Movements of bocaccio (*Sebastes paucispinis*) and greenspotted (*S. chlorostictus*) rockfishes in a Monterey submarine canyon: implications for the design of marine reserves

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Abstract—In August and September of 1997 and 1998, we used SCUBA techniques to surgically implant Vemco V16 series acoustic transmitters in 6 greenspotted rockfish (*Sebastes chlorostictus*) and 16 bocaccio (*S. paucispinis*) on the flank of Soquel Canyon in Monterey Bay, California. Fish were captured at depths of 100–200 m and reeled up to a depth of approximately 20 m, where a team of SCUBA divers anesthetized and surgically implanted acoustic transmitters in them. Tagged fish were released on the seafloor at the location of catch. An array of recording receivers on the seafloor enabled the tracking of horizontal and vertical fish movements for a three-month period. Greenspotted rockfish tagged in 1997 exhibited almost no vertical movement and showed limited horizontal movement. Two of these tagged fish spent more than 90% of the time in a 0.58-km^2 area. Three other tagged greenspotted rockfish spent more than 60% of the time in a 1.6-km^2 area but displayed frequent horizontal movements of at least 3 km. Bocaccio exhibited somewhat greater movements. Of the 16 bocaccio tagged in 1998, 10 spent less than 10% of the time in the approximately 12-km^2 study area. One fish stayed in the study area for about 50% of the study time. Signals from the remaining 5 fish were recorded in the study area the entire time. Bocaccio frequently moved vertically 10–20 m and occasionally displayed vertical movements of 100 m or greater.

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Rockfishes (*Sebastes* spp.) are an important component of the commercial and recreational fisheries on the U.S. west coast. Recent stock assessments conducted by the Pacific Fishery Management Council (PFMC) have indicated large population declines for several species of rockfishes (PFMC[1]). For example, bocaccio (*Sebastes paucispinis*) abundance was estimated by MacCall et al.[2] to be 2–4% of pre-harvest levels, causing bocaccio to be formally designated as overfished by the U.S. National Marine Fisheries Service. This severe population decline prompted conservation organizations such as the World Conservation Union to consider bocaccio to be at high risk of extinction (IUCN, 1996). Even as management regulations have become more stringent, however, bocaccio populations continue to decline (MacCall et al.[2]).

As a result of these population declines, new management techniques, such as marine reserves, have been contemplated for west coast rockfishes (Yoklavich, 1998). Marine reserves currently are being considered as supplements to traditional fishery management schemes in many places around the world (Agardy, 1997; Allison et al., 1998). Marine reserves can serve as undisturbed areas for research, as regions designated for limited harvest, or as fishery exclusion zones where fishes can take refuge from exploitation (Murray et al., 1999). They also can serve as a buffer for management trials and as sources for recruits to fisheries (Johnson et al., 1999; Nowlis and Roberts, 1999). The effectiveness of marine reserves for conservation of heavily fished species, however, is dependent upon the size, shape, and location of reserves and on rates of movement of the protected species (Polacheck, 1990; DeMartini, 1993; Lauck et al., 1998). In this respect, an understanding of the rates and directions of daily movements of rockfishes is vital to understanding the value of marine reserves for these species (Carr et al., 1998; Starr, 1998).

[1] PFMC (Pacific Fishery Management Council). 1999. Status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR.

[2] MacCall, A. D., S. Ralston, D. Pearson, and E. Williams. 1999. Status of bocaccio off California in 1999 and outlook for the next millenium. *In* Appendix: status of the Pacific coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000: stock assessment and fishery evaluation. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, OR.

Few studies have described the movements of commercially caught rockfishes in water deeper than 100 m, however, because of the difficulty in achieving high survival rates for fish tagged at those depths. Most rockfishes have physoclistous swim bladders that expand with the reduced pressure as these fish are brought to the surface. The resulting barotrauma causes death for almost all fish when captured from waters deeper than 20–30 m, rendering traditional tagging techniques ineffective.

We developed techniques to surgically implant sonic transmitters at depth, thus reducing tagging mortality (Starr et al., 2000). These techniques enabled us to estimate the movements of two rockfishes with different life history characteristics. In 1997, we placed sonic transmitters in six greenspotted (*S. chlorostictus*) rockfish, a species presumed to be relatively sedentary (Yoklavich et al., 2000). In 1998, we tagged 16 bocaccio, a more mobile species (Love, 1996). In both years, we tracked the horizontal and vertical movements of tagged fish for a three-month period.

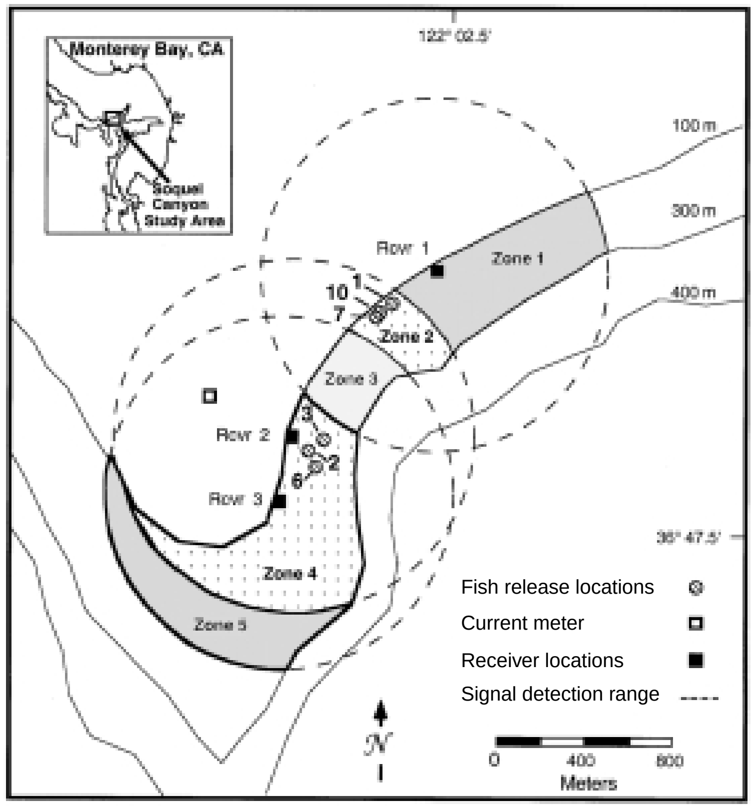

Figure 1

Fish-release locations and tag numbers, receiver locations, current meter location, expected signal detection range, and resulting receiving zones for the 1997 study of greenspotted rockfish.

Materials and methods

Field procedures

Our study site was located on the flank of the submerged Soquel Canyon in 100–250 m of water, approximately 20 km off shore in Monterey Bay, California (Fig. 1). Soquel Canyon contains steep sediment slopes and rock walls interspersed with 50–100 m wide benches. comprising soft sediment and rock outcrops (Yoklavich et al., 2000). Several of the rock outcrops located at the rim of the canyon are 10–20 m high by 50–100 m long scarps with boulders at the bases of the linear rock walls.

In 1997, we caught greenspotted rockfish using longline fishing gear deployed from a research vessel. In 1998, we hired a commercial fisherman to catch bocaccio using modified trolling gear. In both years, fishing lines were retrieved at about 20 m/min. Fishes were brought to a depth of about 20 m and held there for tagging. Divers then surgically implanted Vemco V16 (Vemco Ltd., Nova Scotia, Canada) sonic tags into the captured fish. Following surgery, tagged fish were placed in a recovery-release cage, then towed to the differential GPS location at which they were caught, whereupon the cage was lowered to the seafloor and fish were released. We used the *Delta* submersible to verify that tagged fish were alive after release. A more complete description of tagging and underwater tracking procedures is provided in Starr et al. (2000).

Vemco VR-20 receivers were moored on the seafloor for the duration of the study as a means of tracking tagged fish. The positions of receiver deployment spanned the distribution of release locations of the tagged fish. To increase the amount of positional information available from the receiver data, we placed the tagged fish and receivers along the side of a submarine canyon that stretched northeast to southwest. On 7 October 1997, we placed three receivers on a ledge at a depth of about 160 m along the wall of the canyon (Fig. 1). The receivers spanned a distance of 1500 m and recorded signals for 6 minutes out of every half-hour. We retrieved them on 5 January 1998.

In 1998, we deployed two receivers on surface buoys from 17 August through 10 September because tagging operations commenced one month before the submersible was scheduled to deploy the underwater moorings. These receivers were placed near the locations at which fish were released, in the northeastern portion of the Soquel Canyon study area (site 1, Fig. 2) and in the southwestern portion of the study area (site 2, Fig. 2). On 16 September 1998, we placed six receivers at various depths about 1000 m apart (Fig. 2) and retrieved them on 30 December 1998. Two of the receivers were located in about 100 m of water on the relatively flat substrate above the canyon rim. The other four receivers were placed in deeper water on flat benches or gently sloping walls below the canyon rim. These receivers recorded signals for 12 minutes every hour. In both years, battery life of the tags exceeded the length of time the receivers were moored.

Signal detection range of the moored receivers was about 800 m (Starr et al. 2000). Thus, if a signal was recorded at a particular time by only one receiver, we knew

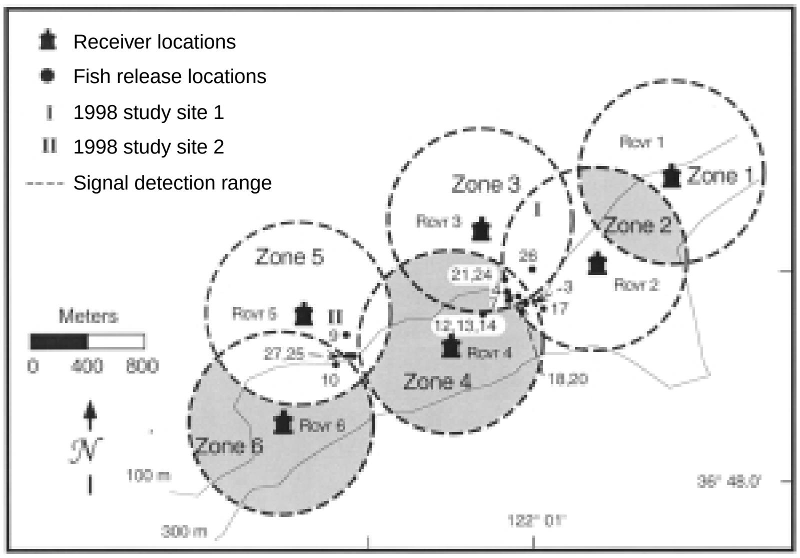

Figure 2

Fish-release locations with tag numbers, receiver locations, current meter location (moored with receiver 1), expected signal detection range, and resulting receiving zones for the 1998 field study of bocaccio.

Table 1

Patterns of signal receptions that define "receiving zones." Signals recorded concurently by the listed combinations of receivers were assigned a receiving zone that represents an approximate location of a tagged fish in a specified time period.

1997		1998	
Receivers (by receiver number) that recorded signals	Receiving zone no.	Receivers (by receiver number) that recorded signals	Receiving zone no.
1	1	1	1
1,2	2	1,2	2
2	3	2	3
2,3	4	2,3	3
3	5	2,3,4	3
		2,4	3
		3	3
		3,4	4
		4	4
		4,5	5
		5	5
		5,6	5
		6	6

the tag was located within 800 m of that receiver and outside the range of detection of other receivers. If a signal was recorded at the same time by two or more receivers, we knew the tag was somewhere within the intersection of the circles that represented the overlap of detection range for the respective receivers. We defined the combinations of intersections or exclusions of overlapping 800-m detection ranges as "receiving zones." In 1997, five such receiving zones were detected (Table 1). We labeled the northeasternmost receiving zone (signals only recorded by receiver 1) as zone 1. Zone numbers increased to the southwest. Because we knew the depths of all the greenspotted rockfish tracked in 1997, we were able to refine estimated locations of a tag to the area in each receiving zone that was between the 100–300 m isobaths (Fig. 1).

In 1998, the same method provided 13 combinations of overlapping detection ranges—too many to permit the patterns of fish movement to be understood easily. Consequently, we grouped combinations of overlapping detection ranges into six receiving zones by their spatial distribution

(Table 1). This enabled us to use signal location and tag depth data to more effectively estimate fish positions and movements. Again, the most northeastern receiving zone (signals only recorded by receiver 1) was labeled as zone 1; zone numbers increased to the southwest (Table 1, Fig. 2).

Each year we placed an S-4 current meter with recording thermometer and salinometer on a mooring near the seafloor to determine if changes in current, salinity, or temperature affected fish movement. In 1997, the current meter was located in 100 m of water on the shelf about 400 m away from receiver 2 (Fig. 1). In 1998, the current meter was moored with receiver 1, and was located in 100 m of water (Fig. 2).

Data analysis

Receivers logged the tag number, date, time of day, acoustic frequency, and tag depth each time a signal was detected. Receivers also recorded signal strength, noise, gain, and error messages provided by the receiver software. Data collected by the moored receivers were downloaded as text files and imported into a database for analysis. Tag depth was plotted versus time of signal reception for each tag and each receiver. Differences in fish depths by time of day were analyzed with ANOVA and Scheffe's *F*-test *post-hoc* analysis (Sokal and Rohlf, 1997).

In 1997, we grouped signals into half-hour time intervals to compare signal receptions between receivers. In 1998, we grouped signals into hourly intervals. We labeled each interval a time "bin" and standardized bin numbers among all receivers. Thus, any signal recorded by a receiver in a given time period (bin) could be directly compared with signals from other receivers in similar time bins. In 1997, the study included 4309 half-hour time bins. In 1998, the study included 2535 hourly time bins.

Each signal was thus assigned a time bin and a receiving zone according to the time interval of signal reception and the combination of receivers recording signals from that tag number. Treating each receiving zone number as a numeric rank enabled us to use a simple average of rank to identify the predominant receiving zone that a fish occupied in the time bins that occurred during a week (336 weekly bins in 1997 and 118 weekly bins in 1998). A difference in average ranking among weeks indicated the fish had moved; the value of the average indicated the direction in which the fish moved. For each tag, a chi-square test of heterogeneity was used to test for differences in average ranking among weeks. In 1997, week 2 of the study was the first week for which there were transmissions from all tagged fish; thus week 2 was used to represent the expected fish distribution by receiving zone for the chi-square test. In 1998, we used week 1 to represent the expected distribution. We also used the unplanned test of homogeneity of replicates tested for goodness of fit (Sokal and Rohlf, 1997) to determine if the average location of a fish (average rank) was similar between weeks. This method enabled us to group weeks in which a fish was in a similar location. In addition to generating weekly distributions, we used the ranking system to plot semihourly (1997) or hourly (1998) movements of tagged fish.

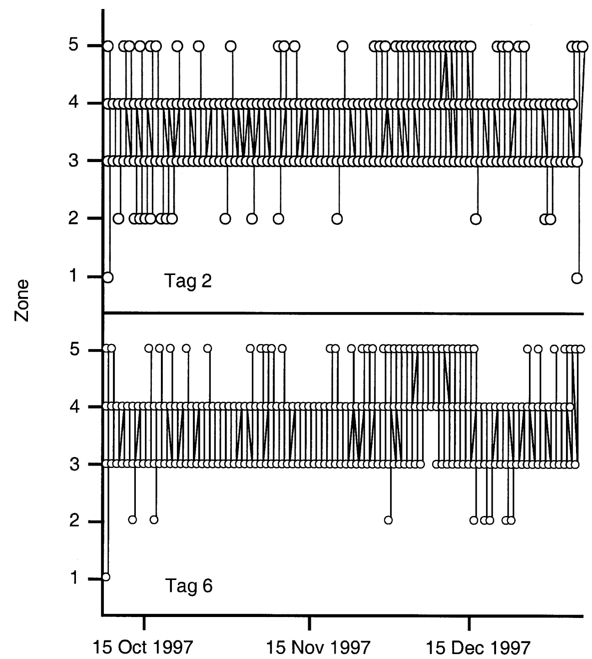

Figure 3

Movements of tagged greenspotted rockfish (tag-2 and tag-6 fish) across study area in 1997, as depicted by changes in receiving zones that were derived from patterns of signal receptions.

Results

Greenspotted rockfish

In 1997, we tagged six greenspotted rockfish, ranging in total length from 35 to 39 cm (Starr et al., 2000). Lea et al. (1999) reported that greenspotted rockfish in this size range are 11–15 yr old and probably mature. The three moored receivers recorded signals throughout the study period from all tags except tag 1. Signals from tag 1 were recorded for 18 hours, then not again until 67 days later. The total number of transmissions recorded from each tagged fish ranged from 156 to 24,132 (Starr et al., 2000).

Except for tag-1 fish, tagged greenspotted rockfish exhibited two patterns of relatively small horizontal movements. Tag-2 and tag-6 fish remained primarily in the receiving zone in which they were released (zone 4) and exhibited few cross-zone movements (Fig. 3, Table 2). Receivers recorded transmissions from each of these tags in 99% of the time bins. More than 56% of the time, signals originated in receiving zone 4, and 94% of the time signals originated from receiving zones 3 or 4 (Table 2), an area comprising 58 ha, or a linear distance along a ledge of 1200 m. When the fish moved out of zones 3 or 4, they most often moved southwest, towards the mouth of Soquel Canyon (towards Zone 5 in Fig. 3). Chi-square and *post-hoc* analyses indicated similarity in the pattern of signals received from the tags for most weeks, as indicated by the weekly average rank of receiving zone (Fig. 4).

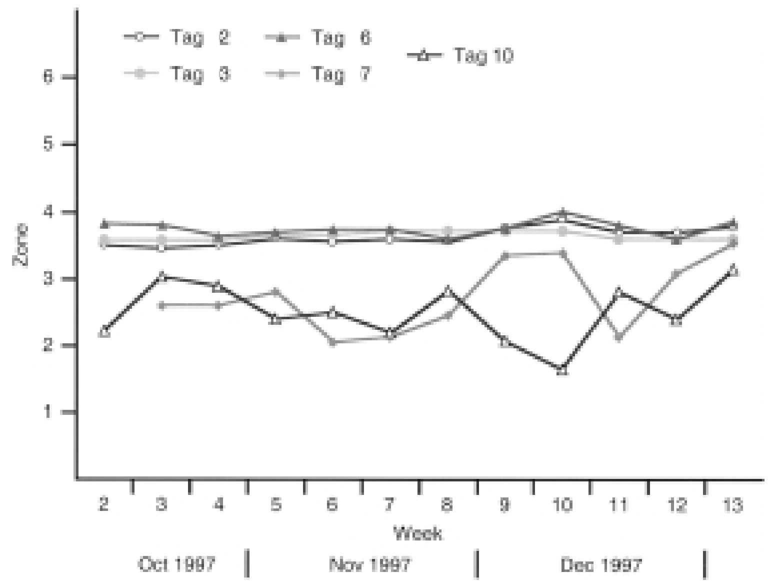

Figure 4

Distribution of tagged greenspotted rockfish in 1997 as depicted by the weekly average rank calculated from receiving zones which were derived from patterns of signal receptions.

Table 2

Percentage of half-hour time bins by receiving zone in which signals were recorded from tagged greenspotted rockfish from 7 October 1997 through 5 January 1998. None = the percentage of time bins in which no signal was recorded.

	Zone number					
Tag number	1	2	3	4	5	None
1	0.1	0.2	0.4	0.3	0.1	98.8
2	0.0	0.4	37.9	56.2	4.4	1.0
3	2.0	3.6	26.5	28.2	14.1	25.6
6	0.0	0.2	26.4	67.3	5.1	1.0
7	11.6	9.6	24.2	8.1	5.2	41.2
10	11.2	12.7	31.6	6.9	2.6	35.0
Zone area (ha)	53.3	11.4	3.9	54.0	36.4	

Table 3

Frequency of time lapse between signals after a time bin in which no receivers recorded signals from tagged greenspotted rockfish in 1997. NA = no signal was recorded for 67 days.

Tag number	0–1 h	1–5 h	5–10 h	>10 h	Max. time (h)
1	NA	NA	NA	NA	
2	7	1	0	0	1.5[1]
3	368	102	7	2	12.5[1]
6	6	0	0	0	1[1]
7	253	107	14	16	30
10	296	101	19	6	27.5

[1] Signals from these fish were not recorded for the first 17 h that receivers were in place and are not included in this table. Signals may not have been recorded because of electronic interference from boats in the area that prevented receivers from recording signals. The other two fish (tag-7 and tag-10 fish) were released a week after receivers were in place.

Tag-3, tag-7, and tag-10 fish moved greater distances, and made relatively frequent short-term movements out of the zone in which they were originally tagged and released (Fig. 5, Table 2). For these tags, 26–41% of the time bins contained no signals. The maximum time recorded for a tag in a single receiving zone was 32% of the time bins, and at least three zones were needed to account for 60% of the signals received from each tag. All three tagged fish showed evidence of moving across the entire study zone, a linear distance of 2940 m, and an area of about 1.6 km^2. Chi-square and *post-hoc* analyses indicated there were significant ($P<0.05$) differences in the weekly average rank of receiving zone for tags 3, 7, and 10 (Fig. 4). Transmissions from these tags were frequently recorded in all receiving zones (Fig. 5) and the fish also moved out of the study area for short time periods. The maximum time between recorded signals from any of these tags was 30 h. More than 90% of the time, the interval between recorded signals was 5 hours or less (Table 3).

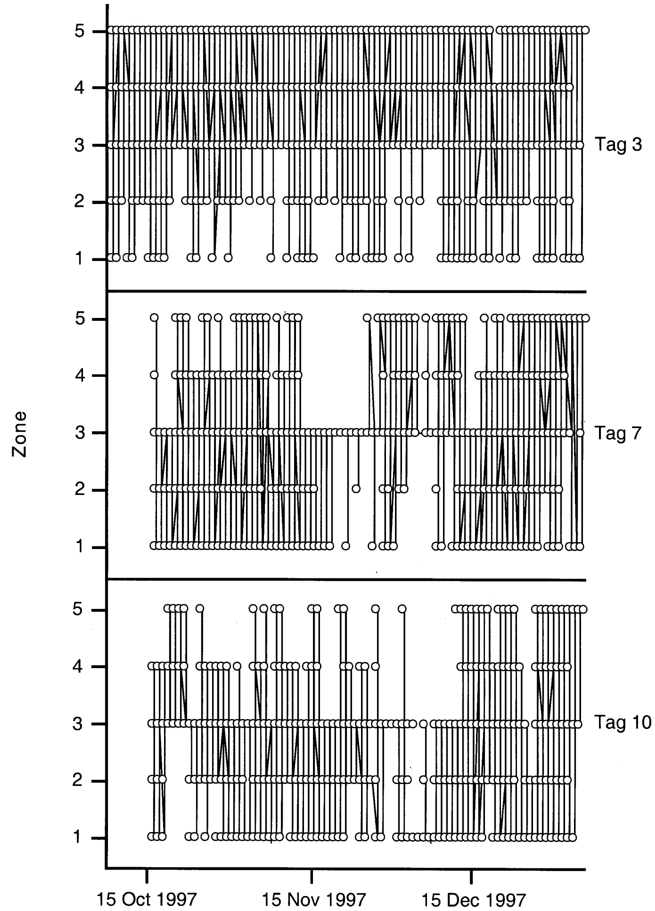

Figure 5

Movements of tagged greenspotted rockfish (tag-3, tag-7, and tag-10 fish) across the study area in 1997 as depicted by changes in receiving zones which were derived from patterns of signal receptions.

All tagged greenspotted rockfish, except tag-1 fish, showed little vertical movement, and 99% of depth transmissions from each tag were within ±3 m (see Fig. 6 for an example of this pattern). This distance is effectively the range of tidal variation and the error associated with the depth sensors in the sonic tags. Some of the fish occasionally made short-term movements to deeper locations. The only exception to this pattern was tag-1 fish that was tracked for 18 hours, lost, then heard again 67 days later. It exhibited vertical movements of about 90 m in the hours before it left the study area (Fig. 7).

Bocaccio

In 1998 we tagged 16 bocaccio, ranging in length from 35 to 58 cm (Starr et al., 2000). Ten of the bocaccio we tagged were larger than the size at 50% maturity reported by Gunderson et al. (1980). The receivers placed on surface buoys in August and early September recorded continuously; the total number of transmissions recorded from each of the tags in that time bin ranged from 0 to 9531 (Starr et al., 2000). The total number of signals recorded by the six subsurface receivers that were deployed from 16 September through 30 December ranged from 0 to 19,213 (Starr et al., 2000). Ten of the tagged bocaccio spent little time in the 12-km^2 study area (Fig. 8). Signals from three tags were recorded only within a few days after tagging and were not heard again (tags 13, 24, 26), either because the fish left the study area or the tags failed to send signals. Lengths of these fish ranged from 47 to 51 cm (Starr et al., 2000). Transmissions from five tags were recorded in the study area for only 1–4 weeks (tags 3, 4, 10, 12, 21). Lengths of these tagged fish ranged from 35 to 52 cm. Three fish appeared to leave the study area and return two weeks to a month later (tags 17, 20, 25). Lengths of these fish ranged from 45 to 55 cm. Signals from the remaining five tags (tags 7, 9, 14, 18, 27) were recorded in the study area the entire time. Lengths of these fish ranged from 47 to 58 cm.

Signals from 10 tags were recorded in less than 10% of the time bins in any zone (Table 4). Signals from one tag

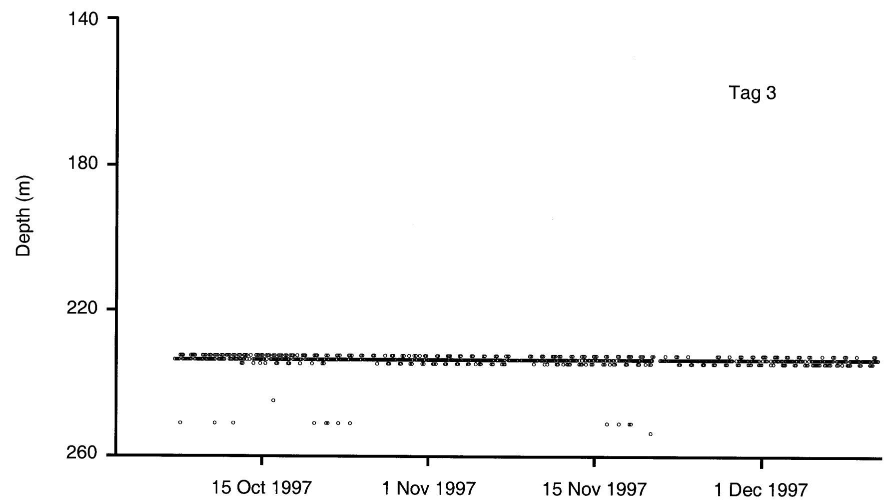

Figure 6

Depth distribution of signals received from tag 3 in 1997. Tag 3 is presented as an example of the depth distributions observed from all tagged greenspotted rockfish, except those of tag 1.

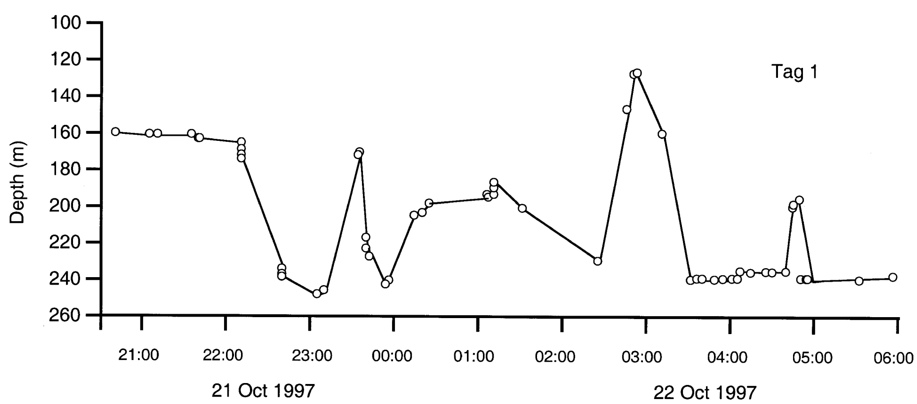

Figure 7

Depth distribution of signals received from tag-1 greenspotted rockfish in 1997.

were recorded about 50% of the time, and transmissions from the remaining five tags were recorded in more than 80% of the time bins. The six fish that remained in the study area 50% of the time or more stayed in a small part of the study area (Table 4). Signals from each of four tags (tags 9, 14, 17, 27) were recorded almost exclusively only where they were released, in receiving zones 4 or 5. These receiving zones comprised an area of 168 ha and 201 ha, respectively. Signals from the other two fish (i.e. tags 7, 18) were recorded primarily in receiving zones 3 and 4, an area of about 400 ha. Chi-square and *post-hoc* analyses indicated all fish stayed primarily in the same receiving zones for the time they were in the study area (Fig. 9).

Although the six fish that stayed in the study area stayed primarily in one or two receiving zones, they often exhibited small movements. Plots of zone numbers of recorded signals indicated that two of the fish (tags 7, 18) frequently moved across all receiving zones (Fig. 10). Additionally, cross-talk from receivers 5 and 6 indicated that tag-27 fish made frequent short-term movements (Starr et al., 2000). Tagged fish also occasionally left the study area. Except for tag 17, which was not recorded in the study area for 27 days, the maximum time interval between recorded signals from any of these tags was 57 h. More than 90% of the time, the interval between recorded signals was 5 h or less (Table 5).

Eight of the 16 tags transmitted information about depth. We recorded signals from five of the eight tags for only short time periods after the fish were released. Two of these five fish (tag-3 and tag-12 fish) moved vertically to within 15 m of the surface 9–12 hours after tagging, then returned below a depth of 90 m for a 12–15 day period before signals were lost (see Fig. 11 for an example of tag-3 fish movements). A third fish (tag-4 fish) fluctuated ±10 m around a depth of 90 m for a week, moved vertically to a depth of 14 m, and returned to a depth of about 90 m for another three weeks before signals ceased. A fourth tag (tag 13) was recorded for 3 days and exhibited frequent fluctuations of 20 m in depth before signals ceased.

Data from the remaining three fish containing depth transmitters were recorded throughout the study. Depth transmissions from tag 14 varied less than 3 m, whereas depth transmissions from tag 7 (Fig. 12) and tag 9 (Fig. 13) indicated cyclical vertical movements of ±10–20 m, and occasional deeper dives. The greatest variation in depth was exhibited from tag 7. That fish made several dives of 100 m; once it moved from 100 m to 220 m and back in a 20-h period. Tag-7 and tag-9 fish also demonstrated a diurnal periodicity in vertical movements. Fish were more active and higher during the day and less active and deeper at night (Fig. 14). The ANOVA and Scheffe's *F* test statistics indicated significant differences in both depth and change in depth between dawn, day, dusk, and night hours (Table 6).

Environmental parameters fluctuated but did not appear to be related to fish movements. Salinity and temperature data from the S-4 current meter at 100-m depth fluctuated within 24-h periods, but there were no obvious trends within or between years. Salinity averaged 33 ppt in 1997 and 34.5 ppt in 1998. Water temperature fluctuated from 10 to 15°C in 1997, whereas in 1998 it was more consistent, ranging from 9 to 11°C. Current speed and direction fluctuated in what appeared to be a tidal basis (Shea and Broenkow, 1982), but since there was no obvious relationship to recorded movements, this relationship was not explored in more detail.

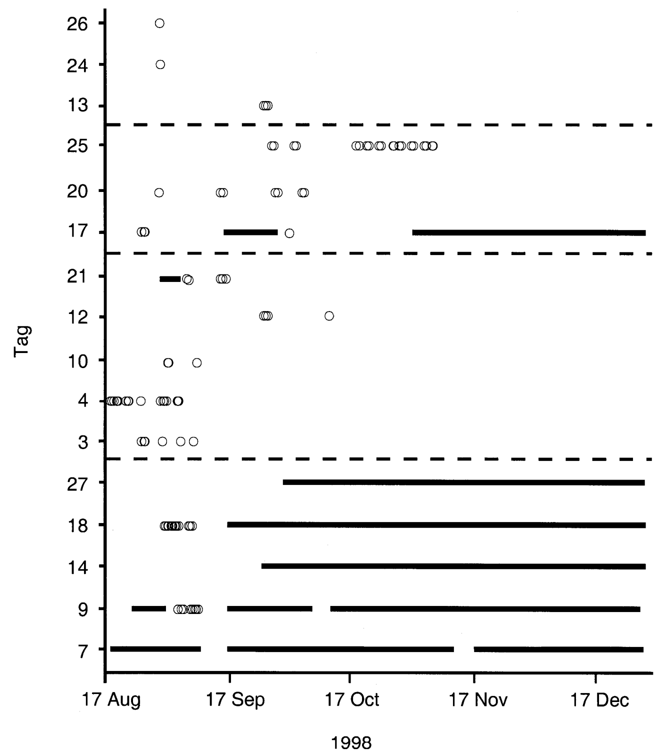

Figure 8

Dates of signal receptions in study area from sonic transmitters implanted in bocaccio in 1998. Circles represent individual occurrences of recorded signals; solid lines represent almost continuous occurrences of recorded signals. Dashed lines on the graph are shown to separate the groups of tagged fish discussed in the text.

Discussion

Fish movements

The *in situ* tagging procedures we developed alleviated many problems associated with surface tagging and provided means for tracking deeper-water rockfishes. We expected greenspotted rockfish to move only small distances because of their affinity to seafloor habitats such as overhangs and crevices (Stein et al., 1992; Yoklavich et al., 2000). Our work confirmed that greenspotted rockfish are relatively sedentary. The greenspotted rockfish we tagged with depth transmitters moved less than ±3 m vertically during the study, except for a few occasions when a fish swam down 20–40 m, only to return to its original depth within 2 hours. This small variation in depth displayed by the tagged greenspotted rockfish indicated that these fish most likely do not leave canyon wall habitats to feed. Love (1996) indicated that they eat mainly small invertebrates, but also cephalopods and fishes. It is possible that prey in the water column is advected toward them along the canyon wall (Isaacs and Schwartzlose, 1965; Genin et al., 1988). They do not appear to migrate vertically to feed on scattering layer organisms as do other rockfishes such as yellowtail rockfish (*Sebastes flavidus*) off Oregon (Pereyra et al., 1969).

Horizontal movements of the tagged greenspotted rockfish were on the order of hundreds of meters to a few kilometers. Receivers 2 and 3 each recorded cross-talk from signals of the same two tags (tags 2, 6) at several different times, indicating that these fish alternately swam close to one receiver, then at a later time swam close to a second receiver that was more than 300 m away (Starr et al., 2000). Although most movements were contained well within the 3-km long study area, half of the fish made sojourns out of the study area for short time periods. We think these small, short-term movements represent foraging activity along the canyon ledge.

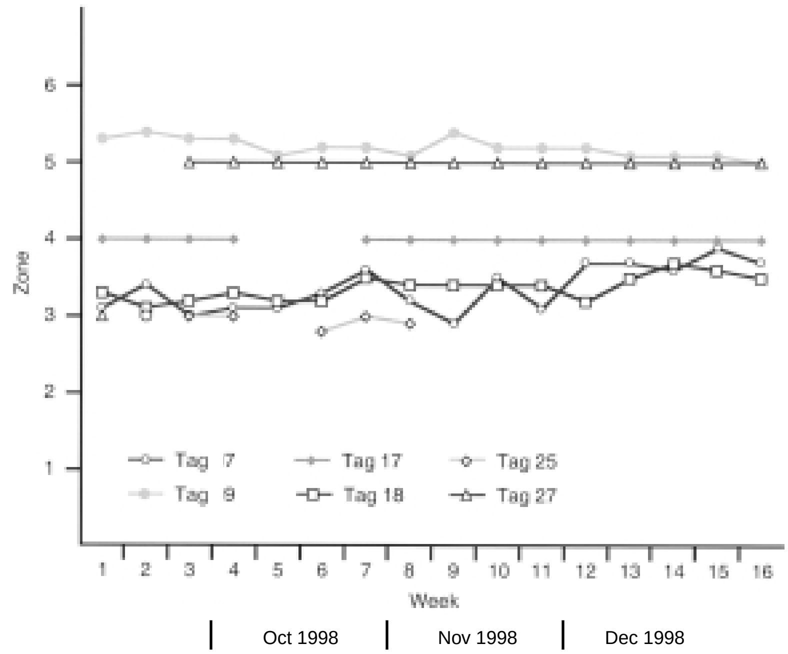

Figure 9

Distribution of six tagged bocaccio in 1998 as depicted by the weekly average rank calculated from receiving zones derived from patterns of signal receptions.

Table 4

Percentage of hourly receiving bins in which signals from tagged bocaccio were recorded from 16 September through 30 December 1998. None = the percentage of time bins in which no signal was recorded.

Tag number	Zone number 1	2	3	4	5	6	None
3	0.0	0.0	0.0	0.0	0.0	0.0	100.0
4	0.0	0.0	0.0	0.0	0.0	0.0	100.0
7	3.3	3.8	41.5	35.3	1.7	0.7	13.7
9	0.0	0.0	0.0	0.2	67.5	17.6	14.7
10	0.0	0.0	0.0	0.0	0.0	0.0	100.0
12	0.0	0.0	0.2	0.4	0.1	0.1	99.2
13	0.0	0.0	0.2	0.4	0.1	0.1	99.2
14	0.0	0.0	0.1	98.0	0.5	0.0	1.4
17	0.0	0.0	0.0	50.4	0.0	0.0	49.6
18	2.0	8.7	29.6	39.3	2.0	0.0	18.4
20	0.0	0.0	0.2	0.0	0.5	0.1	99.3
21	0.0	0.0	0.4	0.4	1.3	0.0	97.9
24	0.0	0.0	0.0	0.0	0.1	0.0	99.9
25	0.3	0.0	5.1	0.0	0.0	0.0	94.7
26	0.0	0.0	0.0	0.0	0.0	0.0	100.0
27	0.0	0.0	0.0	0.0	99.7	0.0	0.3
Zone area (ha)	124.0	75.5	232.2	168.0	201.0	132.4	

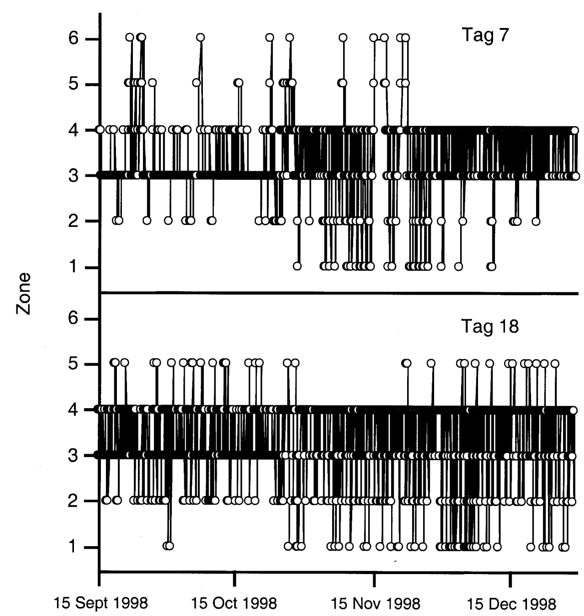

Figure 10

Movements of tag-7 and tag-18 bocaccio across the study area in 1998 as depicted by changes in receiving zones derived from patterns of signal receptions.

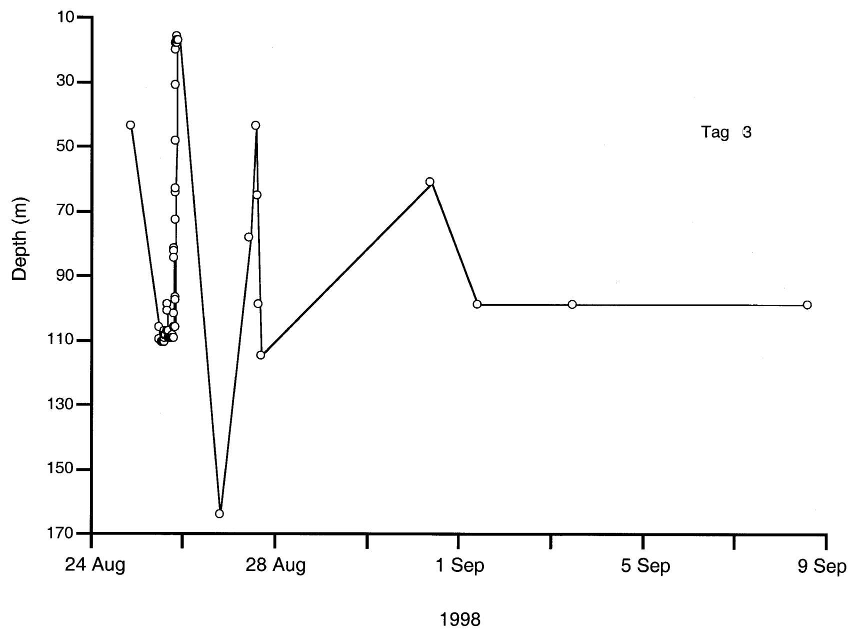

Figure 11

Depth distribution of signals received from tag-3 bocaccio in 1998. Tag-12 bocaccio displayed a similar pattern.

We expected bocaccio to move more than greenspotted rockfish. Bocaccio are frequently caught in midwater trawl nets and are considered more mobile than greenspotted rockfish (Love, 1996). Hartman (1987) reported that juvenile bocaccio moved a maximum of 148 km over two years in tag-recapture studies in southern California. In this respect, young bocaccio are similar to yellowtail rockfish (*Sebastes flavidus*) that have exhibited movements on the scale of hundreds of kilometers in tag-recapture studies conducted in Alaska and British Columbia (Stanley et al., 1994). In Stanley et al.'s studies, 75% of the tag recoveries were within 25 km of the release point, but maximum movement observed was 250 km for Canadian yellowtail rockfish, and 1400 km for Alaskan fish.

Not all studies have shown that yellowtail rockfish move great distances, however. Using ultrasonic telemetry, Pearcy (1992) tracked them from the surface intermittently for periods of several days and reported that tagged fish generally stayed within 2 km of the capture or release location. After a period of 13 days in 1990, 11 of 12 tagged fish were detected within 300 m of the capture site, even though some fish had been displaced. A month after release, eight of 12 tagged fish were within 1.4 km of the capture location.

Pearcy (1992) also suggested that the tagged fish exhibited site fidelity to a pinnacle habitat. Pearcy's work, combined with results from other displacement studies (Carlson and Haight, 1972; Hallacher, 1984; Matthews, 1990; Heilprin, 1992), suggests that several species of rockfish possess homing ability. Half of the bocaccio we tagged either stayed in the study area during the entire time of the study, or left and returned, suggesting some site fidelity. Evidence of site fidelity was also provided by the chi-square analyses of fish location in receiving zones. The analyses indicated that bocaccio remained in the same area over the course of a week, despite the evidence of frequent movements out of a receiving zone on a daily basis.

Table 5

Frequency of time lapse between recorded signals after a time bin in which no receivers recorded signals from tagged bocaccio in 1998. Only tagged fish that remained in the study area for more than 50% of the time are shown.

Tag number	0–1 h	1–5 h	5–10 h	>10 h	Max. time (h)
7	115	30	6	3	57
9	152	66	1	2	28
14	14	2	0	0	1
17	143	86	10	5	660
18	201	86	2	1	12
27	2	0	0	0	1

Although our study was designed to evaluate the residence time of bocaccio in a discrete area, and not to quantify the maximum distance bocaccio move, the relatively small percentage of tagged bocaccio that stayed in our 12-km^2 study area during the entire study period indicated that bocaccio may also move large distances. The results of our study tend to reinforce the hypothesis presented

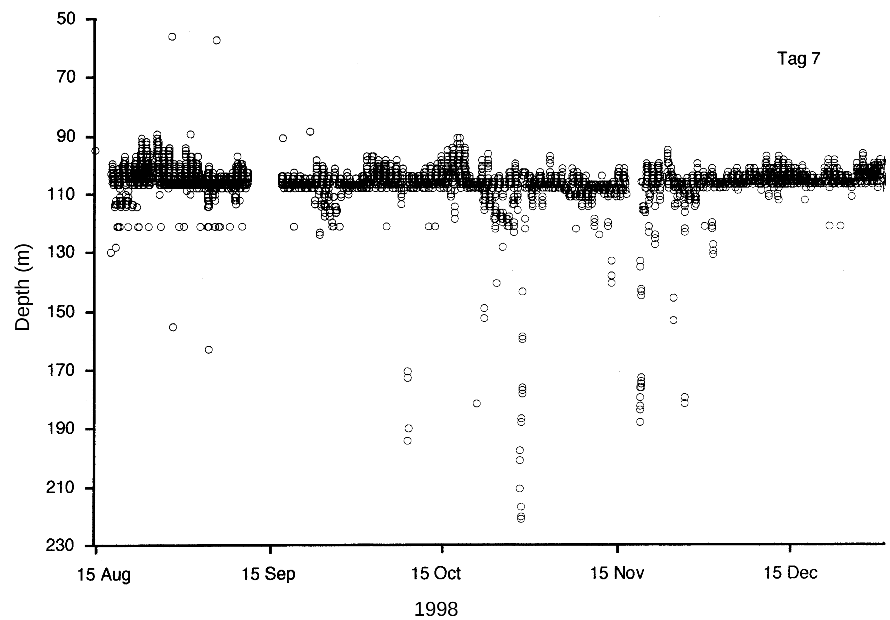

Figure 12
Depth distribution of signals received from tag-7 bocaccio in 1998.

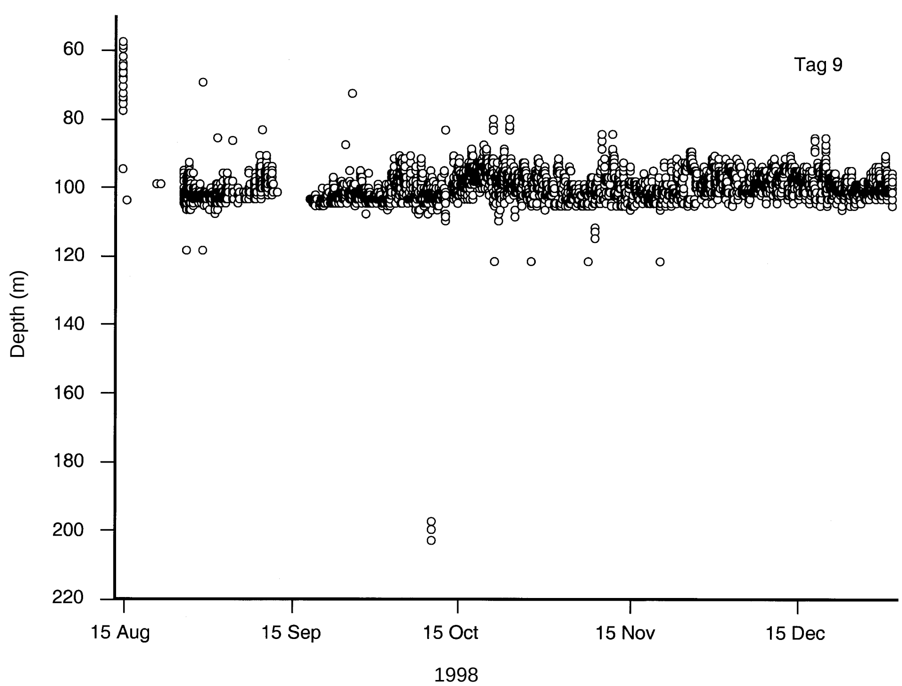

Figure 13
Depth distribution of signals received from tag-9 bocaccio in 1998.

(MacCall[2]) that there are two types of observed movements of bocaccio: pelagic and "refugial." They suggested, from observations of the large sizes of bocaccio observed as single individuals and the occurrence of smaller animals in mid-water trawl catches, that there may be an ontogenic shift from pelagic to refugial habits. They hypothesized that subadults are more mobile than adults, and as the fish increase in size, they become more sedentary. From tag transmissions and submersible surveys, we observed both pelagic and refugial behavior (about 25% of the tagged animals exhibited refugial behavior). The two largest tagged bocaccio were among the five fish that moved the least. The narrow size range of most of the tagged fish, however, precluded an analysis of movements by fish length.

Tagged bocaccio made frequent small vertical movements that were associated with time of day. The magnitude of the vertical movements matched the vertical relief of the habitats used by tagged fish. During submersible operations, we tracked tagged fish in small schools as they moved along rock scarps that were 10–20 m high and 100–200 m long (Starr et al., 2000). These scarps were often at, or just below, the rim of the submarine canyon. The depth transmissions from tags indicated that fish were at the top or just above the rock habitats during the day, and lower and more sedentary at night. We attribute the increased activity during the day to the fact that bocaccio are visual predators (Love, 1996) and are thus more apt to forage during the day.

Four of the eight fish containing depth transmitters made rapid vertical movements. Three of the bocaccio rose vertically to spend a short time near the surface, then returned to depths from which they came. These fish all remained only a few weeks in the study area. A fourth fish made a deep dive to 220 m and back to 100 m in less than a day (Fig. 12). The purposes of these dives are unknown, but such dives reinforce our observations during tagging operations that bocaccio can modify the volume of air in their swim bladder. Pearcy (1992) observed that yellowtail rockfish also are capable of discharging air from their swim bladders in a relatively short time.

For some tags, there were short time intervals when signals were not recorded. This may have been caused by the canyon topography or by fish behavior. The complex topography of Soquel Canyon and the behavior of the rockfishes may have prevented the receivers from receiving all possible transmissions from tagged fish. The hard, steep walls that undulate along the side of the canyon (Yoklavich et al., 2000) occasionally cause echoes and an original transmission to coincide, thus preventing the receivers from recording a valid signal. Other signal lapses may also have been due to the tendency of rockfish to take shelter under rocks or ledges. From the surface, we occasionally heard weak signals that were unusually high-pitched and that sounded "tinny." We have experienced the same type of reception when tracking shallow-water rockfishes that took shelter under a rock or ledge. Signals return to full strength and timbre when the fish leaves the crevice.

Table 6

Results of Scheffe's *F post-hoc* test (*P* values) were used to identify differences in fish depth between different times of the day (i.e. between dawn and day [dawn–day], dawn and dusk [dawn–dusk], etc.) or diel differences in depth and change in depth of signal receptions from tagged bocaccio (tag-7 and tag-9 fish) in 1998.

	Tag 7		Tag 9	
	Depth	Change in depth	Depth	Change in depth
Dawn–day	0.0097	0.0194	<0.0001	<0.0001
Dawn–dusk	0.2840	0.277	0.0040	0.0004
Dawn–night	0.5045	<0.0001	<0.0001	<0.0001
Day–dusk	0.7455	0.9031	0.7312	0.9998
Day–night	<0.0001	0.0065	0.1010	<0.0001
Dusk–night	0.0007	0.0156	0.0440	<0.0001

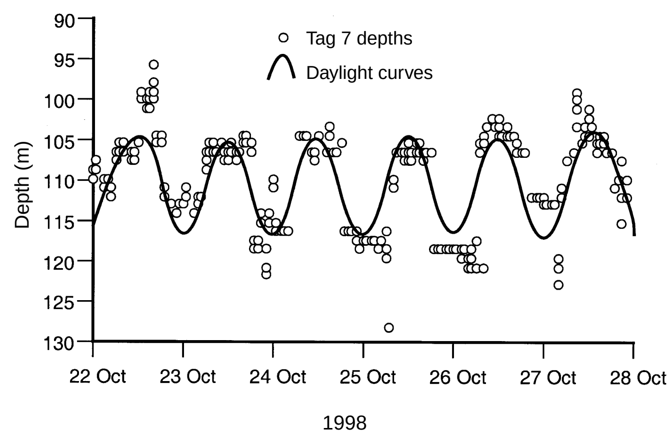

Figure 14

Depth transmissions recorded for tag-7 bocaccio plotted with daylight curve for the period 22–28 October 1998.

Implications for marine reserves

Tag-recapture studies of shallow water (<100 m) demersal rockfishes typically have indicated very little movement; only one species in ten studies exhibited long-term movements greater than 3 km (Stanley et al. 1994; Lea et al., 1999). Results from these studies support the idea that small harvest refugia may effectively protect nearshore rockfishes. This would be fortuitous if almost all nearshore rockfishes have small home ranges, because most of the marine reserves in the eastern Pacific Ocean are very small and have been created without regard to typical movements of species (McArdle, 1997; Starr, 1998; Yoklavich, 1998).

Our results indicate a considerable short-term variation in the movements of individual greenspotted rockfish, which may be masked by the long-term nature of tag-recapture studies. Although almost all fish may remain in a small area over the course of several years, an individual fish may occasionally move longer distances. This raises a question about the efficacy of marine reserves that are designed to account for modal distributions of fish based on traditional tag-recapture studies.

The efficacy of a marine reserve is directly related to its size and shape and the movements of the protected species (Polacheck, 1990; DeMartini, 1993; Nowlis and Roberts, 1999). Thus, without estimates of both the range and frequency of movements of the target species, it is difficult to predict the effectiveness of a reserve for conserving fishes (Carr and Raimondi, 1998). Infrequent foraging excursions out of a reserve, for example, could potentially negate the value of a reserve if its purpose is to act as a harvest refugium. Conversely, small home ranges could preclude a "spillover" effect and diminish a reserve's ability to enhance local fisheries, if that were the goal. Small reserves may appear to protect species that move little, but if protected fishes occasionally move greater distances, as did the tagged bocaccio and greenspotted rockfishes in our study, then larger reserves may be needed to encompass 90% or more of the typical monthly movements of a species. Models that incorporate movement into the theoretical design and evaluation of marine reserves may thus be strengthened by using the probability or percentage of time an animal actually remains in the reserve boundaries rather than modal distributions. The periodic departure of tagged fish from their center of activity suggests that a conservative strategy for the design of marine reserves would be to include a buffer zone to account for these infrequent sojourns.

Only one-fourth of the tagged bocaccio spent more than 80% of their time in the 12-km^2 study area. Yet the Soquel Canyon study area was two times larger than the mean size and four times larger than 70% of marine reserves in California that regulate fishing in any way (McArdle, 1997). Such movement will require that marine reserves intended to effectively protect bocaccio will need to be much larger than most current reserves. Until the full extent of the range and periodicity of movements is known, however, it will be difficult to adequately design a system of marine reserves to protect bocaccio stocks.

After tagging, greenspotted rockfishes returned to rock habitats on the ledges at the side of Soquel Canyon and exhibited small horizontal and vertical movements. Based on the signal receptions for our three-month period, the size of a marine reserve would need to have a diameter of 3 km to account for 95% of the typical movements of the tagged greenspotted rockfish. Bocaccio, however, returned to higher relief habitats near the canyon rim after release and exhibited much greater horizontal and vertical movements. An effective reserve for bocaccio, therefore, would need to be larger than the 12 km^2 area encompassed by our study.

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