

GENDER-MEDIATED PATTERNS IN THE MOVEMENT OF CALIFORNIA SHEEPHEAD IN THE NORTHERN CHANNEL ISLANDS (EASTERN PACIFIC)

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The biology of sex-changing fishes is well-established in tropical coral reef ecosystems, and has been described for selected temperate marine species. Comparatively less is known about the ecology of these fishes, particularly in temperate systems. For instance, the extent to which gender mediates behavior within and among species, and precisely which behaviors are mediated remains unclear for many species. The California (CA) sheephead (*Semicossyphus pulcher* [Labridae]), is a protogynous hermaphrodite found on rocky reefs and in kelp forests along the west coast of North America. Previous studies have shown significant variation in life history characteristics of CA sheephead across the southern portion of its range. In the present study, the movement behavior of 45 adult CA sheephead (26 initial phase [Iph] females and 19 terminal phase [Tph] males) was monitored for 2.5 years by an array of acoustic receivers deployed around Anacapa Island in the northern Channel Islands (California). Results clearly indicated that patterns in the movement of CA sheephead at Anacapa Island were mediated by fish gender. Tph males and Iph females differed significantly with respect to several important behavioral metrics recorded by the passive acoustic receiver array. Further, these results also differed from previous telemetric research conducted at Catalina Island (approximately 102 km to the southeast of the study area), suggesting that the vagility of CA sheephead, like other life history characteristics, changes with local environmental conditions.

Keywords: California sheephead, Channel Islands, hermaphrodite, *Semicossyphus pulcher*

INTRODUCTION

The biology of sex-changing fishes is well-established in tropical coral reef ecosystems (Warner 1975a, Ross et al. 1983, Sadovy de Mitcheson and Liu 2008), and has been described for selected temperate marine species (Warner 1975b, Cowen 1990). Comparatively less is

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known about the ecology of fishes that switch genders over the course of their life histories, particularly in temperate systems (Adreani et al. 2004). For instance, the extent to which gender mediates behavior within and among species, and precisely which behaviors are mediated remains unclear for many species. The implications of this lack of knowledge are particularly acute for successful management and conservation, where gender-mediation of behavior can interact with variable (and frequently unknown) sex ratios to impact local populations and the communities they inhabit (Dill et al. 2003, Hamilton et al. 2007).

The California (CA) sheephead (*Semicossyphus pulcher* [Labridae]), is a protogynous hermaphrodite (Warner 1975b). It is found on rocky reefs and in kelp forests along the west coast of North America. The reported distribution of CA sheephead extends from Monterey Bay, California (USA) in the north to Cabo San Lucas, Baja California (Mexico) in the south, including the northern Gulf of California (Miller and Lea 1972). Hydrographic constraints on dispersal limit the recruitment of CA sheephead, and resulting abundance, to the north of Point Conception except in extreme events such as El Niño (Cowen 1991, Love 1996).

Across the southern portion of its range, both the ecology and life history patterns of CA sheephead have been shown to vary with local environmental conditions. Cowen (1986) showed CA sheephead to be a generalist predator that exhibited flexibility in prey selection at four separate locations from Baja California north to San Nicolas Island. Across the same locations, Cowen (1990) found that CA sheephead attained their largest size at the northernmost location (San Nicolas Island) and that the onset of sexual maturation and sex change varied the greatest at the northernmost site. The extent to which the vagility of CA sheephead also varies in response to local conditions has yet to be demonstrated.

In an ecological context, the movement of organisms within ecosystems has a critical influence on species diversity (Reichenbach et al. 2007). The movement of fishes is of particular interest in the context of exploitation (Lowe and Bray 2006). Data from traditional tag-and-recapture studies suggest that the fidelity of CA sheephead to particular reefs, both artificial (Johnson et al. 1994) and naturally-occurring (Jenn Caselle, personal communication), is strong. However, until recently the difficulties in following individual fish for extended periods of time made precise quantification of fish movement rates one of the most difficult demographic parameters to assess (Jones 1991). Thus with respect to many species, even those for which a great deal of biological data are available, fundamental questions remain as to the movement patterns of individuals of all size classes.

Significant advances in acoustic technology have made possible field deployments of acoustic receivers that record data continuously for months to years (see Lindholm 2005, Heupel et al. 2006). Telemetry has been used to monitor the movements of other Labrids, including *Tautoglabrus adspersus* (Bradbury et al. 1995), *Tautoga onitis* (Arendt et al. 2001a, b) and *Lachnolaimus maximus* (Lindholm et al. 2006). Each of these studies showed high fish fidelity to areas of topographic complexity, both natural reefs and shipwrecks. Patterns in the movement of CA sheephead have been studied at Catalina Island using both active acoustic tracking (Topping et al. 2005) as well as passive acoustic monitoring (Topping et al. 2006). Results indicated that the movement patterns of tagged CA sheephead were mediated both by topographic features of the seafloor (e.g., rocky reefs) as well as seasonal variability in water temperature. Importantly, no difference in movement behavior was observed between males and females.

Important questions remain as to the extent of any gender-based mediation of the vagility of CA sheephead and how such mediation varies with local environmental conditions

elsewhere throughout its range. In the present study, we surgically-tagged adult CA sheephead (both initial phase females [Iph] and terminal phase males [Tph]) with acoustic transmitters and monitored their movements for up to 801 days at Anacapa Island in the northern Channel Islands. We sought to 1) identify any differences in CA sheephead movement patterns that were attributable to fish gender, and 2) to consider these results from the northern Channel Islands in the context of data collected from elsewhere throughout its range.

METHODS

Study Site

The study was conducted at Anacapa Island (Figure 1). The island is composed of three small islets each approximately 8 km in length, which together encompass 290 ha and lie approximately 18 km southwest of the mainland, separated by the Santa Barbara Channel (Harden 1997). The nearest adjacent island is Santa Cruz Island, approximately 7 km to the west. The seafloor surrounding the island is characterized by patchy rock reef and kelp forest, with large areas of sand and mud occurring further seaward (Cochrane et al. 2005). The island is managed as part of the Channel Islands National Park (U.S. Department of Interior) and the Channel Islands National Marine Sanctuary (U.S. Department of Commerce). This study was conducted within and adjacent to the Anacapa Island State Marine Reserve (AISMR) and the Anacapa Island State Marine Conservation Area (AISMCA; Figure 1). Both the AISMR and the AISMCA have prohibited fishing for CA sheephead since April 2003.

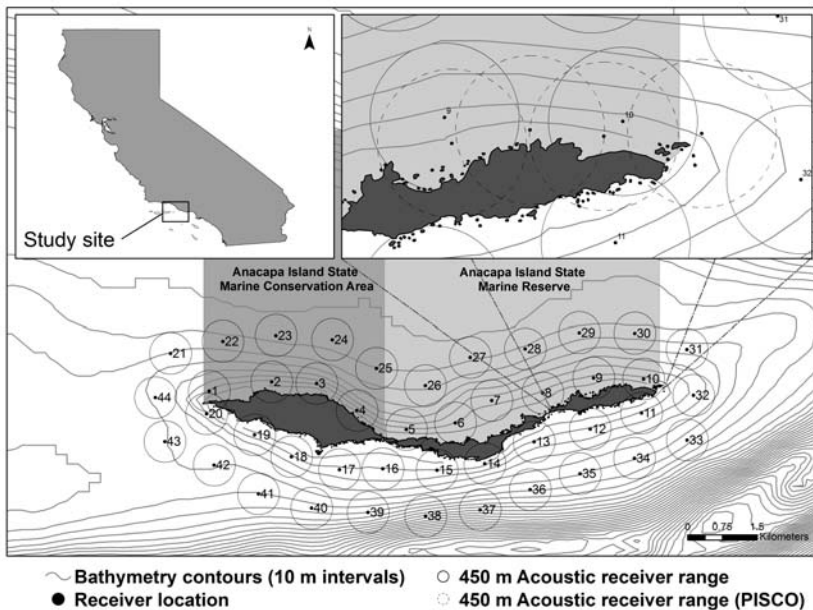


Figure 1. Map of study area at Anacapa Island, including the boundaries of the Anacapa Island State Marine Reserve (light grey) and State Marine Conservation Area (dark grey) and the location of the 44-node passive acoustic receiver array deployed on the seafloor around the island. A 450-m radius of detection is shown for each acoustic receiver.

Fish Capture and Tagging

A total of 45 adult CA sheephead (26 Iph females and 19 Tph males) were captured via baited hook-and-line and baited trap between July 2004 and July 2005. Fish gender was determined visually. Fish were captured in water depths ranging from 5 to 20 m and were brought to the surface slowly to minimize barotrauma and thermal shock. Each fish was maintained in a live-well for a brief period following capture to observe any obvious signs of external stress (e.g., external bleeding, difficulty swimming or station keeping). Fish selected for tagging were inverted on a padded, v-shaped surgical table, covered with a damp cloth, and flushed with chilled, fresh-flowing seawater during surgery. The total length (TL) of each fish was measured, and then a 25-40 mm incision (depending on transmitter model) was made just off the ventral line on the left side of the fish, forward of the vent. V8SC-2L coded acoustic transmitters and V16P-1L coded acoustic depth transmitters (VEMCO Ltd., Shad Bay, Nova Scotia) were coated with triple-antibiotic ointment and inserted into the peritoneal cavity through the incision. The incision was closed using 2 to 3 black monofilament sutures (5-0 Ethilon) and coated with triple-antibiotic ointment. All Iph females received V8SC-2L transmitters, while Tph males received either V8SC-2L or the larger V16P-1L transmitters depending on fish TL. The expected lifetime of the V8SC-2L and V16P-1L transmitters was 520 and 805 days, respectively. Following tagging, each fish was briefly maintained in a live-well and was then released at the same location as its capture.

Acoustic Monitoring of Fish Movement

The movement of tagged CA sheephead was monitored using an array of 44 omnidirectional, single-channel (69 kHz) VR2 acoustic receivers (VEMCO Ltd, Shad Bay, Nova Scotia) deployed around Anacapa Island as part of a larger project occurring throughout the Channel Islands and the southern California Bight (Domeier 2005). Receivers were deployed at 1000 m intervals around the island in two concentric circles (Figure 1). The interior ring of receivers was maintained via SCUBA, while the outer ring of receivers was recovered using ARC 1 acoustic releases (Desert Star Inc., Marina, CA). Range tests using V8SC-2L and V16P-1L transmitters indicated that the range of detection for a tag in the study area was a radius of approximately 450 m around each receiver (based on a detection efficiency of 80% using both transmitter models at that distance), or an area of the seafloor equal to approximately 0.5 km² per receiver. Each receiver was anchored using either a sand auger or multiple sand bags (depending on seafloor substrate type) and was supported 2 m above the seafloor using 2 non-compressible sub-surface floats. An additional 4 VR2 receivers were temporarily deployed inshore of the inner ring of the receiver array (Figure 1) by colleagues with the Partnership for Interdisciplinary Study of the Coastal Ocean (PISCO) who were conducting a parallel project. These receivers, which were in place from the initiation of tagging (June 2004) through September 2005, were not included in the overall analysis but were used to provide additional data on movement patterns of CA sheephead during that period.

Data Analyses

Nineteen Tph fish (mean = 549 mm TL; SD = 63) were tagged between 17 July 2004 and 28 July 2005. Twenty-six Iph fish (mean = 313 mm TL; SD = 35) were tagged between 07 and 09 December 2004. Fish were recorded from the date of release (Table 1) through either the

Table 1. Summary data for 19 terminal phase male and 26 initial phase female *S. pulcher* that were surgically tagged with acoustic transmitters and subsequently Anacapa Island from 2004 – 2006.

Fish #	TL (mm)	Release date	Receivers visited	Total # days recorded	Percent days recorded
Terminal Phase Male					
1	470	17 Jul 2004	4	485	61
2	630	17 Jul 2004	2	157	20
3	550	17 Jul 2004	1	115	14
4	470	17 Jul 2004	3	684	85
5	515	17 Jul 2004	4	320	40
6	530	17 Jul 2004	5	664	83
7	640	17 Jul 2004	3	270	34
8	550	17 Jul 2004	4	757	95
9	585	27 Jul 2004	2	185	43
10	620	08 Dec 2004	5	104	16
11	545	09 Dec 2004	5	614	94
12	550	07 Dec 2004	3	656	98
13	530	17 Jul 2004	4	709	86
14	530	09 Dec 2004	6	11	2
15	550	08 Dec 2004	6	66	10
16	490	08 Dec 2004	6	120	18
17	700	28 Jul 2005	4	81	19
18	455	07 Dec 2004	2	115	22
19	530	17 Jul 2004	1	18	4
Initial Phase Female					
1	355	07 Dec 2004	2	81	16
2	300	07 Dec 2004	2	216	42
3	320	09 Dec 2004	3	321	62
4	330	08 Dec 2004	2	162	31
5	280	08 Dec 2004	1	36	7
6	300	07 Dec 2004	1	153	29
7	380	08 Dec 2004	3	36	7
8	285	08 Dec 2004	1	228	44
9	320	07 Dec 2004	4	61	12
10	330	07 Dec 2004	1	159	31
11	345	07 Dec 2004	1	79	15
12	320	09 Dec 2004	2	334	64
13	270	08 Dec 2004	1	95	18
14	350	07 Dec 2004	2	210	40
15	260	07 Dec 2004	3	145	28
16	380	09 Dec 2004	2	46	9
17	315	09 Dec 2004	1	156	30
18	335	07 Dec 2004	1	333	64
19	350	07 Dec 2004	2	31	6
20	260	08 Dec 2004	1	17	3
21	275	09 Dec 2004	1	107	21
22	310	07 Dec 2004	2	39	8
23	290	07 Dec 2004	2	146	28
24	320	09 Dec 2004	1	147	28
25	285	08 Dec 2004	1	98	19
26	270	09 Dec 2004	1	5	1

end of the study (29 September 2008) or through the predicted expiration date for the transmitter batteries. We excluded data beyond the predicted battery expiration date due to uncertainties in both the quality of the transmitted signal and the resulting detection of tagged fish.

The total number of days recorded was plotted for each tagged fish across all receivers in 24-hour periods up to the lifetime of the transmitter battery or until the study's end. The percent-days recorded for each fish (total number of days recorded / total number of days in the study period) was compared between Iph females and Tph males using a one-way ANOVA (Sokal and Rohlf 1995). Proportion data were arcsin transformed prior to analysis.

To characterize the areas (or ambits) frequented by individual CA sheephead we quantified the number of receivers visited daily by each tagged fish over the course of the study period, where the ambit represented the maximum distance a fish could have travelled within the range of the receivers at which it was detected. The total number of receivers visited per fish was compared between Iph females and Tph males using a one-way ANOVA. To investigate temporal variation (e.g., monthly, seasonally, or annually) in the ambits of tagged fish over the course of the study, a mean daily ambit was calculated for each fish. This mean ambit for each fish was then subtracted from the number of receivers visited by each fish each day to produce a daily deviation (as per Topping et al. 2006). Daily deviations were averaged across all fish for each life history phase. A positive deviation from the mean (an increase in the average number of receivers visited) signified an expansion of an ambit while a negative deviation from the mean signified a contraction. Linear regression was used to evaluate the role of environmental factors in mediating the movement patterns of CA sheephead. The daily deviation for each gender was regressed against mean daily water temperature collected on the north side of Anacapa Island (courtesy of J. Caselle, PISCO).

Variation in movement patterns of fish at the scale of individual 24-hr periods was also investigated. Each 24-hr period of a fish's time at-large was apportioned into twenty-four, 1-hr time bins, standardized across receivers. For example, bin #1 occurred each day from 00:00:00 – 00:59:59, while bin #24 occurred at 23:00:00 – 23:59:59. All signal detections for each individual fish were assigned to particular 1-hr time bins. Diel patterns in fish movement were investigated by calculating the proportion of diurnal and nocturnal 1-hr time bins in which each fish was recorded, weighted for the total number of hours of sunlight and darkness throughout the study period. To compare diel fish movement between genders, a ratio of diurnal/nocturnal 1-hr time bins was calculated. The Kruskal-Wallis test was used to compare the ratio between sampling periods. The daily movements of each fish onshore and offshore were plotted across hourly bins. Where available, data on the maximum depth attained by fish each day were plotted as well to verify movement to the receivers in deeper water.

RESULTS

The total number of days recorded per tagged CA sheephead varied widely within and between the two genders (Table 1), ranging from 11 to 757 days for Tph males and from 5 to 334 days for Iph females. Tph Fish 8 (550 mm TL) was recorded for the maximum number of days (757). The mean number of detections per day (14.8 for Tph males and 13.9 for Iph females) was not significantly different between genders (ANOVA, $F_{1,43} = 0.00$, $P = 0.978$). However, when corrected for fish release date and estimated transmitter battery life, the percent-days recorded per fish (Table 1) was significantly different between treatments

(ANOVA, $F_{1,43} = 5.48, P = 0.024$). A total of seven Tph males and three Iph females were recorded for greater than 60% of the study period.

Plots of the days recorded for each fish across all receivers in the main receiver array (Figure 2, Figure 3) depict wide variability in the behavior among individual fish from both genders. However, three broad patterns in CA sheephead movement behavior are visible: near-continuous presence (e.g., Tph Fish 8 and Iph Fish 3), long-term sporadic presence (e.g., Tph Fish 7 and Iph Fish 15), and short-term presence (e.g., Tph Fish 18 and Iph Fish 5). Each of the seven Tph males that were recorded for greater than 60% of the study period (Table 1) shows near-continuous presence throughout the study (Figure 2). The same is true for the three Iph females recorded for greater than 60% of the study period (Table 1; Figure 3). A second group of fish in each treatment was present throughout the study period, but was recorded more sporadically. The third group of fish was present very briefly during the study period. This group was particularly well-represented in the Iph female treatment, though three Tph males also showed this behavior.

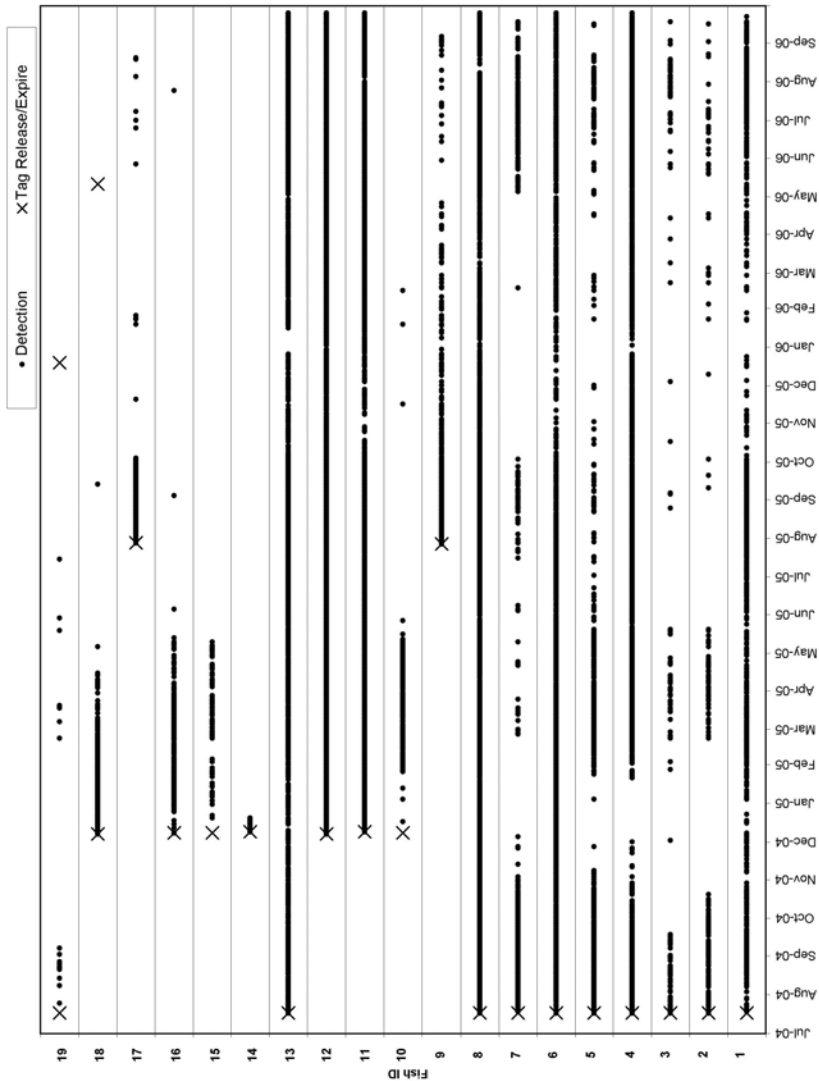


Figure 2. Recorded time at-large for 19 terminal phase CA sheephead tagged at Anacapa Island. Fish movement was monitored from July 2004 through September 2006. Each circle represents a day on which a fish was detected by a receiver, with crosses depicting the release date and expiration date for each transmitter.

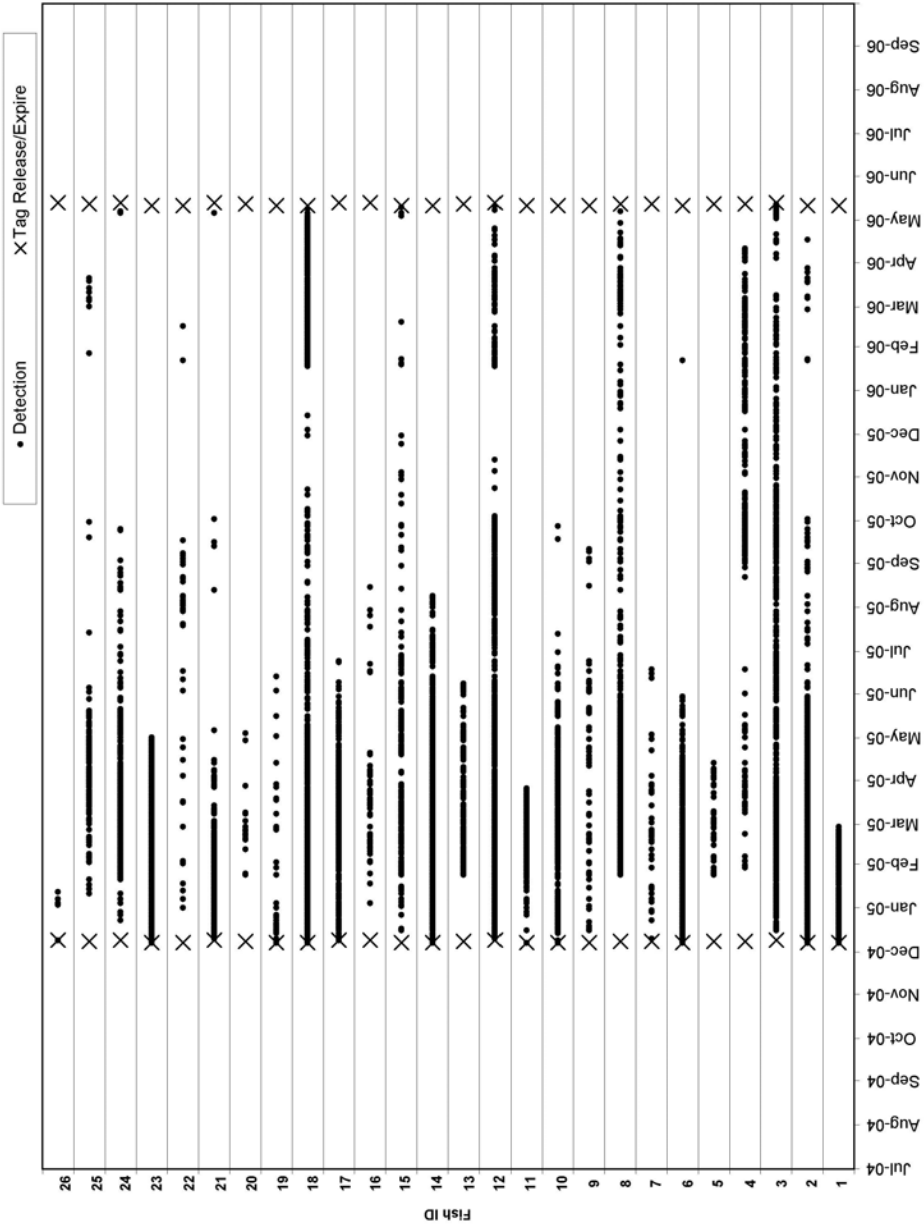


Figure 3. Recorded time at-large for 26 initial phase CA sheephead tagged at Anacapa Island. Fish movement was monitored from December 2004 through May 2006. Each circle represents a day on which a fish was detected by a receiver, with crosses depicting the release date and expiration date for each transmitter.

The total number of receivers visited by each tagged CA sheephead also varied widely within and between the two genders (Table 1). Six Tph males (26.8%) were recorded at five or more receivers over the course of the study, with all but two fish recorded at two or more receivers. The maximum number of receivers visited by Iph females was four, with 13 fish (41.9%) recorded at only a single receiver. The number of receivers visited per fish was significantly different between genders (ANOVA, $F_{1,43} = 29.43, P < 0.001$).

With an estimated radius of detection of 0.45 km for each receiver and a spacing of 1 km between each receiver, the maximum potential ambit recorded for an individual Tph male and Iph female was 4.7 km² and 3.1 km², respectively, with a mean ambit of 2.6 km² for Tph males and 1.11 km² for Iph females. Tph male fish regularly contracted and expanded their ambits throughout the study (Figure 4). Though some ambit expansion was recorded among Iph females (Figure 5), the low number of receivers visited per fish resulted in less change in ambits overall. Results of a linear regression of mean daily water temperature (Figure 4, Figure 5) on deviations from the mean number of receivers visited per fish per day indicated a significant positive relationship between Tph male ambit size and water temperature ($P < 0.001$; $r^2 = 0.25$), with less apparent effect on Iph female ambits ($P = 0.005$; $r^2 = 0.014$).

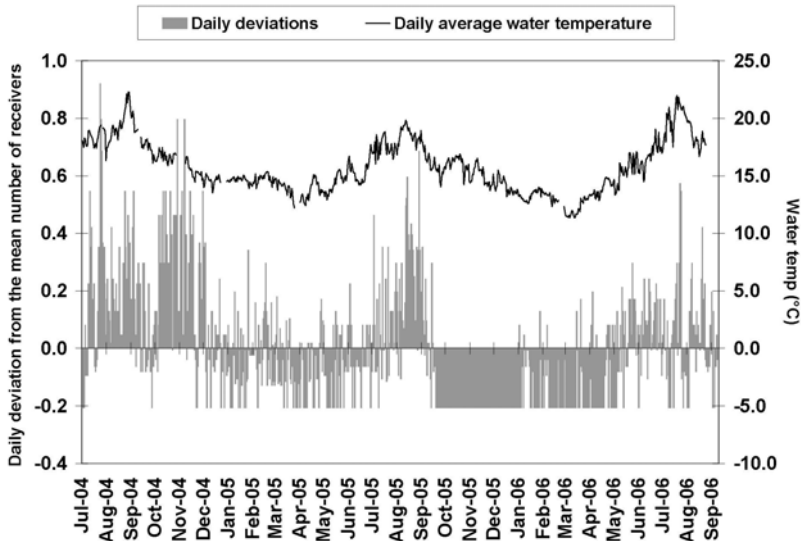


Figure 4. Daily deviations from the mean number of receivers for 19 terminal phase CA sheephead tagged at Anacapa Island. Water temperature is reported in °C.

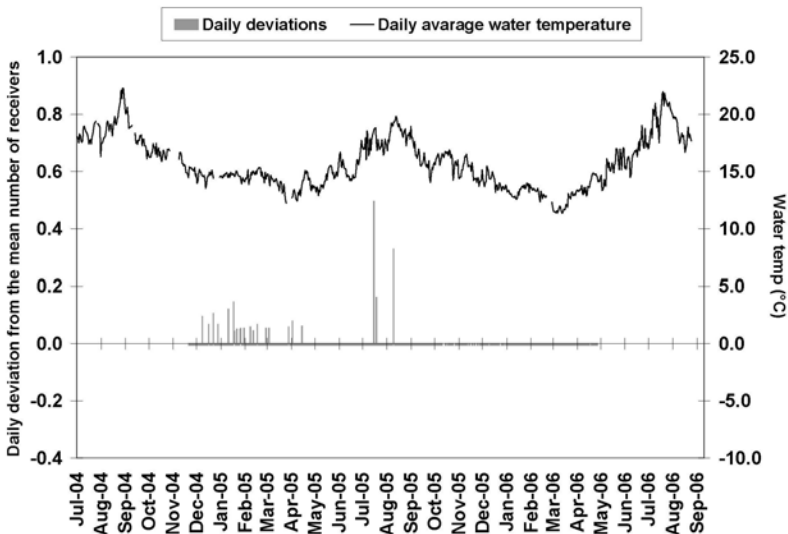


Figure 5. Daily deviations from the mean number of receivers for 26 initial phase CA sheephead tagged at Anacapa Island. Water temperature is reported in °C.

Tagged CA sheephead exhibited clear diurnal movement patterns throughout the study period (Figure 6, Figure 7). No fish was recorded solely during the night hours. A comparison of the day/night detection ratio between Tph males and Iph females indicated no differences in diel movement patterns (Kruskal-Wallis, $H = 2.04$, $P = 0.153$). A total of six Tph males (Figure 6) made repeated offshore movements during daylight hours between 0800 and 1800 hrs local time, primarily in the summer months. Data from the V16P-1L coded acoustic depth transmitters indicated that this group of Tph males often traveled to 40 m water depth, with Tph Fish 8 reaching a depth of 60 m in three separate years. Offshore movement of Iph females was less frequent (Figure 7), with the notable exception of Iph Fish 9, which made frequent forays off-shore in the summer of 2005. The presence of an additional four VR2 acoustic receivers inshore of the main receiver array in 2005 (courtesy of J. Caselle, PISCO) provided insight into the movement behavior of Iph females. While offshore movements were infrequent, data from the inshore receivers indicate that Iph female presence inshore was regular throughout the period that those receivers were in the water (Figure 7).

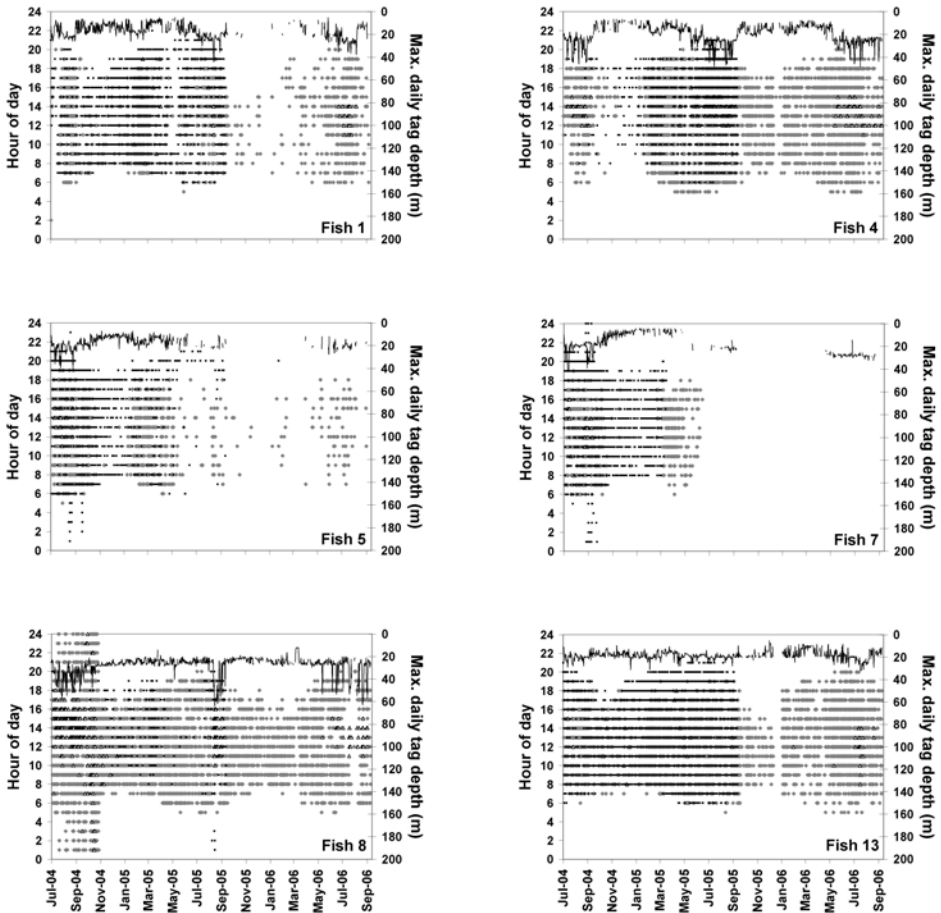


Figure 6. Recorded time-at-large for six terminal phase CA sheephead plotted in 24 hr periods. Each symbol represents a 1-hr bin in which a fish was detected, with triangles representing the outer ring of receivers, grey circles representing the inner ring of receivers, and small black circles representing the four additional receivers deployed at the east end of Anacapa Island. The mean daily water depth of each transmitter is reported in meters.

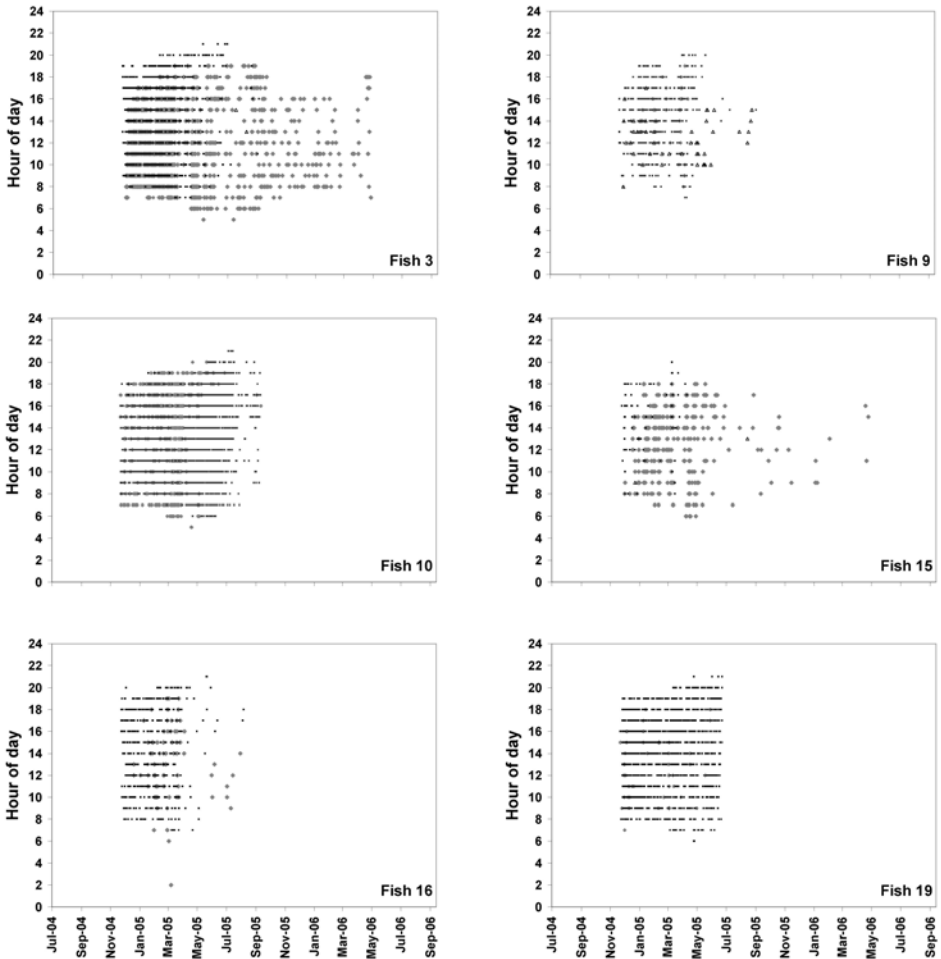


Figure 7. Recorded time at-large for six initial phase CA sheephead plotted in 24 hr periods. Each symbol represents a 1-hr bin in which a fish was detected, with triangles representing the outer ring of receivers, grey circles representing the inner ring of receivers, and small black circles representing the four additional receivers deployed at the east end of Anacapa Island.

DISCUSSION

The results of this study clearly indicated that patterns in the movement of CA sheephead at Anacapa Island were mediated by fish gender. Tph males and Iph females differed significantly with respect to several important behavioral metrics recorded by the passive acoustic receiver array. Further, these results also differed from previous telemetric research conducted at Catalina Island (approximately 102 km to the southeast of the study area) suggesting that the vagility of CA sheephead, like other life history characteristics, changes with local environmental conditions.

Schoener (1971) suggested that time spent in foraging activities should depend on the energetic calculations that organisms make with respect to their reproductive success. Hoffman (1983) identified gender-related differences in the foraging of hogfishes (*Bodianus*

spp.) where larger males spent a significantly smaller proportion of their time foraging when compared to smaller females. In the present study, the gender-mediated movements of acoustically-tagged CA sheephead were predicted to differ significantly between Tph males and Iph females, with large Tph males expected to have smaller ambits than the comparatively smaller-sized Iph females. While the prediction of significant differences in movement behavior between genders was confirmed, the nature of these differences in behavior was unanticipated. Tph males, on average, showed wider ambits than Iph females; the seasonal change in ambits was more pronounced among Tph males; and the general directionality of movement appeared to differ between genders as well.

Of particular interest were the differences in fish movement behavior recorded during spawning season (July through September). Adreani et al. (2004) observed large Tph male CA sheephead at Catalina Island occupying and defending small territories (20 m linear distance along a reef) during spawning season, while the smaller Iph females appeared to move opportunistically among these territories. In contrast to this reported behavior, in the present study at Anacapa Island the large Tph males (which would potentially defend small territories) showed a daily increase in their ambits during a period of potential spawning (Figure 4). Iph females (which would be expected to move more frequently among male territories) showed little expansion of their ambits during this same period. Further, multiple Tph males made daily peregrinations offshore into deeper water (Figure 6). This behavior was *only* observed during likely spawning periods, and was rarely accompanied by similar movements among Iph females. Indeed, data from the smaller PISCO receiver array suggested that females remained closer to shore or may have moved inshore during the same period that males were moving offshore.

We are aware of no published account of this type of behavior. Topping et al. (2005) showed strong mediation of CA sheephead movement by topographic relief on the seafloor. The spatial scale of the passive acoustic array used in the present study precluded the quantification of fine-scale fish movements relative to discrete features on seafloor. However, interpreted seafloor maps of the study area (Cochrane et al. 2005) indicate that the patchy rock reef present in the nearshore area extends offshore into the area encompassed by the outer ring of acoustic receivers. The fact of the tagged fish movement offshore, coupled with water depth data from the pressure transmitters (Figure 6), indicated that habitat-mediated fish movement was a strong possibility. Yet, the underlying causative factors driving the daily movement of a benthivorous species offshore, habitat-mediated or otherwise, remain unclear and require additional study.

It is also important to note that Tph males were recorded more frequently than Iph females throughout the study period (Figure 2, Figure 3). This was not unanticipated and may have resulted from a number of factors, prominent among them the effects of habitat on acoustic transmitter detection by the fixed acoustic receiver array. The east-end of Anacapa Island, where many of the CA sheephead were tagged in this study, was characterized by extensive kelp beds in the nearshore throughout the study period. Due to the known (but not-yet-quantified) difficulties in recording tagged fish movement within a kelp forest canopy, it is likely that the detection of Iph females, which did not move away from the internal ring of receivers as frequently as the Tph males, would be differentially impacted by kelp interference in signal detection.

It is possible that fish tagged as females transitioned to become males during the study period. The size at transition for CA sheephead has been estimated to occur at

approximately 30 cm SL (Warner 1975b, Cowen 1990), which is smaller than the majority of the Iph females tagged in this study (mean TL = 31.3 cm). However, Cowen (1990) reported significant individual and population level variation in age at transition due to both environmental and demographic factors. Had transition occurred for a tagged fish, it is possible that a demonstrable change in behavior would have been recorded. Though we cannot definitively rule out transition, we did not observe any change in the behavior of the tagged females over the course of the study that would suggest transition occurred.

More broadly, four potential scenarios for the apparent divergence in patterns of CA sheephead behavior during spawning periods from other published accounts merit consideration. First, Tph male CA sheephead may not establish spawning territories at Anacapa Island. Direct observations of CA sheephead mating behavior have been limited to a single study conducted at Catalina Island (Adreani et al. 2004). Additional research across multiple sites will be necessary to determine whether the patterns observed at Catalina Island are typical for the species. Second, spawning territories, if established, may either have expanded during spawning periods, or may have been transient during daily spawning events and may not be occupied throughout the diel period. Each of the movements offshore by Tph males was followed by a return to nearshore habitat prior to twilight, suggesting the occupation of a spawning territory at that time. Third, CA sheephead may not have spawned at Anacapa Island during the study period. Recruitment to Anacapa Island from the south is sporadic, depending on oceanographic conditions, and spawning by CA sheephead at Anacapa Island has yet to be observed. It is not possible to quantify the likelihood of any particular scenario from these passive acoustic telemetry data.

CA sheephead exhibit a wide spectrum of life history characteristics across the geographic range of the species (Cowen 1986, 1990; Hamilton et al. 2007). Other aspects of CA sheephead movement behavior recorded at Anacapa Island were consistent with previous published accounts from Catalina Island (see Topping et al. 2005, 2006). As expected, both Tph males and Iph females showed strong diurnal behavior (Figs. 6 and 7) consistent with the behavior of other Labrid species (Arendt et al. 2001a, 2001b; Lindholm et al. 2006). Also as expected, the ambits of CA sheephead were correlated with local water temperature (Figure 4, Figure 5) and consequently showed predictable changes in movement patterns across seasons. These similarities in behavior between distant locations were not surprising. Even where vagility was expected to vary in response to local environmental conditions, that variation would not be expected to fundamentally change how fish respond to variation in light levels and water temperature.

Ultimately, the objective of this research is to better understand the movement behavior of CA sheephead such that the conservation and management of the species can be optimized. CA sheephead is exploited both recreationally and commercially throughout its range (Stephens 2001). Hamilton et al. (2007) showed that differential fishing pressure on CA sheephead produced variation in key life history parameters, such as growth, timing of maturation and sex change, and the sex ratio of local populations. In the context of fishing-induced alteration of these and other life history parameters, an understanding of gender-specific movement behavior will be critical for successful conservation and management, particularly where spatial management regimes such as marine reserves are planned or in place. Future research will seek to quantify the movements of CA sheephead relative to the boundaries of Anacapa Island State Marine Reserve.

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LITERATURE CITED

- Adreani, M. S., B. E. Erisman, and R. R. Warner. 2004. Courtship and spawning behavior in the California sheephead, *Semicossyphus pulcher* (Pisces: Labridae). *Environmental Biology of Fishes* 71:13-19.
- Arendt, M. D., J. A. Lucy, and D. A. Evans. 2001a. Diel and seasonal activity patterns of adult tautog, *Tautoga onitis*, in lower Chesapeake Bay, inferred from ultrasonic telemetry. *Environmental Biology of Fishes* 62:379-391.
- Arendt, M. D., J. A. Lucy, and T. A. Munroe. 2001b. Seasonal occurrence and site-utilization patterns of adult tautog, *Tautoga onitis* (Labridae), at manmade and natural structures in lower Chesapeake Bay. *Fisheries Bulletin* 99:519-527.
- Bradbury, C., J. M. Green, and M. Bruce-Lockhart. 1995. Home ranges of female cunner, *Tautoglabrus adspersus* (Labridae), as determined by acoustic telemetry. *Canadian Journal of Zoology* 73:1268-1279.
- Cochrane, G. R., J. E. Conrad, J. A. Reid, S. Fangman, and N. Golden. 2005. The nearshore benthic habitat GIS for the Channel Islands National Marine Sanctuary and southern California state fisheries reserves, Vol. II, Version 1.0. U.S. Geological Survey, Open-File Report 2005-1170.
- Cowen, R. K. 1986. Site-specific differences in the feeding ecology of the California sheephead, *Semicossyphus pulcher* (Labridae). *Environmental Biology of Fishes* 16:192-203.
- Cowen, R. K. 1990. Sex change and life history patterns of the Labrid, *Semicossyphus pulcher*, across an environmental gradient. *Copeia* 3:787-795.
- Cowen, R. K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. *Marine Ecology Progress Series* 69:9-15.
- Dill L. M., M. R. Heithaus, and C. J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* 84:1151-1157.
- Domeier, M. L. 2005. Methods for the deployment and maintenance of an acoustic tag tracking array: an example from California's Channel Islands. *Marine Technology Society Journal* 39:74-80.

- Hamilton, S. L., J. E. Caselle, J. D. Standish, D. M. Schroeder, M. S. Love, J. A. Rosales-Casian, and O. Sosa-Nichizaki. 2007. Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecological Applications* 17:2268-2280.
- Harden, D. R. 1997. California geology. Prentice Hall, Inc., Upper Saddle River, New Jersey, USA
- Heupel, M. R., J. M. Semmens, and A. J. Hobday. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research* 57:1-13.
- Hoffman, S. G. 1983. Sex-related foraging behavior in sequentially hermaphroditic hogfishes (*Bodianus* spp.). *Ecology* 64:798-808.
- Johnson, T. D., A. M. Barnett, E. E. DeMartini, L. L. Craft, R. F. Ambrose, and L. J. Purcell. 1994. Fish production and habitat utilization on a southern California artificial reef. *Bulletin of Marine Science* 55:709-723.
- Jones, G. P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. Pages 294-328 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California, USA.
- Lindholm, J. 2005. Acoustic tracking of marine fishes and the design of marine protected areas. *Marine Technology Society Journal* 39:7-9.
- Lindholm, J., A. Knight, L. Kaufman, and S. Miller. 2006. A pilot study of hogfish (*Lachnolaimus maximus* Walbaum 1792) movement at the Conch Reef Research Only Area (northern Florida Keys). National Marine Sanctuary Program NMSP-06-06. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, Maryland.
- Love, M. S. 1996. Probably more than you want to know about the fishes of the Pacific coast. Really Big Press, Santa Barbara, California, USA.
- Lowe, C. G., and R. N. Bray. 2006. Movement and activity patterns. Pages 524-533 in L. G. Allen, D. J. Pondella, and M. H. Horn, editors. *The ecology of marine fishes: California and adjacent waters*. University of California Press, Berkeley.
- Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. California Department of Fish Game, Fisheries Bulletin 157.
- Ross, R. M., G. S. Losey, and M. Diamond. 1983. Sex change in a coral-reef fish: dependence of stimulation and inhibition on relative size. *Science* 221:574-575.
- Sadovy de Mitcheson, Y., and M. Liu. 2008. Functional hermaphroditism in teleosts. *Fish and Fisheries* 9:1-43.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology Systematics* 11:369-404.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. W. H. Freeman and Company, New York, New York.
- Stephens, J. 2001. California sheephead. Pages 149-156 in W. S. Leet, C. M. Dewees, R. Klingbeil, and E. Larson (editors). *California's living marine resources: a status report*. California Department of Fish and Game, Sacramento.
- Topping, D. T., C. G. Lowe, and J. E. Caselle. 2005. Home range and habitat utilization of adult California sheephead, *Semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve. *Marine Biology* 147:301-311.
- Topping, D. T., C. G. Lowe, and J. E. Caselle. 2006. Site fidelity and seasonal movement patterns of adult California sheephead *Semicossyphus pulcher* (Labridae): an acoustic monitoring study. *Marine Ecology Progress Series* 326:257-267.

- Warner, R. R. 1975a. The adaptive significance of sequential hermaphroditism in animals. *American Naturalist* 109:61-84.
- Warner, R. R. 1975b. The reproductive biology of the protogynous hermaphrodite *Pimelometopon pulchrum* (Pisces: Labridae). *Fisheries Bulletin* 73:262-283.

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