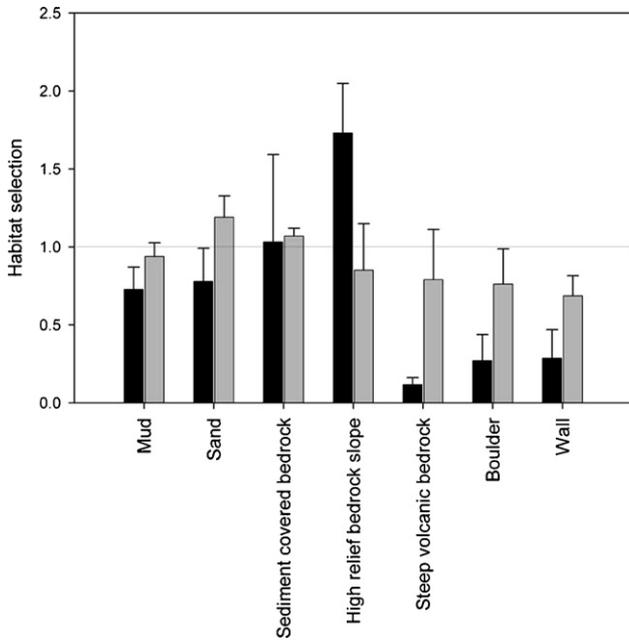
Fig. 3. Mean habitat selection index (+S.D.) between night (black bars) and day (grey bars) periods. The grey horizontal line indicates the neutral reference value of 1.
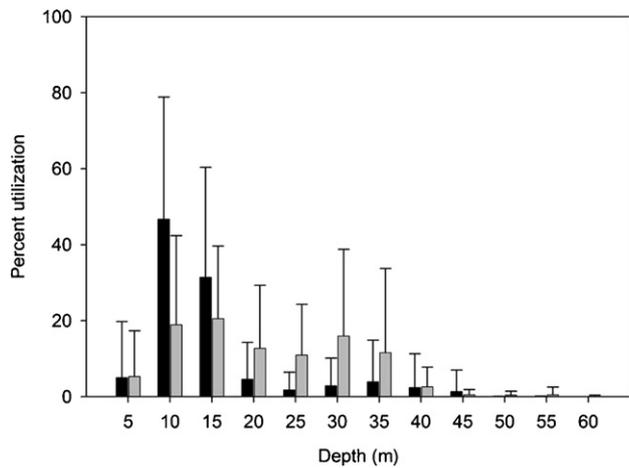

Fig. 4. Mean percent depth utilization (+S.E.) between night (black bars) and day (grey bars). Depth values represent mean depth of the bottom at each position fix, rather than the actual depth of the fish.

4. Discussion

Post-release survival has important implications for fisheries management, especially in southern California where many anglers advocate catch-and-release for conservational purposes. Short-term post-release survival for actively tracked ocean whitefish was high (94%). The one ocean whitefish mortality among 17 actively tracked fish was thought to be a predation event due to unusual increase in rate of movement and depth use, as well as a sudden offshore movement during the night when ocean whitefish generally seek refuge. Potential predators for ocean whitefish include the giant seabass (*Stereolepis gigas*), tope shark (*Galeorhinus galeus*), California sealion (*Zalophus californianus*), and harbor seal (*Phoca vitulina*), which are all
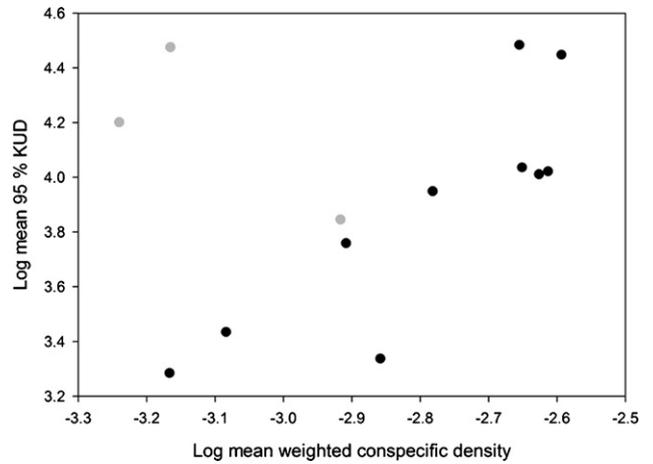

Fig. 5. Log 95% KUD (m^2) vs. log mean weighted conspecific density (number of fishes per m^3). Gray points represent fish # 1–3 that were fed acoustic transmitters and could possibly be the same individual. Only 13 points are shown because 3 of the 16 fish left the surveyed area completely, and as a result, could not be correlated with a density value.
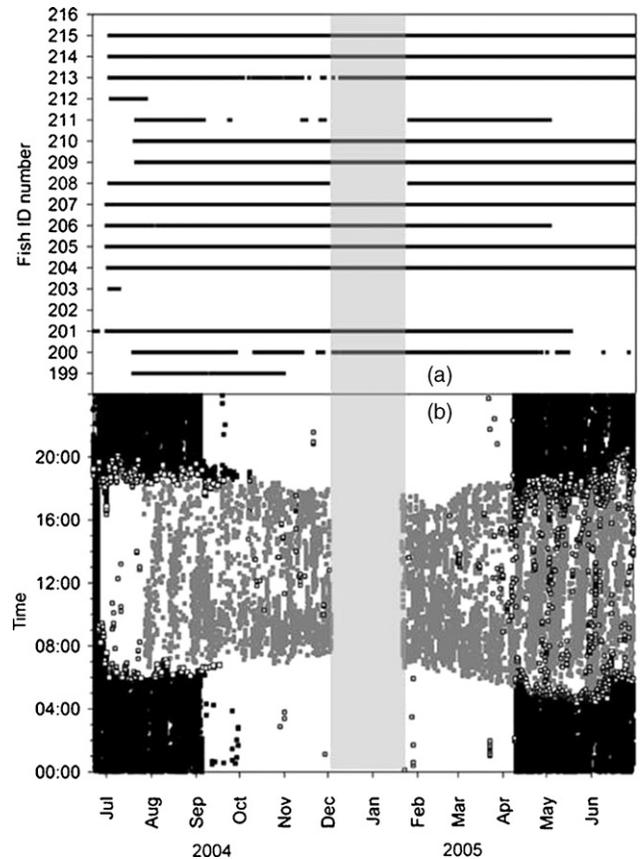

Fig. 6. (a) Detections for all passively tracked fish over the 1-year study period. The grey shaded box represents a gap in temporal coverage at some of the VR1 receivers. (b) All detections for fish #208 at different VR1 receiver locations are indicated by black points (Intake Pipes), grey points (Blue Caverns), grey outlined points (Pumpernickel), or white outlined points (3 Caves). This individual exhibits consistent use of areas inside the reserve at night and outside the reserve during the day, although nighttime area use shifts to areas outside detection range, likely beyond Blue Caverns from September to April. Faint diagonal bands in daytime detections result from tidal effects on detection rate rather than movement.
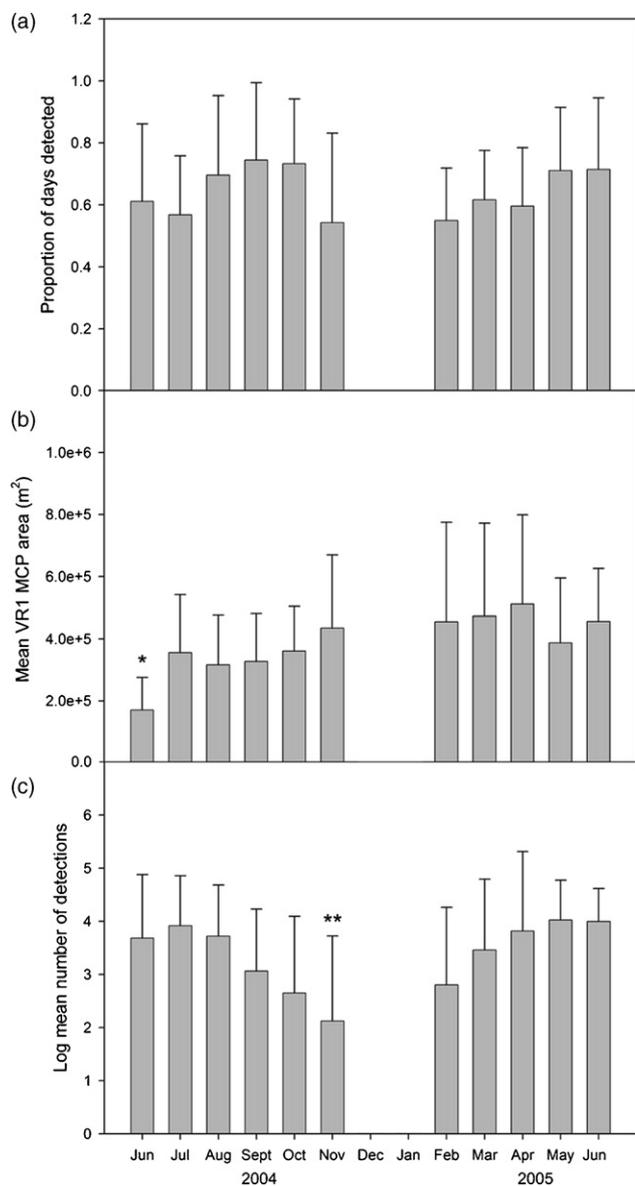
Fig. 7. (a) Mean (±S.D.) monthly proportion of days that tagged fish were detected relative to the total number of effective days that VR1 receivers were deployed, (b) mean (+S.D.) monthly area (m²) used, and (c) log transformed mean (+S.D.) monthly number of detections of tagged fish per number of effective days that VR1 receivers were deployed. ** represents a significant difference ($p < 0.01$) and * represents ($p < 0.05$).

(40 m) may be because the effects of barotrauma are generally not lethal for this species if the swim bladder is properly vented or fish are recompressed.

Despite high survival estimates, physiological and behavioral effects of stress due to catch-and-release could result in restricted movement patterns. Fine-scale active tracking showed no differences in movement between the first and subsequent tracks for fish surgically fitted with transmitters. In addition, only distance traveled was significantly less during only the first track of surgically fitted fish than for fish that were fed transmitters. This indicates that post-release handling stress was short-lived, and resulted in decreased rate of movement rather than decreased area use. Brief periods of stress have been measured for other fish species as well. For example, Lower et al. (2005) measured increased cortisol levels in both carp (*Cyprinus carpio*) and roach (*Rutilus rutilus*) following surgical transmitter implantation, although cortisol levels returned to pre-stress levels within 12 h after tagging. Rate of movement among ocean whitefish decreased without affecting size of activity space because individuals usually traversed their daily activity space several times each day. Thus, rate of movement would only have affected the number of times an individual moved through its activity space rather than the size of the activity space.

All ocean whitefish were diurnally active, exhibiting crepuscular movements between consistent day and night areas, a behavior that has been quantified in other species as well (Meyer et al., 2000; Jadot et al., 2002; Meyer and Holland, 2005; Topping et al., 2005). Mean distance traveled per day (m) generally revealed two types of crepuscular movements among ocean whitefish. Dawn movements were either over short distances (less than 200 m) to daytime areas directly adjacent to nighttime areas (both inside and outside the reserve), or over long distances (greater than 700 m) beyond the reserve boundary. At dusk, individuals returned to the same general nighttime area within the CMLR. These behaviors were exhibited consistently among tracks for all individuals. Meyer and Holland (2005) found similar behaviors with bluespine unicornfish (*Naso unicornis*) within a small Hawaiian marine reserve, and used the terms 'commuting' and 'foraging' to distinguish between the two types of diel movements. However, this species moved over shorter distances than ocean whitefish, possibly because the unicornfish is a reef-associated species with a higher affinity for benthic structure than ocean whitefish.

Ocean whitefish preferred sand habitat during the day and high relief bedrock slope during the night. Because ocean whitefish are diurnal and are known to feed primarily on interstitial invertebrates, this was likely for the purposes of foraging during the day and refuge during the night. Selection for sand habitat during the day in conjunction with some use of rocky habitats, suggests that this species associates with the rock–sand ecotone, yet prefers the sand side of the habitat edge. Differences in day–night habitat use have been documented in other coastal species as well, such as tautog (*Tautoga onitis*; Arendt et al., 2001b), bluespine unicornfish (*N. unicornis*; Meyer and Holland, 2005), and California sheephead (*S. pulcher*; Topping et al., 2005). Actively tracked ocean whitefish also showed a shift towards shallower water at night, with fish using waters 21 ± 8 m

occasionally observed within the CMLR. Such high percentages of short-term post-release survival have been found among other coastal species as well, despite varying methods used for catching and/or tagging (e.g., Matthews, 1990a; Starr et al., 2002; Arendt et al., 2001a; Lowe et al., 2003; Aalbers et al., 2004; Lacroix et al., 2005; Topping et al., 2005). The overall survival for both actively and passively tracked fish was high (91%), despite the number of fish caught with over-inflated swim bladders, which usually required venting via a hypodermic needle. Effects of barotrauma can result in increased post-release mortality as capture depth increases (Gitschlag and Renaud, 1994; St. John and Syers, 2005; Jarvis and Lowe, 2008). The lack of increased mortality of ocean whitefish caught at deeper depths

(±S.D.) deep during the day and 15 ± 7 m during the night. These depth distributions are shallow relative to the reported depth range (10–150 m) for this species, and suggest that ocean whitefish may prefer shallower water habitats at Santa Catalina Island than along the mainland coast. In addition, the selection for shallow rocky habitats at night may be due to the presence of giant kelp (*Macrosystis pyrifera*) growing at depths of approximately 5–15 m, which could provide additional shelter habitat near the holdfast. Interestingly, the behavior of ocean whitefish differs from that of other species of tilefishes. For example, a congener on the Atlantic coast, *Caulolatilus microps*, constructs burrows in soft sediments for refuge (Able et al., 1987), which is a common behavior among several species of tilefishes in both the Caribbean (Dooley, 1978) and Japan (Mitamura et al., 2005), but this behavior has not been documented for ocean whitefish. However, large burrows have been observed from submersibles within the depth range of ocean whitefish in Santa Monica Bay, but it is unclear whether these were constructed by ocean whitefish (J. Allen, pers. comm.).

Association with habitat edges suggests that edge configuration could affect shape of an individual's activity space. The shape of activity spaces using MCP aspect ratios was significantly different between individuals tracked within the cove and individuals tracked along the outside wall of the reserve. Mean aspect ratios revealed more elliptical MCPs along the relatively linear rock–sand ecotone near the outside wall, and more circular MCPs in the cove where individuals were more bounded by habitat edges (Fig. 2a–e). This is consistent with similar analyses conducted with California sheephead (*S. pulcher*) at the same study site (Topping et al., 2005). It is clear that habitat edges do affect animal movements (Kolasa and Zalewski, 1995), although most studies have focused on estuarine (e.g., Peterson and Turner, 1994; Walsh et al., 1999) and freshwater fish species (e.g., Matěna, 1995; Schlosser, 1995). However, studies on Caribbean coral reef fishes have shown that habitat edges and configuration have significant effects on species abundance (Kendall et al., 2003) and assemblage structure (Grober-Dunsmore et al., 2007). This suggests that habitat edge configuration likely affects the movements of some demersal fish species. In the case of ocean whitefish, activity space shapes are influenced by the shape and configuration of reef-sand ecotone habitat.

Variation in size of activity spaces of marine fish species has been attributed to factors such as sex (Bradbury et al., 1995), body size (Kramer and Chapman, 1999), and habitat quality (Matthews, 1990b; Lowe and Bray, 2006). There was no relationship between the body size (TL) of ocean whitefish tracked and size of their activity spaces. However, the size range of fish tracked was 36–60 cm TL, which is only a fraction of their entire size range (largest recorded individual—102 cm TL; Fitch and Lavenberg, 1971). While spatial requirements did not differ among 36–60 cm TL adults, differences could exist for juveniles and the largest adults. Thus, it is possible that ontogenetic shifts in area use exist, but the size range of tagged individuals was not broad enough to detect a size effect. In addition, ocean whitefish exhibit no sexual dimorphism, so it was not possible to determine whether males had larger or smaller activity spaces than females. Other variables such as reproductive requirements, seasonality, food availability, habitat availability/distribution, or inter/intra-specific competition could also affect activity space size. However, active tracking did not reveal seasonal variation in area use among ocean whitefish, which differs from movement studies on other local species. Topping et al. (2006) found that the protogynous haremic California sheephead (*S. pulcher*) exhibited home range expansion during winter months, possibly to increase the frequency of social interactions. Because ocean whitefish are not known to be territorial and do not maintain harems, it is less likely that conspecific social factors influence their area use; however, foraging and refuge seeking behaviors combined suggest an interaction between habitat distribution and food availability likely influences activity space size of ocean whitefish.

Conspecific densities could also affect the activity space sizes of individuals based on density-dependent effects on resource availability and intra-specific competition (Kramer and Chapman, 1999; Abesamis and Russ, 2005; Lowe and Bray, 2006). While most studies focusing on density-dependent movements in fishes have only done so from a theoretical perspective (e.g., Kramer and Chapman, 1999; Nowlis and Roberts, 1999; Roberts et al., 2001; Sullivan et al., 2003), Abesamis and Russ (2005) found supporting empirical evidence for density-dependent emigration, or spillover, of surgeonfish (*Naso vlamingii*) from a marine reserve. This study employed visual survey methods to measure a gradient in both adult densities and competitive interactions between conspecifics that decreased with increasing distance from the reserve. However, density-dependent spillover after reserve implementation could only be inferred from gradual increases in density outside the boundary, and actual relocation of activity spaces to areas beyond the reserve was rarely observed. The density of ocean whitefish within the CMLR showed no significant effects on activity space size of individuals actively tracked. However, evidence suggests that three of these fish (fish # 1–3), which were all fed transmitters via SCUBA, were actually the same individual. They were all estimated to be 60 cm TL, which was the largest size observed within the CMLR, all were fed in the same location within the CMLR, all exhibited similarly behavior towards divers, and exhibited very similar home range sizes/shapes (Fig. 2a). Consolidation of these three fish yields significant density influence on activity space size, possibly due to intraspecific competition for resources. This may explain why some individuals traveled from the reserve to Two Harbors to forage almost 1 km away, yet return to their same refuge areas at dusk within the reserve.

Longer-term movements of ocean whitefish using passive acoustic tracking indicated site fidelity with periodic shifts in area use, although these spatial shifts did not appear to be seasonal (Fig. 6). Duration of day–night movements was clearly a function of day length because all individuals exhibited the same diel periodicity in detections as seen in Fig. 7. The mean number of detections showed a seasonal trend, although there was only a significant decrease in November among all individuals. Changes in the number of detections can be caused by variation in the degree of site fidelity to an area or changes in

the rate of movement when site fidelity is constant (Topping et al., 2006). If an individual moves at a faster rate, there is a lower probability of being detected when it swims within range of a VR1 receiver. Thus, the November 2004 reduction in the mean number of detections in conjunction with relatively constant monthly site fidelity (proportion of days detected) implies that individuals exhibited an increased rate of movement during that month. This could be related to reproductive behaviors, and would be consistent with peak GSI values in November from ocean whitefish studied in Baja (Elorduy-Garay and Ramirez-Luna, 1994). Record levels of storm activity during the winter of 2004–2005 could have affected movement patterns or detection rate of ocean whitefish. However, there was little storm activity during November 2004 relative to December and January. Thus, decreases in detection frequency during November were likely due to other factors. In addition to days detected and detections per day, area use was measured with monthly MCPs around frequented VR1 receivers to assess expansion or contraction of home ranges over the one-year period. Aside from the first month after release for each tagged fish, there was no difference in MCP size for detection by different VR1 receivers among months. This difference in the first month was likely an artifact of transmitters being deployed toward the end of the first month (20 June), thus allowing only 10 days to measure total area used during the month of June.

5. Conclusion

The results from this study indicate that overall post-release survival is high (91%) despite signs of catch-related barotrauma. In addition, behavioral effects of post-release stress and barotrauma are minimal and short-lived. Therefore, catch and release practices could be implemented as a conservation measure for ocean whitefish. Ocean whitefish exhibit consistent home ranging behavior, and most individuals spend a large proportion of their time outside the boundary of the CMLR. Thus, small marine reserves such as the CMLR may be less effective for more mobile species such as ocean whitefish than for less mobile species, such as kelp bass (*Paralabrax clathratus*). Ocean whitefish select for deeper sand habitats during the day while foraging, and shallower high relief rocky reef and kelp habitats are selected at night for refuge. Depths utilized at Santa Catalina Island are quite shallow relative to their described general depth range. These habitat selection patterns differ from known behavior of many nearshore rockfish species, and should be considered when managing the recreational fishery for ocean whitefish. Consistent site fidelity was exhibited over a 1-year period, although frequent shifts occur to areas beyond the reserve boundary, and there is no significant conspecific density-dependent effect on home range size. This behavioral information has important implications for management of the recreational fishery for ocean whitefish in the southern management region. The data suggest that more effective management of the recreational fishery for ocean whitefish could be achieved by implementing size limits and could allow separating this species from the groundfish regulations in some locations.

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