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RESEARCH ARTICLE

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Home range and habitat utilization of adult California sheephead, *Semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve

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Abstract The California sheephead, *Semicossyphus pulcher* Ayres (Labridae), is a carnivorous, temperate, rocky-reef/kelp-bed species that is highly sought in recreational and commercial fisheries. Fine-scale acoustic telemetry tracking was used to ascertain the home range and habitat utilization of *S. pulcher*. Sixteen adult *S. pulcher* (26–38 cm SL) were surgically fitted with small acoustic transmitters and manually tracked for up to 144 h during multiple, 24-h periods between March 2001 and August 2002 within the Catalina Marine Science Center Marine Life Reserve (33°26′N; 118°29′W). A geographic information system was used to calculate home range sizes (95% kernel utilization distributions) and habitat use. Tracking of the first five fish over 24 h confirmed that *S. pulcher* were strictly diurnal, so the remaining 11 fish were tracked from 1 h before sunrise to 1 h after sunset. Home ranges varied greatly, from 938 to 82,070 m^2, with a mean (±SD) of 15,134±26,007 m^2. Variability in home range sizes among fish was attributed to differences in habitat shape (embayment vs. contiguous coastline) and to natural habitat boundaries (deep, sandy expanses) in adjacent areas within the reserve. There was a significant relationship between fish length and proportion of time spent in different habitats (sand vs. reef). *S. pulcher* were found within rocky-reef areas 54% of the time, and, within these areas, a greater percentage of daytime was spent in high-relief areas. Based on the relatively small size and persistence of home ranges of adult *S. pulcher*, no-take reserves, if they contain appropriate habitat, would provide adequate protection for their stocks.

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Introduction

The number of studies on the effectiveness of marine reserves for protecting fish stocks has recently increased (Roberts 1994; Johnson et al. 1999; McClanahan and Mangi 2000; Meyer et al. 2001; Roberts et al. 2001), but critical information on movement patterns, space use, and habitat preference of fished species is still lacking (Gerber et al. 2003). New marine reserves are being developed in the absence of this critical information, but knowledge of the relationship between habitat use and movements of fished species can be used to quantify the effectiveness of established reserves and serve as a basis for development of future reserves (Kramer and Chapman 1999; Eristhee and Oxenford 2001; Lowe et al. 2003).

Movement patterns vary widely among fish species, but marine reserves would be predictably most effective for species that use a home range, an area consistently occupied for feeding, reproduction, and shelter seeking (Barrows 1996). Most coral- and rocky-reef-associated fishes are thought to have defined home ranges, although the size and fidelity may vary ontogenetically and seasonally and with habitat availability (Matthews 1990; Kramer and Chapman 1999; Lowe et al. 2003). How much home ranges vary within reef-associated species and how nearshore microhabitats influence size and fidelity of home ranges remain uncertain for many species.

The California sheephead *Semicossyphus pulcher* (Labridae) is a carnivorous, temperate, rocky-reef/kelp-bed fish, which is highly sought in recreational and commercial fisheries in California and Mexico. Current regulations are based primarily on minimum size restrictions (> 25 cm SL) (CA DFG regulations, 2004). Dietary studies indicate that *S. pulcher* feeds on a wide variety of macroinvertebrates (e.g. mollusks, echinoids, brachyurans, polychaetes, and bryozoans) while foraging over rock and sand habitats (Cowen 1986; Hobson and Chess 1986, 2001; Johnson et al. 1994). *S. pulcher* are considered essential in regulating urchin populations, which forage on kelp, and therefore have an indirect effect on kelp density and distribution (Cowen 1983, 1986; Dayton et al. 1998). In situ diver observations indicate that *S. pulcher* is diurnally active, returning to a home shelter at night (Wiley 1974; Ebeling and Bray 1976; Hobson et al. 1981). A previous tag and recapture study of *S. pulcher* at an artificial reef suggests that these fish exhibit strong fidelity to the reef (Johnson et al. 1994). Nevertheless, diver observations and tag and recapture methods may be insufficient for resolving fine-scale movement patterns and habitat use of fishes.

Because *S. pulcher* is a protogynous hermaphrodite, environmental and social factors can affect the size at sex change and population sex ratio (Warner 1975; Cowen 1990), thereby making it difficult to predict the extent to which traditional management strategies (i.e. size and bag limits) protect stocks. The species' economic value, complex life history, and ecological importance make it a candidate for management using a reserve system. Furthermore, study of this species may provide critical insight into the influence of habitat on movement patterns of reef-associated species.

In this study, we used short-term (multiple, 24-h periods), high-resolution tracking via acoustic telemetry to determine the home range size and habitat use of adult, legal-sized (> 25 cm SL) *S. pulcher* in the Catalina Marine Science Center Marine Life Reserve at Santa Catalina Island. A geographic information system (ArcView GIS) was used to overlay movement data over high-resolution benthic habitat maps, which enabled us to better understand the effect of habitat on the movement patterns of *S. pulcher*. Data acquired in this study were used to determine the effectiveness of the reserve in protecting the areas and habitats necessary for the foraging, spawning, and refuge-seeking behaviors of adult *S. pulcher*.

Materials and methods

Study site

The study was conducted at Catalina Marine Science Center Marine Life Reserve, Santa Catalina Island, California (33°26′N; 118°29′W) (Fig. 1), a no-take reserve designated in 1988 encompassing 130,000 m^2 (Senate Bill 2131, 1988). This reserve is on the wave-protected leeward side of the island, and includes kelp beds, rocky reefs, and mud/sand habitats. There are also anthropogenic habitats, such as a boulder riprap, a pier, a floating dock, and mooring blocks. The reserve has two distinct areas: a large, sandy cove (250 m×300 m) and a long, narrow stretch of rocky reef (600 m) bordering the coastline. The Cove is bordered on two sides by steep rocky reefs and a rock rubble beach opposite its mouth. Depths in the Cove range from 0 to 40 m. The

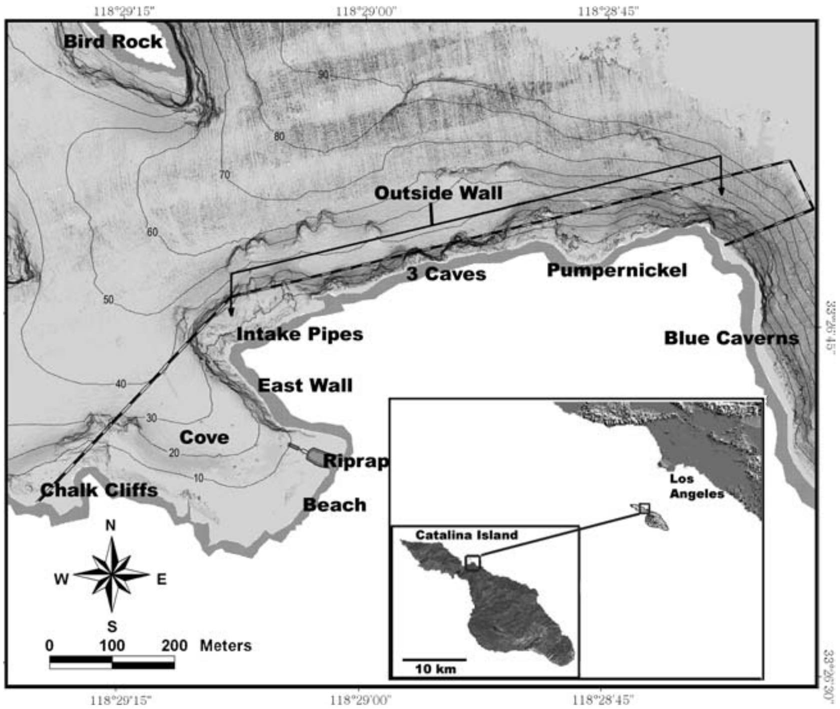


Fig. 1 Shaded relief map of Catalina Marine Science Center Marine Life Reserve at Santa Catalina Island, California, showing bottom topography. Reserve boundary represented by *black dashed line*. *Dotted bathymetry lines* represent 10-m depth increments. Pier/dock complex extends out from boulder riprap area

narrow, contiguous reef (Outside Wall), directly east of the Cove, is made up of steeply sloping rock walls and rocky rubble. This reef extends 50–80 m from the land, sloping quickly to a depth of 50 m, where it meets a sand/mud habitat. The reserve boundary passes just outside the mouth of the Cove and closely borders (within ~50 m) the length of the Outside Wall (Fig. 1).

Tracking

Sixteen *Semicossyphus pulcher* Ayres were caught by hook and line at various locations within the reserve. Fish were anesthetized to level 4 (total loss of equilibrium) with MS-222 (Finquel 0.15 g l^{-1}) (Summerfelt and Smith 1990). A 1-cm incision was made 1 cm from the ventral midline between the pelvic fins and the anus, and a small acoustic transmitter (Vemco V8SC-6L and -1L, 22 mm×8 mm diam. or 26 mm×8 mm diam., respectively) was placed within the visceral cavity. The incision was closed with two to three surgical sutures (Ethicon Chromic Gut 2–0), and the fish were transferred to a tub of seawater for recovery. The time from capture to release was 6–15 min. During recovery, the standard length (SL) of each fish was measured and the fish was tagged externally in the dorsal musculature with a plastic dart tag for visual identification. The sex of each fish was determined visually by its color pattern (Warner 1975).

Each fish was released at the site of capture and followed continuously from a 5-m Boston Whaler equipped with a side-mounted directional hydrophone (Vemco model V10) and an acoustic receiver (Vemco model VR-60), as described by Holland et al. (1993). Each fish's position was determined at 15-min intervals using GPS (Garmin-48). Fish were tracked over multiple (2–6) 24-h periods (24 h after initial position fix) for up to 5 months after tagging. Initially, fish were tracked during both day and night periods ($n=5$ fish/3 tracks each); however, these tracks and diver observations confirmed the quiescent state of *S. pulcher* at night, as observed previously in diver surveys (Wiley 1974; Ebeling and Bray 1976; Hobson et al. 1981). The remaining 11 fish were tracked during periods from 1 h before sunrise to 1 h after sunset, but the nighttime location of each fish was periodically checked throughout its tracking period.

Data analysis

Position fixes derived via fine-scale tracking were plotted on a geo-referenced map of the reserve (supplied by California State University Monterey Bay Seafloor Mapping Lab) in ArcView GIS. We estimated home ranges using ArcView GIS (ver. 3.2) with the "Animal Movements Analyst Extension" (AMAE; Hooge et al. 1999, 2001). To describe each fish's home range, we calculated a 95% kernel utilization distribution (KUD), an area that a fish has a 95% probability of being found within during a given time (total duration of track) (Worton 1989; White and Garrott 1990; Seaman and Powell 1996). When using the AMAE to calculate the KUD, the ad hoc value was used for the smoothing function. The KUD crossed over land in some locations, and this area was subtracted from the total area. Home range sizes of males and females were compared using a *t*-test, and linear regression was used to examine relationships between fish size and movement patterns (i.e. home range size and distance traveled per day). Total distance traveled per day was calculated by taking the mean of the cumulative distances between each successive position fix determined for each day a fish was tracked, which was normalized by the total number of position fixes. A minimum convex polygon was drawn around the outermost position fixes for each fish to determine the aspect ratio of a fish's home range (Eristhree and Oxenford 2001). To calculate the aspect ratio of a home range, the maximum distance across the polygon (max. length) and the maximum distance perpendicular to max. length (max. width) were determined, and then the max. width was divided by the max. length. The aspect ratio was used to describe the shape of the home range polygon, with a number closer to 1 representing a circular home range and closer to 0 describing an elongated home range.

Home range sizes were examined in relation to the reserve size as a percentage of the total reserve area (130,000 m^2). In addition, the percentage of time that each fish spent outside the reserve boundary was calculated using only daytime position fixes due to *S. pulcher* being quiescent at night.

The geological habitat map was derived from multibeam side-scan sonar data of the reserve (H.G. Greene and R. Kvitek, personal communication) and adjacent areas (2-m grid resolution) and plotted in ArcView GIS. For biological habitat, the location of giant kelp (*Macrocystis pyrifera*) in the reserve was determined by taking GPS positions of kelp canopy, including the fronds that reached the surface, to create a geo-referenced kelp coverage map. We overlaid position fixes over kelp cover to examine the association of *S. pulcher* with kelp. To simplify this analysis we separated kelp (biotic habitat) from geological habitat, due to the ubiquitous coverage of kelp over each category of rocky substratum to depths of 25 m. Kelp cover was only determined once (May 2001) due to the difficulty of taking the measurements each time a fish was tracked. A habitat selection index (HSI) was used to determine each fish's preference or avoidance of the habitat (geological and biological) available within its home range. This index is calculated by dividing habitat utilization (percent of position fixes over a given habitat) by habitat availability (percent of each habitat type available in the reserve). Thus, relative preference or avoidance is shown by the degree of deviation in a positive or negative direction from a value of 1 (Winter and Ross 1982). Habitat availability was calculated by measuring the proportional area of each habitat within the total area of a minimum convex polygon encompassing 100% of the position fixes for that fish.

Results

Sixteen adult *Semicossyphus pulcher* (26–38 cm SL) were each tracked for up to 144 h (range: 51–144 h) over multiple days between March 2001 and September 2002. Nine of the 16 fish tracked possessed male coloration and ranged from 26.5 to 38 cm SL, while females ranged in size from 26.5 to 36.5 cm SL. Males and females were not significantly different in length ($t = 1.75$, $P = 0.11$).

Home range size

Home range sizes of fish varied greatly, ranging from 938 to 82,070 m^2, with a mean (± SD) of 15,134 ± 26,007 m^2 (Table 1; Fig. 2a–c). Mean home range sizes were not significantly different between males (14,111 ± 24,849 m^2) and females (16,448 ± 29,395 m^2) ($t = 0.17$, $P = 0.86$). All fish tracked showed overlap in daily activity spaces of each successive 24-h period, but there was some variability in daily activity space size (Table 2). The overall maximum linear distance each fish moved varied from 61 to 848 m, with a mean of 205 ± 191 m. Total distances traveled per day ranged from 554 to 3,320 m, with a mean of 1,357 ± 952 m day^{-1} (Table 1).

There was no significant relationship between home range size and fish SL ($F = 2.27$, $R^2 = 0.22$, $P = 0.17$), but there was a significant positive relationship between mean distance traveled per day and SL ($F = 5.60$, $R^2 = 0.29$, $P = 0.03$) (Fig. 3). Fish within the Cove had significantly smaller home ranges than fish tracked along the Outside Wall, just east of the Cove (Mann–Whitney *U*-test: $U = 66$, $P = 0.02$). Home ranges within the Cove area tended to be elliptical in shape (mean aspect ratio: 0.57 ± 0.05), while home ranges along the Outside Wall were significantly more elongate (mean aspect ratio: 0.21 ± 0.02) (Mann–Whitney *U*-test: $U = 111$, $P = 0.003$).

All six of the *S. pulcher* tracked along the Outside Wall crossed the reserve boundary, with between 2% and 98% of the position fixes of these fish lying outside the reserve. Fish no. 13 had a home range in an area where the marine reserve boundary was located just 50 m from land; and, while it used the rocky area within the reserve at night, its daytime use of the nearby sand habitat was primarily outside the boundary (98%). Only three fish (nos. 12, 14, and 15) of the ten caught and tracked within the Cove crossed the boundary, and < 1% of their total position fixes were outside the boundary. Individual home ranges occupied on average 11.6 ± 20.0% (mean ± SD) of the total reserve area (130,000 m^2), with a range of 0.7–63.1% (Outside Wall fish: 1–63% and the Cove fish: 0.7–5%) (Table 1). Although several, *S. pulcher* spent considerable time outside the reserve, none of the fish ever entirely left the reserve to establish a home range in another area over successive tracks. The fish consistently revisited the same locations during each successive track, indicating strong site attachment.

Diel activity patterns

Tracking data confirmed that all *S. pulcher* were strictly diurnal. The fish tracked continuously throughout the night did not move more than a meter at any time, and none of the fish ($n = 43$) tracks that were discontinued an hour after sunset were ever found in a different location when reacquired the subsequent morning prior to sunrise. Fish left their rest area just after first light (nautical twilight) and moved 30–800 m away to a foraging area

Table 1 *Semicossyphus pulcher*. Sheephead tracked at Catalina Marine Science Center Marine Life Refuge, Santa Catalina Island, California. Home ranges determined using 95% kernel utilization distribution. Distance traveled per day is the summation of distances between position fixes in each successive 24-h period. Locations caught were Big Fisherman's Cove (*C*) or along the Outside Wall (*OW*). *Percent of reserve area* represents home range as a percentage of the total reserve area (130,000 m^2).*Aspect ratio* is the max. width/max. length of minimum convex polygon home range (*SL* standard length;*M* male; *F* female; *C* Cove;*OW* Outside Wall)

Fish no.	Sex	SL (cm)	Dates tracked	Home range (m^2)	Distance traveled day^{-1} (m)	Location caught	Percent of reserve area	Aspect ratio
1	M	34.0	Mar–Jun 2001	3,521	1,096	C	3	0.29
2	M	33.5	Jun–Jul 2001	1,130	757	C	1	0.25
3	F	26.5	Jun–Jul 2001	2,013	728	C	2	0.68
4	F	28.5	Jun–Nov 2001	6,580	1,049	C	5	0.53
5	M	29.6	Jun–Oct 2001	6,690	1,195	C	5	0.47
6	F	26.5	Jul–Sep 2001	16,356	1,618	OW	13	0.18
7	F	36.5	Aug–Sep 2001	82,070	3,162	OW	63	0.11
8	M	31.0	Sep–Oct 2001	2,634	1,161	OW	2	0.23
9	M	26.5	Oct–Nov 2001	1,803	718	C	1	0.57
10	M	31.0	Nov–Dec 2001	75,247	3,121	OW	58	0.08
11	M	33.0	Feb–Mar 2002	3,620	850	C	3	0.75
12	M	34.0	Mar 2002	938	554	C	1	0.76
13	F	28.0	Apr–May 2002	1,930	667	OW	1	0.49
14	F	31.0	Jun–Jul 2002	4,676	1,003	C	4	0.43
15	F	28.0	Jul 2002	1,515	719	C	1	0.95
16	M	38.0	Aug 2002	31,424	3,320	OW	24	0.17

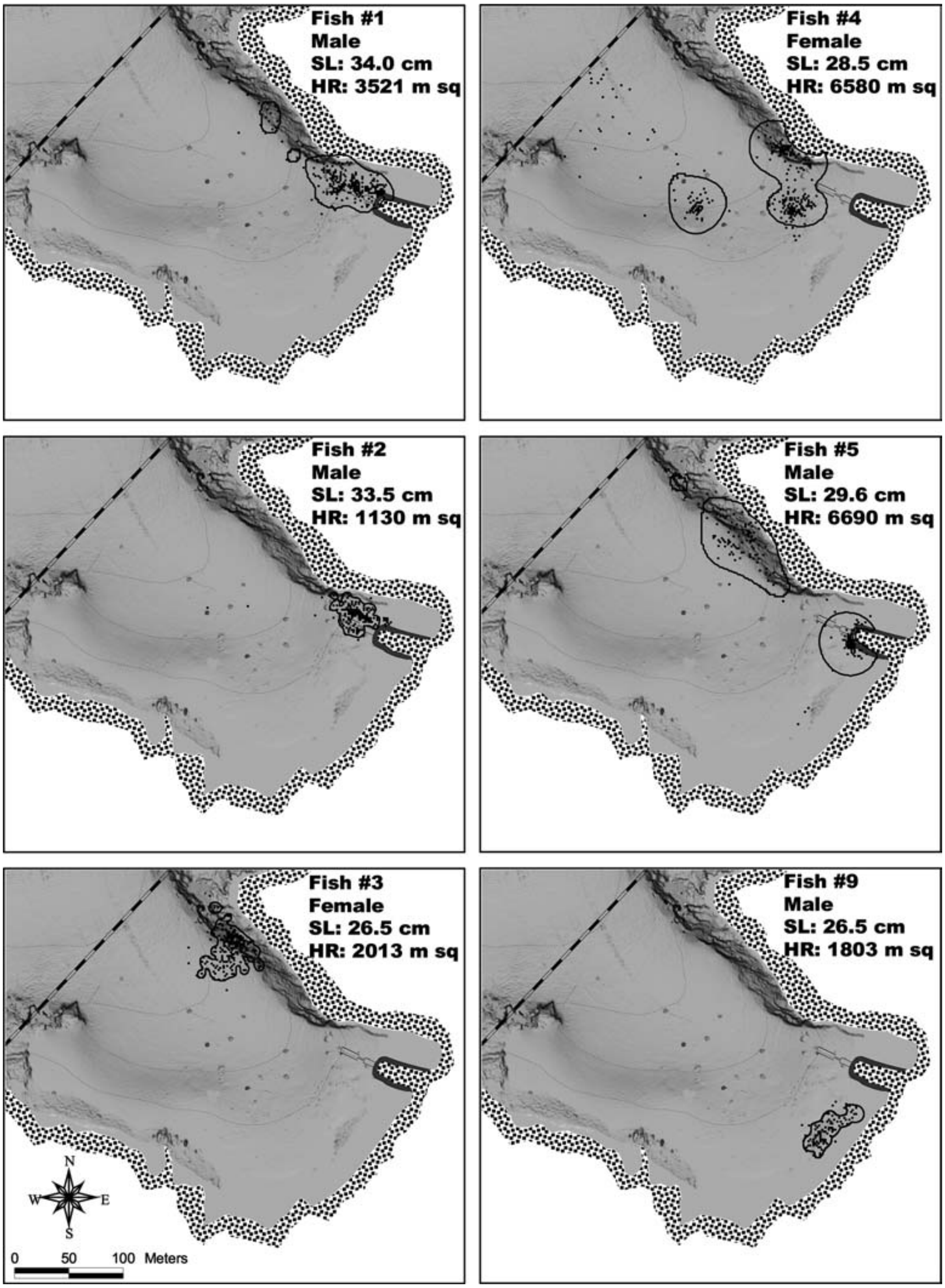


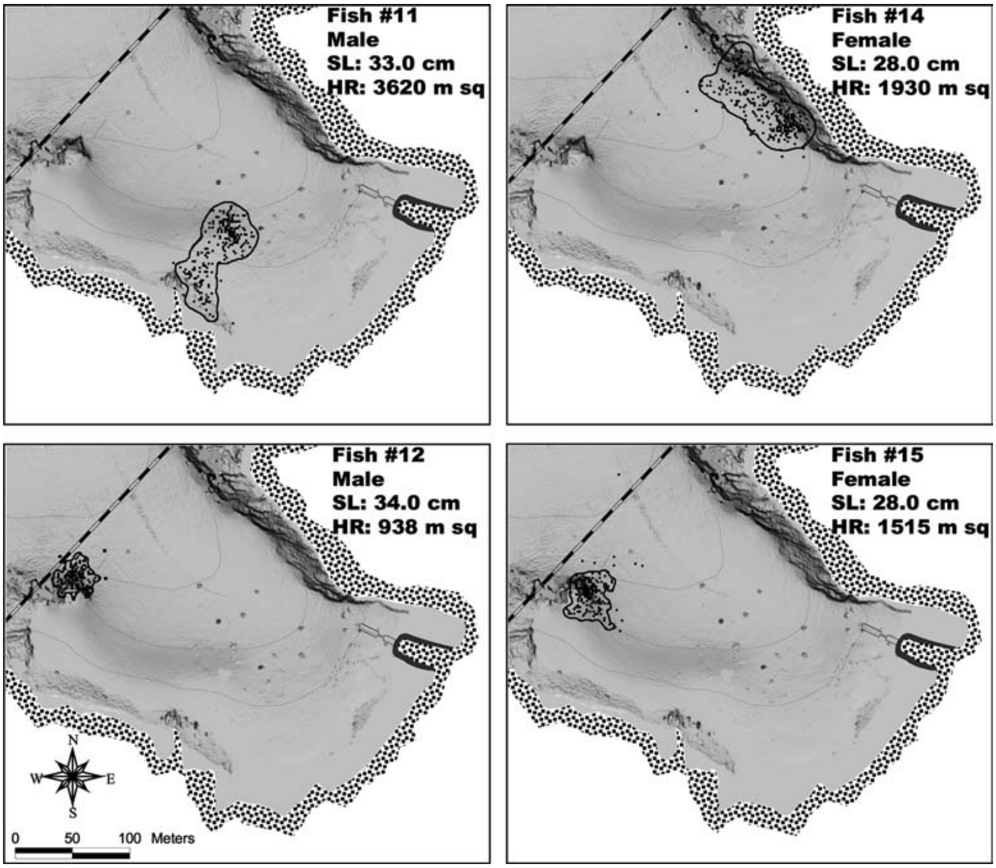
Fig. 2a–c *Semicossyphus pulcher*. Shaded relief maps of the reserve showing bottom topography with overlying position fixes and 95% kernel utilization distribution home range estimates for: **a** fish nos. 1, 2, 3, 4, 5, and 9; **b** fish nos. 11, 12, 14, and 15; and **c** fish nos. 6, 7, 8, 10, 13, and 16. Sex, standard length (*SL*, cm), and home range size (*HR*, m^2) given for each fish. Home ranges defined by several polygons represent shifts between nighttime and daytime locations

before returning to the same rocky rest area (within 2 m) each night just after sunset. One fish (no. 4) used a different nighttime location on one of the six nights it was tracked, but all other fish returned to within a few meters of their previous nighttime refuge, indicating high site fidelity to night refuges.

Habitat use

The categories of geological habitat type as determined by multibeam side-scan sonar were generally described as rocky wall (> 15° slope solid bedrock), steep rocky rubble (> 12° slope, loose rocks over bedrock), boulders (rocks > 1 m diam.), rocky rubble (< 12° slope, loose rocks over bedrock), and mud/sand (Electronic Supplementary Material S1). Biological habitat was described as areas of kelp (*Macrocystis pyrifera*) cover (Electronic Supplementary Material S1). During daylight, *S. pulcher* exhibited the highest mean percent use of mud/sand (46 ± 32%) followed by rock wall (22 ± 17%), steep rocky rubble (17 ± 24%), boulder (7 ± 12%), and rocky rubble (8 ± 20%) (Fig. 4). Mean percent use of kelp (*M. pyrifera*) by *S. pulcher* during

Fig. 2a–c (Contd.)



daylight hours was 47 ± 31% (Fig. 4). Mean percent utilization of the four rocky reef types combined, was 54 ± 32%. The degree of habitat preference or avoidance was calculated as the HSI for each fish for each habitat. *S. pulcher* exhibited the greatest HSI for boulders (4.56 ± 7.73) followed by rock wall (3.15 ± 2.74), steep rocky rubble (0.74 ± 0.41), mud/sand (0.71 ± 0.50), and rocky rubble (0.66 ± 0.86) (Fig. 4). *S. pulcher* exhibited selection for kelp areas with an HSI of 1.65 ± 1.44 (Fig. 4). There was a significant positive relationship between the percent use of mud/sand habitat and fish size (SL) inside the Cove, with the larger fish having a greater percentage of position fixes over mud/sand ($R^2 = 0.41$, $F = 5.6$, $P = 0.04$); however, there was an inverse relationship for fish in the Outside Wall area, with larger fish utilizing rocky reef areas at a higher percentage than sand areas ($R^2 = 0.62$, $F = 6.5$, $P = 0.06$) (Fig. 5). *S. pulcher* used only rocky areas during nighttime resting periods, regardless of sex, size, or home range location. Of the *S. pulcher* tracked, 38% used rock wall at night, followed by steep rocky rubble (31%), boulders (19%), and rock rubble (13%). Of the 16 fish tracked, only one fish (no. 4) changed its night rest area during a tracking period, moving from rock rubble to rock wall habitat over two successive tracks, but returning to its original rest area on the fourth night.

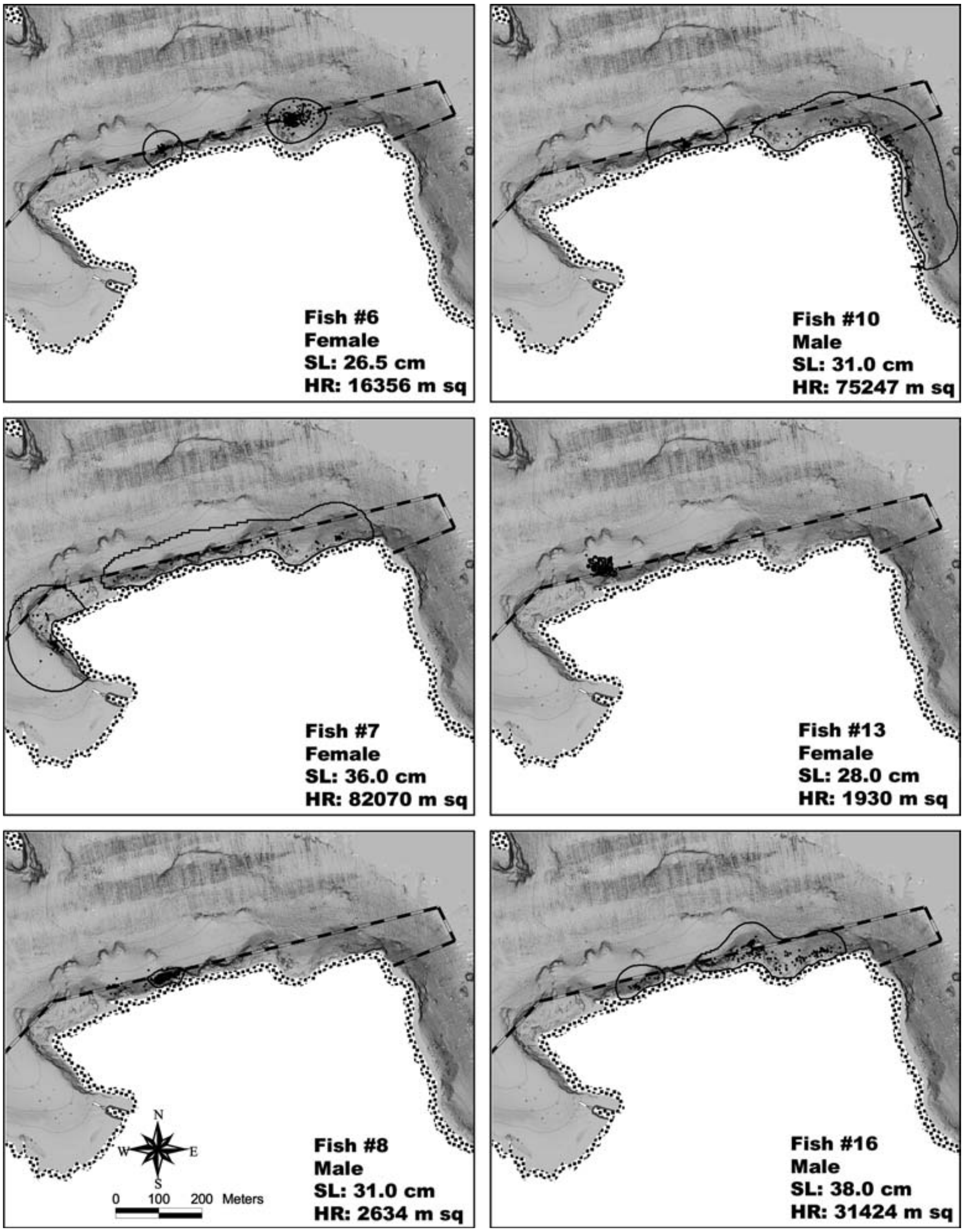
Discussion

This study examined fine-scale movement patterns of legal-sized adult *Semicossyphus pulcher* for the first time. In addition, the combination of fine-scale acoustic tracking with the use of high-resolution habitat maps provided a powerful tool to ascertain the effects that different habitat types may have on the size and shapes of fishes' home ranges. All fish tracked were representative of the adult size classes found within the Catalina Island population (Warner 1975).

Home ranges of adult *S. pulcher* varied considerably among individuals (938–82,070 m^2). Intraspecific variability in movement patterns of fishes have been explained by numerous factors, including body size (Fitch and Shapiro 1990; Morrissey and Gruber 1993; Kramer and Chapman 1999), sex of fish (Hoffman 1983; Shpigel and Fishelson 1991; Bradbury et al. 1995), reef shape (Barrett 1995; Zeller 1997; Eristhee and Oxenford 2001), and habitat availability (Matthews 1990).

Although there was not a positive relationship between home range size and body size (SL) for *S. pulcher* in this study, the distance traveled per day (rate of movement) was positively related to body size. In mammalian systems, the relationship between home range size and body size is well documented and varies

Fig. 2a–c (Contd.)



with trophic position (i.e. herbivore/carnivore) (Harestad and Bunnell 1979). Several studies on fish have found that body size influences home range and rate of movement (Morrissey and Gruber 1993; Kramer and Chapman 1999) and that resource demand increases with body size (Brett 1965). In *S. pulcher*, because there was a positive relationship between fish size and rate of movement and not with home range size, rate of movement may be a better indicator of resource demand than home range size.

Male and female *S. pulcher* had overlapping home ranges, and there was no difference in home range size between the sexes. Typically, differences in home range size between sexes for labrid species are due to their mating system and territoriality (Hoffman 1983; Martel and Green 1987; Bradbury et al. 1995). *S. pulcher* are not typically considered territorial; however, a study by Adreani et al. (2004) found that male *S. pulcher* were increasingly territorial throughout the day during periods of spawning activity. Spawning activity occurs around sunset, so it may be that they only have differences in space utilization for short periods (late afternoon) on various days during the spawning season (June–September). Because we only tracked fish of lengths above the recreational and commercial size limits (>25 cm SL), this limited our study to the upper size classes of mature females at Catalina Island (Warner 1975). Therefore, it is possible that the lack of

Table 2 *Semicossyphus pulcher*. Daily activity spaces for 16 sheephead. Each daily activity space represents the 95% kernel utilization distribution (*KUD*) calculated for each 24-h period (daylight), indicated as days 1–6

Fish no.	Day 1 (m^2)	Day 2 (m^2)	Day 3 (m^2)	Day 4 (m^2)	Day 5 (m^2)	Day 6 (m^2)	Mean daily KUD (m^2)	Standard deviation (m^2)
1	10,913	1,844	1,673	1,286			3,929	4,662
2	1,298	1,105	820				1,074	240
3	801	498	3,536	1,393			1,557	1,371
4	4,334	1,519	16,672	7,066	1,875	1,182	5,441	5,937
5	9,906	5,754	7,454	10,726	2,436		7,255	3,339
6	20,367	7,739	18,722	23,461	19,432	16,771	17,749	5,374
7	76,842	126,938					101,890	35,423
8	6,326	3,046	1,790				3,721	2,342
9	1,860	1,479					1,670	269
10	74,840	62,088	93,780				76,903	15,946
11	1,611	3,992	3,321	4,497			3,355	1,259
12	769	505	1,060				778	278
13	914	1,874	2,201				1,663	669
14	3,235	3,231	5,053	3,350	4,898		3,953	936
15	1,273	674	2,128				1,358	731
16	38,434	35,060	29,081				34,192	4,737

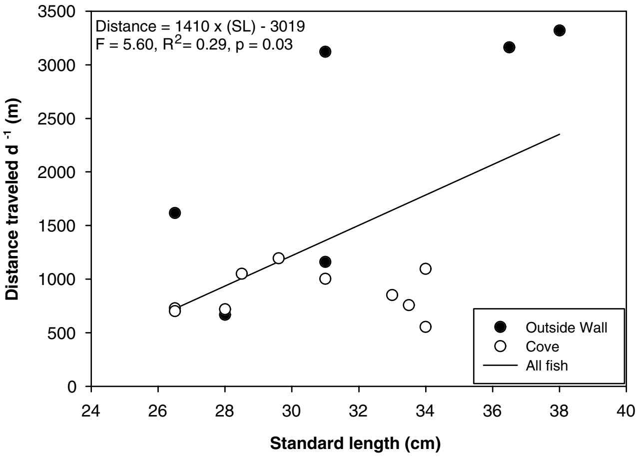


Fig. 3 *Semicossyphus pulcher*. The relationship between standard length (*SL*) of sheephead tracked and the total distance traveled day. Points categorized by area where the fish were tracked

a difference in home range size between males and females is simply due to not having smaller females in the sample. Regardless of any spawning-related movements, no difference was detected in home range sizes of males and females during the spawning period.

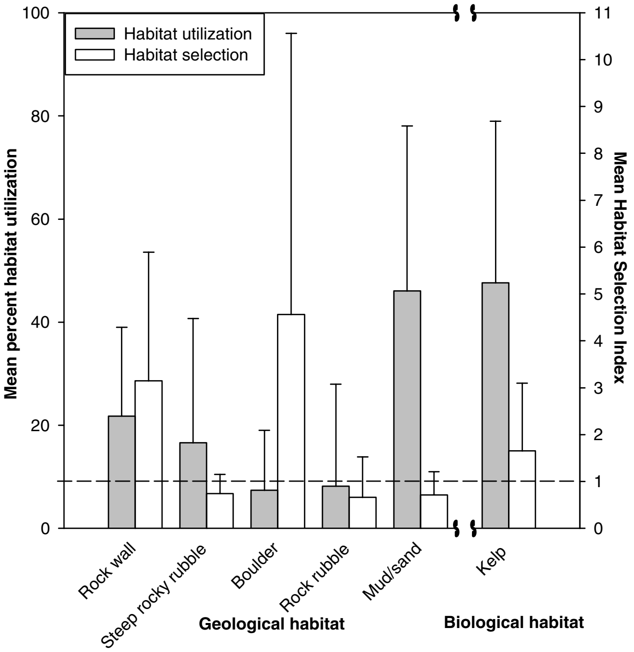


Fig. 4 *Semicossyphus pulcher*. Mean percent utilization (+SD) of geological (rock wall, steep rocky rubble, boulders, rock rubble, and mud/sand) and biological (*Macrocystis pyrifera*) habitat types by the 16 sheephead and mean habitat selection index (HSI, +SD) for each habitat type, calculated as percent of habitat used/percent of habitat available. *Dashed line* represents HSI = 1, the value when percent habitat used equals percent habitat available

Habitat shape (embayment vs. narrow, contiguous rocky coastline) and habitat type (sand/mud vs. rocky reef) appeared to have the greatest influence on the size and shape of home ranges of *S. pulcher* in this study. Fish tracked along the Outside Wall followed the reef contours and had larger home ranges with lower aspect ratios than fish within the Cove. Thus, the size and shape of the Cove may have reduced the size and affected the shape of those home ranges. Eristhee and Oxenford (2001) found that home range shape of *Kyphosus sectatrix* (Kyphosidae) was more elongated (low aspect ratio) on a narrow fringing reef with a steep depth gradient, when compared to home ranges in a nearby area with a wide patch-type reef. Zeller (1997) also observed that home ranges for *Plectopomus leopardus* (Serranidae) on fringing reefs were more elongated than on isolated patch reefs; however, contrary to the present study, home ranges of *P. leopardus* were smaller on linear fringing reefs than on patch reefs. This difference between *S. pulcher* and *P. leopardus* in home range shape and size may be simply related to their difference in foraging strategies, in that *S. pulcher* searches for benthic invertebrates, while *P. leopardus* is a sit-and-wait piscivore.

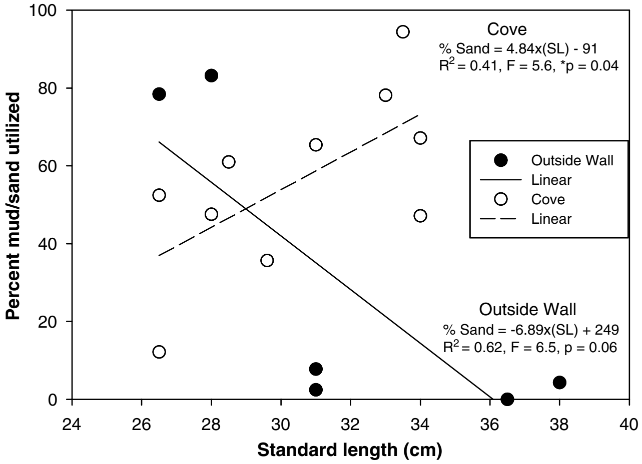


Fig. 5 *Semicossyphus pulcher*. Percent use of mud/sand habitat by sheephead inside the Cove and along the Outside Wall. Relationships shown between standard length (*SL*) of fish (cm) and the proportion of position fixes when fish were in mud/sand at two different locations

In the present study, *S. pulcher* had a larger home range than was found in a study of similar-sized temperate labrids. Labrids, being reef/structure-associated fish, are generally thought to exhibit high site attachment and have relatively small home ranges (e.g. Barrett 1995; Bradbury et al. 1995; Chapman and Kramer 2000). Two of the larger labrids (*Notolabrus fucicola* and *N. tetricus*) in temperate waters in the southern hemisphere had smaller home ranges (225–725 and ~1,750 m^2, respectively) than *S. pulcher*; however, these estimates were based on 1-h SCUBA observations. If *S. pulcher* were tracked for short periods (1 h), home ranges would be grossly underestimated, having a range of 154–9,434 m^2, approximately ten times smaller than our estimates made over longer tracking periods. Thus, it is important to define the temporal scales at which a home range or a fish's site fidelity is measured and to understand the limitations at those scales.

In this study, fish were found in a variety of habitats and were associated with rocky-reef areas (rock wall, steep rocky rubble, boulders, or rock rubble) 54% of the time, only 8% more often than mud/sand habitat. In a study of diet and prey distribution, Johnson et al. (1994) estimated that *S. pulcher* used artificial rocky-reef habitat 70% of the time, followed by ecotone (sand/reef interface) (15%), and sand habitats (5%). Although fish in the present study did appear to follow reef contours and use reef habitat in a slightly greater proportion than sand, the estimate of reef use was significantly less than reported by Johnson et al. (1994). The difference between these two studies may reflect differences in prey composition and prey availability between an artificial reef and a natural habitat. For the most part, the movement and habitat use patterns determined in the present study agree with previous fish count and gut content/prey studies, in which *S. pulcher* was considered mainly a rocky-reef- and kelp-bed-associated species, with occasional to frequent foraging forays within sand habitats (Hobson and Chess 1986, 2001; Johnson et al. 1994).

S. pulcher was not strictly associated with kelp (*M. pyrifera*), but did utilize areas with kelp a significant portion of the time and showed a preference for this habitat. Kelp was the dominant macroalga in the reserve and covered a majority of the rock habitat. Because *S. pulcher* prey on urchins that graze on kelp, increased numbers of *S. pulcher* may result in an increase in kelp density (Dayton et al. 1998). Therefore, *S. pulcher* may be selecting areas with kelp due to increased habitat complexity, which likely offers additional feeding opportunities and potential refuge from large predators (e.g. Hobson and Chess 1986, 2001; Johnson et al. 1994).

Sand habitat within the reserve appears to be used more than expected by *S. pulcher*, based on other studies that emphasize use of the rocky reef. The pattern of sand habitat utilization in the reserve follows the availability of this habitat (HSI = 0.71), so fish may alter their use of sand habitat in different areas depending on its availability. Of the reef substratum, daytime habitat use appeared to follow an order consistent with increasing substratum relief, namely rocky wall > steep rocky rubble > boulders > rocky rubble. Rock wall was used (~22%) more than was expected based on its availability (~10%), suggesting that fish selected this habitat (HSI = 3.15). Matthews (1990) found a similar high-relief habitat selection behavior by rockfish and attributed this habitat preference to the higher densities of prey and cover available in high-relief habitats. Boulder habitat had the highest mean habitat selection index value (HSI = 4.56), which may be partially attributed to a large percentage of position fixes around sunrise and sunset within this frequently used nighttime resting habitat and to the scarcity of this habitat in the reserve.

Fish tracked within the Cove showed a relationship between body size and habitat use, with larger fish using sand significantly more than smaller fish. *S. pulcher* have been reported to vary their diet with availability of prey in different locations and to exhibit ontogenetic shifts in prey selection (Cowen 1986; Hobson and Chess 1986, 2001). Hobson and Chess (2001) and Cowen (1986) found that larger *S. pulcher* (>25 cm) shift to more heavily armored prey. The difference observed in the time that larger fish in the Cove spent over the sand might simply be due to their ability to excavate out larger prey (mollusks) within the sediment. However, the opposite relationship was found for the fish tracked along the Outside Wall, that is, larger fish spent less time in sand habitats and more time in reef habitats than smaller fish. This pattern may have been due to site-specific differences in types of available prey. Two other studies in the reserve found significantly lower abundances of *Centrostephanus coronatus*, a reef-dwelling urchin, in the Cove than along the Outside Wall (S. Sharfi 2000 and B. Kay 2003, unpublished data). Nelson and Vance (1979) found that only larger sheephead could successfully prey on these urchins. Because they are abundant along the Outside Wall, larger fish may spend more time over the reef than sand, in order to utilize this prey. This difference in prey availability may also explain the disparity in time allocated to different habitats by larger fish (i.e. they may switch to the most available prey within the different locations). More information is needed about the prey composition and availability in these two areas relative to the diets of different-sized *S. pulcher*, in order to determine how foraging may influence these movement patterns.

The home ranges observed for *S. pulcher* were relatively small compared to the size of the reserve, with fish spending most of their time within the reserve. However, all six fish tracked along the Outside Wall crossed the reserve boundary at some point, primarily where the reef contours cross the boundary. Their movements were mainly along and near the base of the reef in the sand ecotone, appearing to avoid traversing the 40-m-deep sand channel between the Outside Wall and Bird Rock (~200 m north). If the reserve boundary were 40 m seaward from its present location, none of the six Outside Wall fish would have been found outside the boundary. In a similar telemetry study in the reserve, Lowe et al. (2003) found that kelp bass (*Paralabax clathratus*) also did not cross the deep sandy expanse between the Outside Wall and Bird Rock. This suggests that the habitat break (long stretches of sand without reef) bordering the reserve may serve as a natural boundary for reef-associated species such as *S. pulcher*, in some cases increasing the degree of protection provided within a relatively small area.

Although the deep sand area bordering the Outside Wall limited *S. pulcher* movement away from the reef, this narrow habitat tended to increase the distance moved along the reef, the directionality, and the size and shape of their home ranges. This increased the probability of the fish crossing the boundary at the ends of the reserve. Fish tracked within the Cove rarely exceeded its confines, and these fish showed more circular paths than fish on the Outside Wall. Therefore, the shape of the habitat relative to the reserve boundary may influence the degree that fish cross the boundary, and thus may result in varying density gradients across differing types of habitat.

Kramer and Chapman (1999) suggested that maximizing the area to boundary length ratio would effectively increase population sizes and mean fish size within a reserve. If the Cove and the Outside Wall areas were considered separate reserves, the Cove had a 4.5 times greater area to boundary length ratio (188:1) than the Outside Wall (42:1) and had the lowest percentage of fish crossing the boundary. This provides evidence to support this theory.

Reserves must contain the habitat essential for *S. pulcher* feeding (reef and sand), reproduction, and shelter (rocky holes and crevices); however, given these, the next most important factors may be the size of the reserve and its shape. By increasing the area to boundary length ratio, spillover would be minimized and a larger stock of fish could be protected. Alternatively, if a greater spillover potential is desired, the area to boundary length may be adjusted. This study provides the foundation to assess the potential for spillover and to predict the overall effectiveness of reserves to manage *S. pulcher* stocks. Considering the increased global use of reserves for management and the number of species assumed to be protected by reserves, movement studies are necessary for other target species.

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