



Movements of small adult black rockfish: implications for the design of MPAs

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ABSTRACT: Off the coast of central California, USA, small black rockfish *Sebastes melanops* (individuals below the length at 50 % maturity) comprise a large percentage of the catch in recreational fisheries, yet little is known about the movements of these small fish. To better understand their movements, we implanted acoustic transmitters into 23 black rockfish (29 to 41 cm total length) in Carmel Bay, California, USA. Tagged fish were monitored over a 16 mo period between August 2006 and January 2008. Their vertical movements were correlated with environmental variables such as atmospheric pressure, wind speed, upwelling, and wave height. From October to May, black rockfish moved to deeper waters offshore during the day and returned at night. In the summer, diurnal movements of black rockfish decreased in frequency, perhaps due to locally abundant food resources associated with seasonal upwelling. About two-thirds of the tagged black rockfish (14 fish) displayed a high degree of residency to the study area (>11 mo). The remaining third (9 fish) left the study area within 6 mo of release; signals from 4 of these fish were later detected on other acoustic receiver arrays >50 km north of Carmel Bay. Storms may have caused those fish to move northward in winter. When in residence, the mean home range of tagged fish was 0.25 km². Our results indicate that a better understanding of the variability of fish movements among age classes is necessary to design marine protected areas (MPAs) that are intended to protect all life stages of a species.

KEY WORDS: Acoustic telemetry · *Sebastes melanops* · MPA · Central California · Residency · Home range · Movements · Migration

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INTRODUCTION

Resource managers are increasingly using marine protected areas (MPAs) to supplement existing fisheries management strategies. The reduction of fishing pressure within no-take MPAs has been shown to increase the numbers and sizes of fishes within reserve boundaries (Halpern & Warner 2002, Micheli et al. 2004), and may enhance fisheries yields via movements of fishes to areas outside reserve boundaries (Starr et al. 2004, Russ et al. 2005, White et al. 2008). The conservation benefits afforded by no-take

MPAs, however, are primarily accrued for fish that stay within reserve boundaries, i.e. fishes with home ranges that are smaller than the reserve. To date, most information used to design MPAs has been based on the net movements of adult fishes, and has been derived from tag-recapture studies. Without information about daily and seasonal movements of immature as well as mature fishes, it is difficult to evaluate the performance of a MPA in achieving an expected level of protection (Botsford et al. 2008).

Historically, the black rockfish *Sebastes melanops* has been described as a species with strong site

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fidelity, and is typically managed as part of a complex of nearshore, residential rockfishes *Sebastes* spp. that may benefit from MPAs. Estimates of movements of adult black rockfish have been based primarily on tag-recapture studies, which have shown net movements of about 5 km, with about 10% of tagged fish exhibiting greater (up to 600 km) movements (Coombs 1979, DeMott 1983, Mathews & Barker 1983, Culver 1986, Starr & Green 2007). Tag-recapture studies, however, provide estimates of net movements only and do not account for short-term (e.g. daily) movements; this lack of temporal resolution about movements creates uncertainty with respect to MPA benefits. If black rockfish demonstrate strong site fidelity throughout their life, then MPA benefits would be greater than if movements of black rockfish vary with life stage.

Parker et al. (2007) represents the only published study that provides information about the daily and seasonal movements of black rockfish. They used acoustic telemetry techniques to provide information about the home ranges and vertical movements of adult black rockfish off Oregon, USA. However, in California, adult black rockfish are uncommon in the recreational catch (Mason 1998, O'Farrell & Botsford 2006), and individuals in central California above the length at 50% maturity typically represent <5% of the recreational catch (Starr & Green 2007). To provide information about the movement patterns of smaller size-classes of black rockfish, we conducted a study to track the movements of small adult black rockfish using acoustic telemetry techniques in Carmel Bay, California, USA. The specific objectives of the present study were to: (1) describe the daily and seasonal movement patterns of small adult black rockfish and (2) quantify the home range and residence times of small adult black rockfish.

MATERIALS AND METHODS

Study site

We tagged black rockfish *Sebastes melanops* in a 4 × 2 km area located within Carmel Bay, California (Fig. 1). Benthic habitats in Carmel Bay include high-relief rock areas and sand flats mixed with occasional low rocks. The high-relief areas are comprised of large boulders and rock outcrops up to 5 m in height. Sand flats gently slope to deeper waters, and the sand areas scattered rocks contain rocks or boulders with from 1 to 2 m in size. Seasonal beds of canopy-forming kelp *Macrocystis*

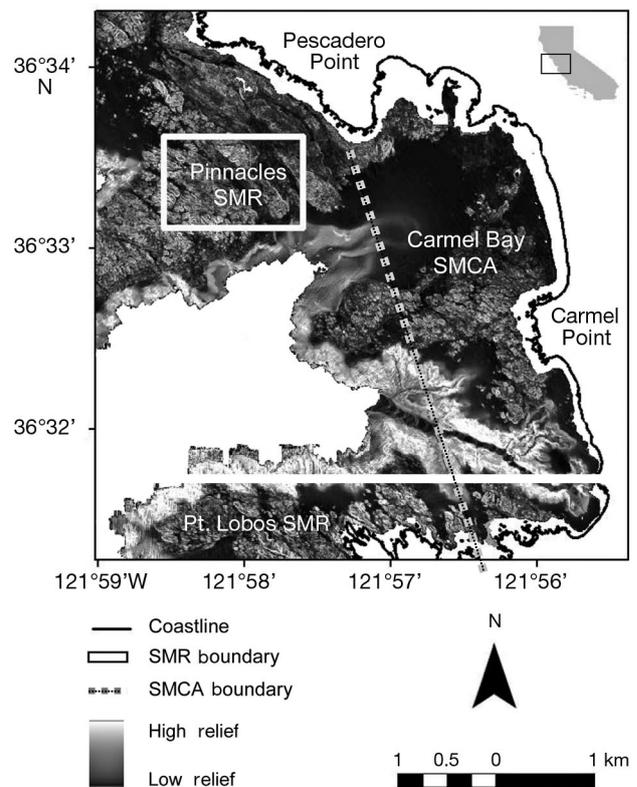


Fig. 1. Carmel Bay, Central California. Multibeam bathymetry imagery with Marine Protected Area boundaries. SMCA: State Marine Conservation Area; SMR: State Marine Reserve (data from the Seafloor Mapping Laboratory, California State University of Monterey Bay)

pyrifera and *Nereocystis luetkeana*, and perennial understory algae *Pterygophera californica* are abundant in the rocky habitats. The majority of the study area is within the boundaries of several MPAs (Fig. 1). The Carmel Bay State Marine Conservation Area (SMCA) allows recreational fishing but prohibits commercial fishing. The Carmel Pinnacles State Marine Reserve (SMR) and the Pt. Lobos SMR prohibit take of all marine species.

Fishing, tagging, and data collection

We caught black rockfish with rod and reel fishing gear during the fall of 2006 and summer of 2007 and tagged individuals that were between the mean length at first maturity (25.0 cm) and mean length at 50% maturity (41.0 cm for females and 36.0 cm for males), as described by Wyllie Echeverria (1987). Thus, tagged fish were either large immature juveniles or small mature adults. For the

present study, we termed these fish 'small adults,' because we could not determine maturity in the field. The sex of each fish was determined by the presence or absence of external papillae. Captured black rockfish were anesthetized by placing them in a solution (0.1 g l^{-1}) of tricaine methanesulfate (MS222). In 7 fish, we surgically implanted Vemco V13-1H-S256 acoustic transmitters (Vemco Ltd.) into the peritoneal cavity. In 16 fish, we implanted Vemco V13P-1H-S256 acoustic transmitters that contained pressure sensors as well. Transmitters emitted coded signals at a random interval between 90 and 270 s. Predicted battery life for each tag was 445 d. An external T-bar anchor tag imprinted with a unique tag identification number was also implanted into the dorsal musculature of the fish in case of angler recapture. Fish were released at the location of capture.

We placed 31 acoustic receivers (Vemco VR-2 omni-directional acoustic monitors) along the coastline between Pescadero Point and Carmel Point, at depths from 7 to 40 m (Fig. 1). Receivers were individually anchored to a 40 kg mooring weight using a line that extended ~ 5 m above the sea floor. A subsurface float was attached on a line above the receiver to maintain line tension and keep the receiver upright in the water column. Range tests indicated that the receiving range of moored receivers was ~ 150 m (Greenley 2009). Temperature loggers (Onset StowAway Tidbit Underwater Data Loggers, programmed to record water temperature every 15 min) were attached on the mooring line of 4 receivers. Each receiver had 3 temperature loggers, positioned at a shallow (12 to 16 m), mid (18 to 24 m), and deep (26 to 34 m) depth interval. Data from moored receivers and temperature loggers were downloaded every 4 to 6 mo between August 2006 and January 2008.

Oceanographic and atmospheric data were acquired from the historical data archives of the National Oceanic Atmospheric and Administration (NOAA). Wave height (m), wind speed, and barometric pressure (mb) were recorded from Monterey Buoy 46042 (www.ndbc.noaa.gov). Tidal height (m) was recorded from Monterey Tide Station 9413450 (<http://tidesonline.nos.noaa.gov/>). Day lengths were derived from the historical archives of the US Naval Observatory from Carmel, California (<http://aa.usno.navy.mil/data/>). Daily and monthly upwelling indices, expressed as $\text{m}^3 \text{ s}^{-1}$ per 100 m of coastline at 36°N , 122°W were obtained from NOAA Fisheries Pacific Fisheries Environmental Laboratory (PFEL) (www.pfeg.noaa.gov/products/PFEL).

Data analyses

Residence time for all tagged black rockfish, except fish carrying Tag 228, was calculated by dividing the total number of days a fish was present in the array by the predicted battery life of the transmitter. Daily presence in the array was defined as ≥ 2 signal detections in a 24 h period. Residence time for fish carrying Tag 228 (recovered in the recreational fishery) was reported as a ratio of the days present in the study area to the number of days from release to recapture. The percentage of days each fish was absent from the array was calculated as the number of days absent divided by the number of days from release to the day the last tag transmission was recorded. Occasionally, receivers were temporarily missing from the array because they were moved or lost in storm events. For both residence time and absence calculations for a given fish, we excluded the dates from analyses for which a receiver was missing due to storms, if the lost receiver was the primary receiver that recorded signals from that tagged fish. By removing these dates and locations from analyses, we avoided reporting false absences for a tagged fish.

Diel changes in presence of black rockfish were characterized by calculating the percentage of hours a fish was detected in the study area during the day versus at night. Day hours were defined as the time period between sunrise and sunset. Night periods were defined as the time from 1 h after sunset until 1 h before sunrise. Crepuscular hours (1 h before sunrise and 1 h after sunset) were excluded from analyses. A fish was considered to be present in an hour if there was ≥ 1 tag detection in that hour. The amount of time (hours) a tag was detected during the day or night on each date was normalized by the total night or day hours available on that date and summed to create a contingency table with the expected and observed percentage of hours detected for night periods versus day periods. Fisher's exact test was used to test the null hypothesis that there was no difference in fish presence in the study area, either between day and night periods annually or for selected seasons.

Vertical movements of black rockfish were examined by comparing differences in depth anomalies of tagged fish. To calculate daily depth anomalies, we subtracted the mean depth of a given fish on each date of the study from the annual mean depth for that fish. Depth anomalies were averaged across all fish on each date of the study to obtain a mean anomaly for each day and for day and night periods. Mean day

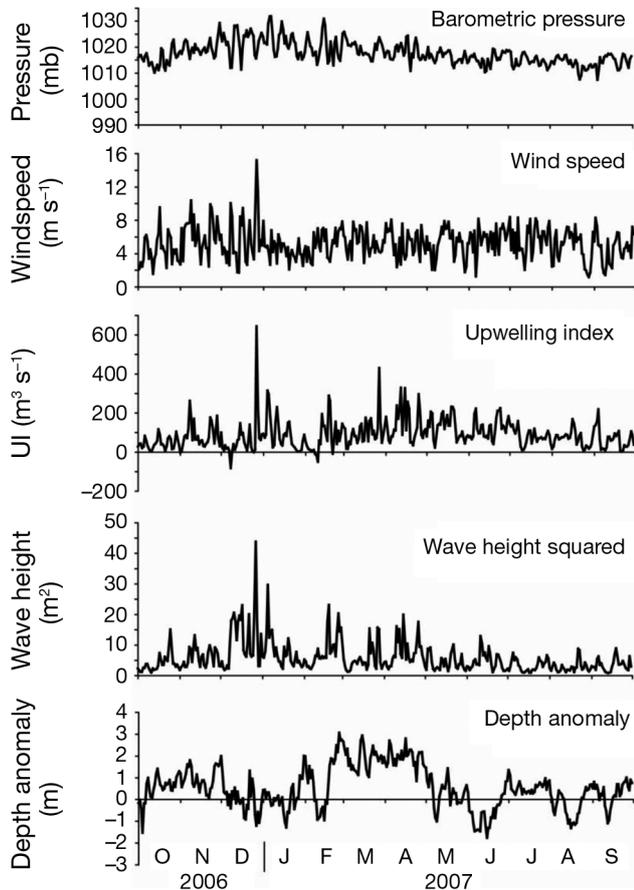


Fig. 2. Plots of mean daily barometric pressure, wind speed, upwelling index (per 100 m of coastline), mean wave height (squared), and depth anomalies of tagged black rockfish *Sebastes melanops* in or near the study area in Carmel Bay, CA. See 'Study site' for sources of data. A daily depth anomaly was obtained by subtracting the mean depth of a fish in a day from that individual's annual mean depth. Positive (negative) anomalies represent deeper (shallower) mean depth than the annual mean depth

depths were compared to mean night depths using *t*-tests.

We used cross correlation analysis to compare daily depth anomalies of black rockfish with daily water temperatures, tidal stages, the square of mean wave heights, wind speeds, upwelling indices, and barometric pressures (Fig. 2). We removed the effect of autocorrelation before computing the cross correlations, as suggested by Katz (1988). Serial correlation was excluded by fitting univariate models to the X and Y time series, using these fitted models to obtain estimated residuals, and then determining the cross correlation function between the 2 residual time series. We conducted the cross correlation analysis for 3 time periods: the entire study period, the high upwelling season (April to June), and the low up-

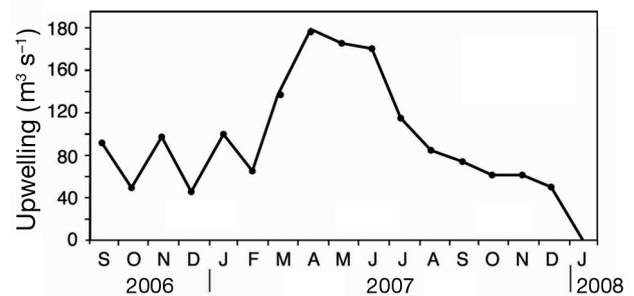


Fig. 3. Monthly upwelling index (per 100 m of coastline) at 36° N, 122° W obtained from Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/products/PFEL)

welling season (December to February), as defined by monthly upwelling indices (Fig. 3).

We calculated a measure of home range for each tagged fish in the following manner. For each hour that a fish was present in the array, it was assigned 1 or more locations, based on the receiver(s) that recorded signals from the tagged fish. The number of hours detected at each receiver location was tallied for each fish. Receiver locations that ranked in the 90th percentile of the total hours that a fish was recorded during time at liberty were used to calculate the home range of that fish. In ArcGIS, a polygon of best fit was drawn around these receiver locations, using the receiver detection radius of 150 m. The area encompassing home range for each fish was then calculated using the ArcGIS spatial analyst extension, XToolsPro.

RESULTS

Fishing and tagging

A total of 23 small adult black rockfish was captured, tagged, and released in the study area between August 2006 and July 2007 (Table 1). Total length (TL; mean \pm SE) of the 23 black rockfish was 32.7 ± 0.7 cm. Of the 23 black rockfish implanted with transmitters, 13 were females (TL 33.7 ± 1.0 cm) and 10 were males (TL 31.5 ± 0.6 cm) (Table 1). One fish (Tag 92) was only present in the study area for 2 d, and another fish (Tag 81) only for 23 d. There were no complications for these fish during surgical procedures, and both fish were observed swimming upon release, but were excluded from the majority of the analyses due to lack of data. The largest female black rockfish (41 cm; Tag 228) released in this study was captured by a recreational angler on 30 June

Table 1. *Sebastes melanops*. Tag numbers of small black rockfish released in Carmel Bay. Sex denoted as F (female) or M (male). Total days detected (Total days det.): number of days in which ≥ 2 signals were recorded in a 24 h period for an individual. Residence time (Res. time): total number of days detected for each fish divided by the total number of days available in the battery life of a transmitter. TL: total length

Tag no.	TL (cm)	Sex	Release date	Total days det.	Res. time (% of d)
78	31.5	F	28 Sep 2006	88	21.2
80	35.0	F	5 Oct 2006	366	82.2
81	33.0	M	22 Aug 2006	23	5.2
82	34.0	F	29 Aug 2006	369	82.9
83	33.0	F	3 Oct 2006	336	81.0
84	32.0	M	5 Oct 2006	427	96.0
85	30.0	F	28 Aug 2006	391	88.7
86	38.0	F	3 Oct 2006	115	27.7
87	29.5	F	5 Oct 2006	382	85.8
88	33.5	F	11 Sep 2006	70	15.7
89	36.5	F	4 Sep 2006	445	100.0
90	34.5	M	1 Sep 2006	433	97.3
91	32.0	M	7 Oct 2006	100	25.6
92	29.0	M	9 Oct 2006	2	0.4
93	30.0	M	11 Oct 2006	372	83.6
94	35.0	F	11 Oct 2006	409	91.9
95	32.0	M	9 Oct 2006	445	100.0
227	30.5	F	11 Oct 2006	445	100.0
228	41.5	F	15 Oct 2006	216	86.4
229	29.0	F	15 Oct 2006	423	95.1
4054	29.5	M	20 Jun 2007	53	10.2
4058	29.0	M	20 Jun 2007	168	32.3
4060	34.0	M	7 Jun 2007	181	34.8

2007, after 198 d at liberty, near the Pinnacles SMR, close to the site where it was originally released.

Residence times

Residence times of small adult black rockfish in the study area ranged from <1 to 100% (2 to 445 d) of the expected battery life of transmitters (Fig. 4). Residence time (mean \pm SE) of all fish was 272.0 ± 33.0 d. We could detect no differences between residence times of female and male fish in a 2-sample *t*-test ($p = 0.483$). Of the 23 fish released, 14 were highly residential, i.e. were detected for $>75\%$ of the days during the transmitter battery life of each tag. Of these 14 small adult black rockfish, 8 fish were detected in the receiver array between 75 and 95% of the days of transmitter battery life (i.e. detected in the array for 11 to 14 mo), and 6 fish were detected for $>95\%$ of the days of transmitter battery life (>14 mo in the array). The remaining 9 small adult black rockfish were present in the study area for a mean of 34.8% of the days of transmitter battery life or <6 mo before permanent departure. After the study, we were notified by other researchers that signals from 4 of these fish were detected on receiver arrays north of the study area. Signals from Tag 83 were detected on 7 December 2007 on a receiver located near Año Nuevo Island, California, 52 km north of the study area, 3 d after it last recorded in our study area. Sim-

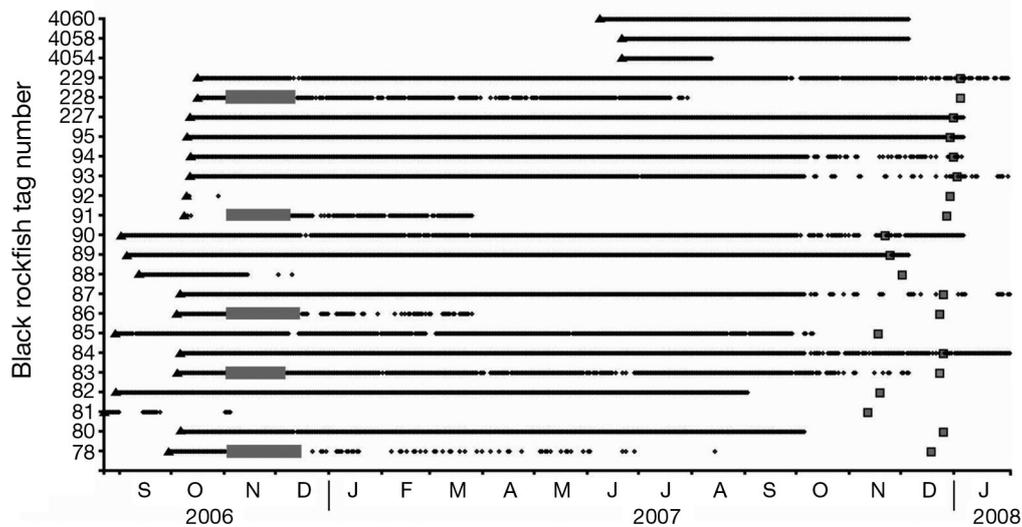


Fig. 4. *Sebastes melanops*. Residence times of small adult black rockfish as indicated by presence or absence in Carmel Bay. Tag number of each fish is listed on the y-axis. ◆: detection of signals from a tagged fish; ▲: date of tag and release of each fish; ■: projected battery life of tags (not indicated for tagged fish 4054, 4058, and 4060 as batteries expired after the study end); grey bars: time periods during which a receiver that was within the home range of a tagged fish was missing from the array

ilarly, signals from 2 other tagged fish were recorded 186 km north of the study area (off Point Reyes, California); 7 and 4 d, respectively, after they were last detected in the study area (4 December 2007 and 5 January 2008). Also, a single detection for Tag 227 was recorded on a receiver located >1000 km north of our study area, near Neah Bay, Washington, on 21 June 2010. This tagged fish was last detected in Carmel Bay on 5 January 2008.

Absences

Of the 23 tagged black rockfish, 7 individuals were detected every day during time at liberty. Of the 16 fish that did exhibit absences from the study area, 7 were absent <7% and 4 were absent <15% of the total time at liberty. The remaining 5 individuals had longer absences (26 to 84%) of total time at liberty. The number of absences (mean \pm SE) from the receiver array for small adult black rockfish was 9.5 ± 2.0 . Duration (mean \pm SE) of absences was 2.9 ± 0.2 d for all fish combined, 2.8 ± 0.3 d for females and 3.6 ± 0.7 d for males. We could detect no differences between the duration of absences for males and females in a 2-sample *t*-test ($p = 0.548$). We could detect no synchronous absences and returns from the study area among fish, although, for 7 individuals, the frequency and/or length of departures from the study area increased in the fall and winter (September to December 2007; Fig. 4).

Diel movements

The number of signal detections of small adult black rockfish in the study area during the night was significantly greater than during the day for the entire year (Pearson's chi-squared = 29.867; $p <$

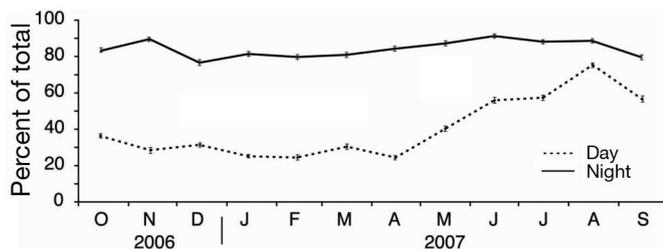


Fig. 5. *Sebastes melanops*. Monthly percentages of hours (mean \pm SE) that black rockfish were present in the study area during the day (1 h after sunrise till 1 h before sunset) and night (1 h after sunset till 1 h before sunrise)

0.001), and for both the high and low upwelling seasons (April to June, Pearson's chi-squared = 21.001; $p = 0.004$; December to February, Pearson's chi-squared = 21.019; $p = 0.007$). The annual percentage of hours (mean \pm SE) tagged fish were detected was $74.6 \pm 0.04\%$ of the night hours and $41.8 \pm 0.04\%$ of the day hours. The monthly mean percentage of hours in which tagged fish were detected at night was relatively constant (between 77 and 89%) throughout the year; however, the mean percentage of daytime hours in which all tagged fish were detected was lowest ($23.8 \pm 1.1\%$) in April 2007. This coincided with the peak of mean monthly upwelling (Fig. 3). In late May 2007, detections of small adult black rockfish began to increase during the day, peaking in August when the mean presence of all tagged fish was $75.0 \pm 1.2\%$ of the day hours (Fig. 5).

Vertical movements

Water depths in the study area ranged from 10 to 20 m. The annual depth (mean \pm SE) of all small adult black rockfish was 11.6 ± 0.8 m; mean depths of individuals ranged from 4.3 to 15.5 m. Vertical movements of small adult black rockfish were highly variable. Depth changes from 5 to 10 m occurred frequently over short time intervals (5 to 20 min). The difference between mean daily minimum and mean daily maximum depths for all fish during the study period was 6.4 ± 0.1 m. Mean day depths were significantly greater than mean night depths for 16 small black rockfish (Table 2) over the October 2006 to September 2007 period (paired *t*-test; $p = 0.026$).

Environmental correlations

Cross correlation analyses using data from a 1 yr period indicated that depth anomalies of tagged black rockfish were positively correlated with upwelling indices ($p < 0.001$) and the square of wave heights ($p = 0.045$) with a lag of 1 d. When evaluated with respect to the months with the highest mean monthly upwelling indices (April to June), depth anomalies were positively correlated with atmospheric pressure, wind speed, the square of wave height, and the upwelling index, all with lags of 1 to 3 d (Table 3). Although cross correlation analyses showed a negative correlation between the upwelling index and water temperature ($p = 0.028$) with a lag of 1 d over 1 yr period, we could detect no significant relationships ($p > 0.05$) between depth anom-

alies and water temperature or the difference in water temperatures between 16 and 34 m. However, when we plotted mean daily temperatures, it was apparent that tagged fish were deeper from mid-February through mid-June when mean daily temperatures were low (Fig. 6). Tagged fish were significantly deeper in these months than at other times of the year (2-sample *t*-test; $p < 0.001$). Cross correlation analyses of depth anomalies and environmental vari-

Table 2. *Sebastes melanops*. Mean day and night depths for small adult black rockfish over a 1 yr period (1 October 2006 to 30 September 2007). Mean day (night) depth (m) is the mean annual day (night) depth for each individual black rockfish. Day depth > night depth (% of d) is the percentage of days in the year in which the mean day depth of a tagged fish was greater than the mean night depth of that fish on a particular date

Tag no.	Mean depth (m)		Day depth > night depth (% of d)
	Day	Night	
78	14.9	13.9	61.4
80	11.1	10.6	44.4
83	16.8	14.6	73.2
84	16.6	15.5	81.6
85	4.8	4.3	61.1
86	14.7	14.5	56.9
87	14.6	15.0	26.8
88	7.6	7.1	45.3
89	10.1	10.5	29.8
90	11.6	11.6	40.4
93	14.2	15.0	33.5
94	11.8	11.0	56.0
95	10.1	7.8	77.8
227	15.2	15.2	49.0
228	11.5	10.2	51.4
229	12.4	12.5	55.6

Table 3. *Sebastes melanops*. Lag in days, correlation, and *p*-values associated with cross correlations among selected environmental variables and the depth anomalies of tagged black rockfish for 1 April 2007 to 30 June 2007. Positive correlations indicate that tagged fish move deeper when atmospheric pressure, wind speed, upwelling index, or wave height increases (NS = not significant, $p > 0.05$)

	Lag (d)	Correlation	<i>p</i>
Atmospheric pressure	2	0.236	0.026
Wind speed	3	0.227	0.033
Upwelling index	1	0.309	0.003
Wave height (squared)	1	0.274	0.009
Tidal stage			NS
Temperature			NS

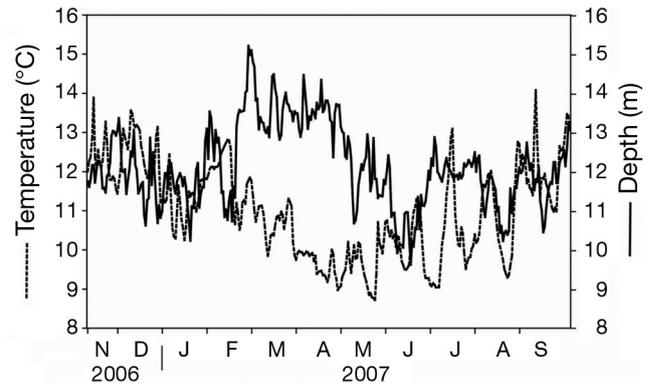


Fig. 6. *Sebastes melanops*. Mean daily water temperatures (°C) at 16 m depth and mean daily depth anomalies (m) for black rockfish during the period 10 November 2006 through 30 September 2007

ables conducted for the months with the lowest mean monthly upwelling indices (December to February) revealed no relationships at the 95 % level of significance, but upwelling and the square of wave height were both positively correlated to depth anomalies with $p = 0.080$. We could detect no significant relationships between depths and tidal stages.

Home range

Home ranges of small adult black rockfish were centered near the original site of release for each fish (Fig. 7). Home range areas for small adult black rockfish varied from 0.07 to 0.56 km². Home range area (mean \pm SE) was 0.25 ± 0.04 km², and a mean of 2.6 ± 0.3 receiver locations was used in these home range estimations. Mean home range area for the 13 female fish was 0.28 ± 0.05 km² and was 0.20 ± 0.05 km² for the 8 male fish. We detected no significant differences in mean home range area between males and females (2-sample *t*-test; $p = 0.364$), and regression analysis revealed no significant relationship between total length and home range areas by sex, nor for all fish combined ($p = 0.100$).

DISCUSSION

Residence time and absences from the array

The site fidelity of an individual fish to a given area is related to many factors, including life-history characteristics, ontogeny, environmental variability, and resource availability. Acoustic telemetry studies have

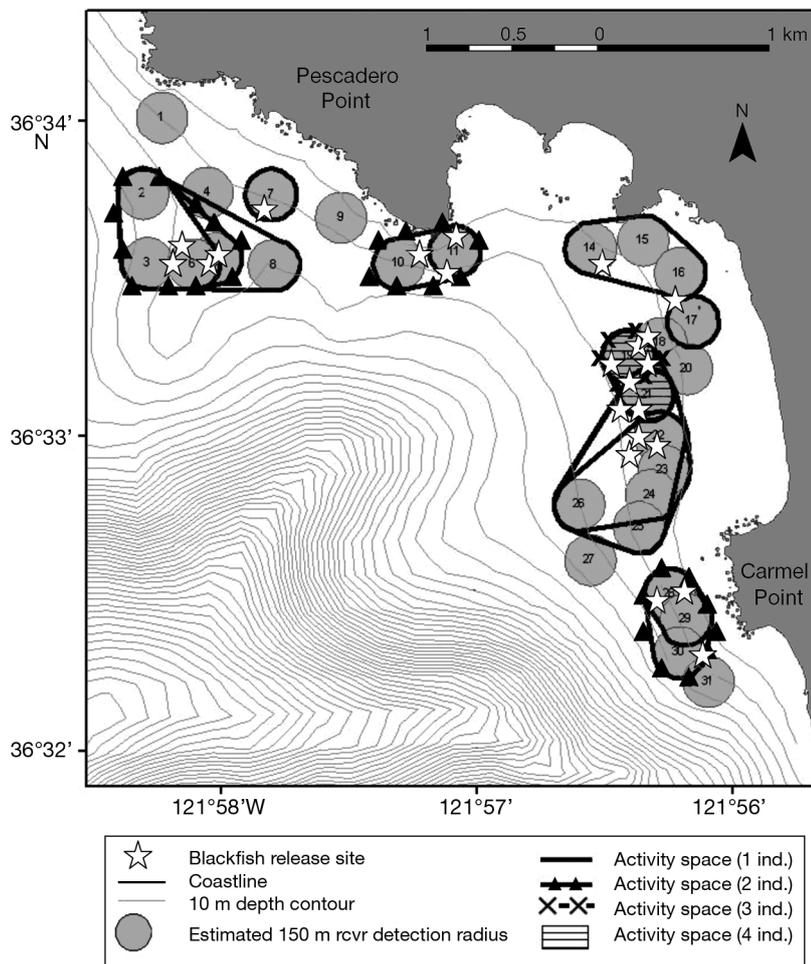


Fig. 7. *Sebastes melanops*. Release locations (☆) and estimated home range areas for tagged black rockfish in the study area. Polygons represent the home range of a tagged fish based on the receiver locations where the fish was recorded during 90% of the hours at liberty. Polygons: solid black outline = home range used by 1 individual; with triangles = home range used by 2 individuals; with × = home range used by 3 individuals; filled with stripes = area used by 4 individuals; numbered grey circles: receiver locations with estimated detection area

shown that several nearshore rockfishes exhibit high site fidelity (Matthews 1990, Jorgensen et al. 2006, Parker et al. 2007, Lowe et al. 2009). In those studies, a few tagged fish departed the study area within a few months of release, but the departures were considered to be outliers rather than indicative of normal behavior. In our study, many of the tagged small adult black rockfish *Sebastes melanops* exhibited residence times that were similar to those of other nearshore rockfishes, however, the tagged black rockfish in our study differed in that more than one-third of the fish displayed short residence times (<6 mo) and moved out of the study region. At least 4

fish in our study migrated north; signals from fish carrying Tag IDs 83, 89, 94, and 227 were recorded on receiver arrays maintained by other researchers north of our study site. These detections of our tagged fish at distances north of the study area corroborate information about long-distance northward movements presented in several unpublished tag-recapture reports (Coombs 1979, DeMott 1983, Starr & Green 2007).

The short residence times documented for the 9 small adult black rockfish in our study could be the result of handling mortality, tag malfunction, fishing mortality, natural mortality, or undocumented emigration from the study area. Mortality due to tagging complications would be most likely to occur in the first week after release (Starr et al. 2000, Lowe et al. 2009), and only 1 fish in our study (Tag 92) was detected for <2 d. We cannot discount handling mortality or predation for this individual, but it seems unlikely for others. All tags were tested before deployment, and other acoustic studies have shown that the Vemco tags we used have a low (<1%) failure rate (Voegeli & Starr 2000). At least 1 tagged individual was a known fishing mortality, and it is possible that others were caught and we were not notified. However, we estimated expected mortality using a survivorship equation (Wilson & Bossert 1971) and determined that the natural and fishing mortality rates would each need

to have been 3 times greater than rates used in stock assessments to account for the reduction in tagged fish recorded. There is no reason to expect fishing and natural mortality rates to be that high in the MPAs we studied. The evidence of northward migrations documented for the 4 small adult black rockfish that were recorded on other acoustic receiver arrays indicate that emigration is a likely hypothesis for the short residence times exhibited by the tagged fish that were detected in the study area <6 mo after release.

If our assumption of emigration is correct, we suggest 2 hypotheses why small adult black rockfish left

Carmel Bay. (1) Movements were triggered by major storm events. Fish emigration has been correlated with the onset of winter storm activity in temperate environments for juvenile rockfish (Johnson et al. 2001) and summer flounder (Sackett et al. 2007). In tropical environments, Ingram & Patterson (2001) showed that movements were larger and more frequent for fish at liberty during tropical storms than periods without storms, and Heupel et al. (2003) described greater movements of small sharks immediately prior to arrival of a tropical storm. In our study in Carmel Bay, the last detections of 10 fish coincided with major storm events. Four small adult black rockfish were last detected during a storm on 4 December 2007, and 4 others, on the storm of 5 January 2008. An additional 2 fish were last detected a few days before a major storm on 27 March 2007. Signals from 4 of the 10 fish that were last detected during storms were recorded on receivers located at the very north end of the study area, despite the fact that these fish had previously exhibited strong site fidelity to a different area of the array. On all occasions, storms were characterized by sustained swells of >4.5 m over a 24 h period, with recorded maximum wave heights of up to 10 m. Cross correlation analyses indicated that tagged fish moved deeper with increasing wave heights. The high wave heights associated with large winter storms may have led to movements to deeper waters and then to a northward migration. (2) Emigration from the study area was related to an ontogenetic shift in habitat use. A common trait observed in rockfishes is the use of shallow water habitats as juveniles and a transition to deeper water habitats as adults (Boehlert & Yoklavich 1983, Love et al. 1991). Adult fish in some reef-associated species have greater site fidelity and increased homing ability than juvenile fish (Hallacher & Roberts 1985), and Parker et al. (2008) speculated that adult black rockfish maintain small home ranges by making frequent descents to the bottom for visual spatial reference. However, if a major storm caused tagged black rockfish to lose visual contact with the bottom, the small adult black rockfish in Carmel Bay may not have the same navigation ability of older conspecifics to return to a home area. The greater residence times for black rockfish documented by Parker et al. (2007) may be attributed to differences in the size or maturity of the tagged black rockfish in their study. Greater emigration rates for small adult black rockfish in Carmel Bay may be representative of ontogenetic changes in movement patterns as these fish transit to maturity.

Regardless of the cause of emigration of small adult black rockfish from the study area, our data indicate that fish that left the study area moved northward in winter. We do not know what the mechanism is for this movement, but note that it occurred in winter, when the Davidson current becomes shallower and moves north at higher speeds (Hickey 1979, Huyer et al. 1989). One possibility is that, as black rockfish lose visual contact with the bottom, they are carried northward by the Davidson current. Another possibility, however, is that small black rockfish are moving in search of prey. Dorman et al. (2011) modeled winter ocean conditions to describe how krill *Euphausia pacifica* are advected poleward in the winter. It is possible that small adult black rockfish move northward to stay in water masses that contain more food than is available in kelp beds in winter.

Diel movements

Differences in habitat use between day and night periods have been documented in many fish species. In coral reef fishes, crepuscular 'commutes' between distinct day and night habitats are common (Mazeroll & Montgomery 1995, Holland et al. 1996, Meyer et al. 2007). Diel vertical movements have been noted for juvenile black rockfish (Leaman 1976, Carr 1991), and directed crepuscular and nocturnal movements have been reported in this region for tagged rockfishes (Starr et al. 2002, Jorgensen et al. 2006, Tolimieri et al. 2009) and sharks (Carlisle & Starr 2009, Dawson & Starr 2009). In our study, small adult black rockfish in Carmel Bay exhibited repeated diurnal movement patterns: departing the study area in the morning crepuscular hours and remaining outside the study area during the next 10 to 12 h before returning to the study area in the evening.

Although small adult black rockfish moved outside of receiver reception range during the day, the change in depth use between day and night periods enabled us to determine the direction of movements. The deeper depths recorded during the day than at night are indicative of movement offshore during the day. Although depth data recorded during daytime were limited to time periods when fish were entering and exiting the array, an increase in mean depth was observed during the day for >50% of all tagged individuals. These greater depths during the day indicate that small adult black rockfish in Carmel Bay moved to deeper waters outside the kelp forest during daytime, and returned to shallower depths inside the kelp forest at night.

Seasonal movements

The seasonal movements that we observed for black rockfish are consistent with the hypothesis that movements of fishes may be driven by prey distribution (Hallacher & Roberts 1985). A large portion (up to 73%) of the black rockfish diet is composed of young-of-the-year (YOY) *Sebastes* spp. in the summer upwelling season (Hallacher & Roberts 1985, Hobson et al. 2001), an important feeding time when rockfishes increase their fat reserves for winter (Guillemot et al. 1985). In our study, a reduction in home range to shallow kelp habitats by tagged small adult black rockfish coincided with typical peak settlement of YOY *Sebastes* spp. to the kelp forest (Miller & Geibel 1973, Hallacher & Roberts 1985, Hobson et al. 2001, Studebaker & Mulligan 2008).

Hallacher & Roberts (1985) observed that diets of black rockfish change seasonally, with a switch from fish to invertebrates during the non-upwelling season. This, along with the increase in the percentage of empty black rockfish stomachs, led them to speculate that food is a limiting resource for black rockfish during the non-upwelling season. In our study, diurnal movements out of the study area were greatest for small adult black rockfish in the winter and spring, and corresponded to the decrease in black rockfish densities observed by Hallacher & Roberts (1985) in Carmel Bay kelp forests during the non-upwelling season.

Vertical movements and environmental correlations

Similar to the results reported by Parker et al. (2008), small adult black rockfish in Carmel Bay exhibited many different vertical movement patterns. Given the degree of vertical activity in black rockfish and the relatively weak behavioral coherence among black rockfish described in Parker et al. (2008), we did not attempt to categorize vertical movement behavior in the same way. Instead, we compared depth anomalies and environmental parameters, hypothesizing that over long periods of time, small adult black rockfish may be responding in the same way to certain environmental cues. The positive correlations observed between black rockfish depth anomalies and atmospheric pressure, wind speed, upwelling, and wave heights are examples of how wind stress and resulting upwelling, as well as low pressure storm systems, affect black rockfish and other nearshore species in the California current. The in-

creased primary productivity associated with upwelling fronts results in increased zooplankton abundance; a primary prey source for rockfishes during strong upwelling events in central California (Hayward et al. 1999). Just as we hypothesized that small adult black rockfish in Carmel Bay maintain smaller home ranges in kelp habitats in the summer during the peak YOY rockfish settlement, it is likely that during the winter and spring upwelling seasons, the distribution of locally abundant prey affects movements of small adult black rockfish (Ainley et al. 1993, Schwing et al. 2000).

Positive correlations between the depth distribution of small black rockfish and barometric pressure and wave heights may have been a response to seasonal environmental conditions such as increased storm activity. For example, blue rockfish move to deeper waters to avoid winter storm turbulence (Miller & Geibel 1973). Hallacher & Roberts (1985) and Parker et al. (2008) reported that black rockfish were significantly closer to the bottom in winter. Another possible reason for the deeper depths of black rockfish during the winter and spring is that black rockfish are avoiding increased water turbulence from wave action during seasonal periods typified by higher storm activity.

Although cross correlation analyses indicated no significant relationship between depth anomalies and water temperature over the entire year, tagged fish in our study were significantly deeper from mid-February through mid-June, when water temperatures were at an annual minimum. Many fish species respond to changes in ambient water temperature by changing depths (e.g. Shrode et al. 1982). The coldest ambient water temperatures in Carmel Bay occurred from March through July 2007, with the lowest mean monthly temperature occurring in April. It is possible, however, that this depth pattern is not entirely driven by water temperature. Hallacher & Roberts (1985) reported that black rockfish were significantly closer to the bottom during fall and winter, during which time invertebrates comprised a large proportion of black rockfish diets. If black rockfish are relying mostly on invertebrates for food during the non-upwelling season, changes in seasonal depth distributions of small adult black rockfish observed in the study area may be related to prey depth distributions.

Implications for management

Often, for species that demonstrate high rates of residency, the small percentage of fish that move

long distances are considered anomalies and ignored in management. Data from this study, and from a tag-recapture study at Duxbury Reef near Bolinas, California (Starr & Green 2007), however, indicate that black rockfish exhibit a bimodal distribution in movements, and between 10 and 40% of the small black rockfish have low site fidelity, and may move long distances, indicating that black rockfish should not be characterized as displaying limited movements.

Small MPAs may be an effective fisheries management technique, if the management goal is to protect the proportion of a population that has strong site fidelity or to facilitate spillover of individuals. The large adult black rockfish tagged in the Parker et al. (2007) study, and many of the small adult black rockfish in our study, had small home ranges during the time they were present, a good characteristic for MPA protection. However, more than one-third of the small adult black rockfish we tagged exhibited low fidelity to the study area. Thus, although MPAs may provide protection for adult black rockfish that exhibit strong site fidelity, not all life stages of black rockfish would be protected by small reserves.

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