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Notes from the Editor

This final issue of 2019 contains a variety of articles including marine, freshwater, and terrestrial species. Ronald Russo, a frequent contributor to the Journal, offers a method for determining sexual maturity in male leopard sharks in the Pacific Ocean. Dr. Vern Bleich, former editor of this Journal and also a frequent contributor, and his colleagues discuss habitat selection by bighorn sheep in southern California finding support for both seasonal and sex differences in selection. Dr. Frederick Feyrer from the USGS's California Water Science Center provides notes on the spawning ecology of the endemic, CESA Threatened Clear Lake hitch. And finally, Jean Davis and her colleagues from the Marine Region of CDFW compare video and visual survey techniques for censusing barred sand bass.

We have one more new addition to our editorial staff, Jennifer Nguyen. Jennifer is currently acting director of the Department's Cannabis Program. Before that, she was a supervisor in our Region 2 office in Rancho Cordova providing leadership in our Habitat Conservation Program, focusing on CESA, CEQA, Natural Community Conservation Plans, and Mitigation Banking. She has worked for the Department since 2005 after receiving her B.S. in Biology at California State University-Fresno.

The Journal is continuing to update and change! In the next issue (106-1), the first of 2020, you will see not only a newly redesigned cover, but a new name: *California Fish and Wildlife Journal*. As was discussed in the spring issue (105-2), the Department's focus has changed over the decades to reflect current environmental and conservation issues in our state. Just as the Department's name was changed from "Fish and Game" to "Fish and Wildlife" in 2012, so too will the Journal's name change to accurately reflect all the species we are charged with managing and protecting.

I would also like to do one final push for the three special issues of the Journal that we are working on this year: cannabis, fire, and human recreation and their impacts on fish and wildlife resources in the state. Please pass the word along to those you know who do research on these topics. If you would like to find out more about our Special Issues, please see our webpage: <https://www.wildlife.ca.gov/Publications/Journal/Special-Issues>.

Ange Darnell Baker, PhD

Editor-in-Chief

California Fish and Game Journal (soon to be California Fish and Wildlife Journal)

Determining sexual maturity in male leopard sharks in San Francisco Bay, California

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Key words: calcification, catch events, claspers, spermatozoa, vas deferens

The leopard shark (*Triakis semifasciata*) is endemic to the eastern North Pacific ranging from Mazatlan, Mexico and the Gulf of California to Oregon. It is an inshore species generally found in shallow water < 91 m deep (Smith 2001; Ebert 2003). This species is one of the most researched elasmobranchs along the Pacific Coast of North America with several aspects of its biology well defined (Ackerman 1971; Russo 1975, 2013, 2015, 2018, 2019; Talent 1976, 1985; Smith 1984, 2001, 2005; Smith and Abramson 1990; Cailliet 1992; Kusher et al. 1992; Au and Smith 1997; Smith et al. 2003; Hight and Lowe 2007; Lewallen et al. 2007; Carlisle and Starr 2009, 2010; Nosal et al. 2013a,b, 2014; Launer 2014; Barker et al. 2015). Various reproductive studies have occurred for leopard sharks (Ackerman 1971; Talent 1985; Ebert and Ebert 2005; Smith 2005; Nosal et al. 2013a, b, 2014; Launer 2014; Russo 2015, 2018, 2019). Although these studies have found sexual segregation the specifics of male sexual maturity remain unknown. Additionally, little detail is known concerning the process of sexual maturation in males from known breeding locations within its range.

Male leopard sharks may reach sexual maturity at a total length (TL) ranging from 70 to 120 cm (Ebert 2003), a range currently thought to be based on various known breeding locations and research methods. However, details regarding the length at which calcification of claspers and production of mature spermatozoa occur in male leopard sharks are poorly known.

Several reports on calcification of claspers and production of spermatozoa of various species have been published (Pratt 1979; Joung and Hsu 2005; Huveneers et al. 2007; Awruch et al. 2008). Clark and Von Schmidt (1965) and Chen et al. (1988) have suggested that calcified claspers and the ability of the rhipidion to splay is a measure of sexual maturity. Yet, other studies maintain that a more reliable indicator of sexual maturity involves clasper length and calcification in combination with swollen testes and the presence of spermatozoa (Peres and Vooren 1991; Jensen et al. 2002; Lucifora et al. 2005; Conde-Moreno and Galvan-Magaña 2006; Awruch et al. 2008; Dharmadi and Wiadnyana 2013; Natanson and Gervelis 2013; Gracan and Lackovic 2016). The purpose of the present study was to determine whether calcification of claspers is correlated with production of spermatozoa and thus an indicator of sexual maturity in leopard sharks. Data first reported herein, shows that in male leopard sharks in South San Francisco Bay, there is a time delay between the

length at which claspers calcify and spermatozoa is produced.

Between 1970 and 2001, data collection was conducted monthly primarily between the San Francisco Bay Bridge (37.800 N, 122.3667 W) and the entrance of Alviso Slough (37.450 N, 122.017 W) at the south end of San Francisco Bay (Figure 1). There were 224 catch events (one technique, location, date, and time) using long-lines (n = 146), rod and reel (n = 36), and otter trawl (n = 42) (Russo 2019).



Figure 1. Map of the study area of San Francisco Bay with all catch events (red circles) in this study restricted to South San Francisco Bay and close to known parturition or mating sites. Map courtesy of the East Bay Regional Park District.

I collected data on sex, external parasites, and general condition of every shark. All measurements of individual sharks were made in centimeters total length (cm TL), whereas groups of sharks were calculated in centimeters mean total length (cm MTL). I physically examined male claspers for flexibility, extent of calcification and length from the tip to the posterior margin of the cloacal opening. I also examined clasper tips for spurs, hooks, or spines used in holding the clasper in the female cloaca, but none were found in the field and samples were not removed for microscopic examination later (Pratt and Carrier 2004). Clasper length was plotted against total length for analysis with color designations at the points at which calcification of claspers and production of spermatozoa occurred. Both sperm sacs and seminal vesicles were examined for presence of spermatozoa in the field along with the condition of the vas deferens, which are coiled in mature sharks. I took samples back to the laboratory for microscopic examination.

In this study, 4,121 elasmobranchs were captured mostly from South San Francisco Bay including 2,478 (60.1%) leopard sharks composed of 1,299 males and 1,179 females (Russo 2019). I selected a group of 99 male leopard sharks as a representative sample of all potential stages of maturity (Table 1, Figure 2A). These individuals ranged in size from 44.4 to 124.4 cm TL (86.3 cm MTL \pm 19.6 SD) and were captured in six male-dominated long line events during the months of expected sexual activity from April to early July (1977 - 1990) (Ebert and Ebert 2005, Russo 2015, 2018, 2019) and close to known parturition sites defined in Russo (2019) (Figure 1). Clasper length ranged from 2.5 to 14.6 cm (5 cm MTL \pm 1.3 SD). This analysis broadly defined the length “markers” at which calcification of claspers occurred along with the production of spermatozoa. Calcified claspers ranged in length from 6.3 cm to 14.6 cm (12.4 cm MTL \pm 2.04 SD). Of these, 44.4% (44/99) possessed calcified claspers and 32.3% had possessed spermatozoa (Table 1, Figure 2a). Of the 44 males with calcified claspers, 72.7% (n = 32) were sexually mature, while the remaining 27.3% (n = 12) with calcified claspers were sexually immature.

Additionally, there was a familiar relationship between clasper elongation and TL. This relationship shows rapid clasper elongation from 6.4 cm to 14 cm (+7.6 cm) between 86 and 101 cm TL, which is where calcification begins between 86 and 92.7 cm TL (Table 1), along with weight gain from 2 kg (86 cm TL) to > 6.3 kg (> 100 cm TL; Russo, unpublished data; Kusher et al. 1992). Similar patterns in rapid clasper elongation coinciding with weight gain prior to or during calcification have been found in school sharks (tope) (*Galeorhinus galeus*; Peres and Vooren 1991), bonnethead shark (*Sphyrna tiburo*; Kajiura et al. 2005), shortfin mako shark (*Isurus oxyrinchus*; Joung and Ysu 2005) and the blackspotted smoothhound (*Mustelus punctulatus*; Gracan and Lackovic 2016). Whereas most of these studies focused

Table 1. Summary of 99 males captured in six male-dominated catch events between 1977 and 1990. Examination of body and clasper lengths were used to determine length “markers” when calcification of claspers occurs and onset of spermatozoa. n = no calcification or spermatozoa found at these size ranges.

Size range		Clasper length		Number		
cm/cm	MTL	cm/cm	MTL	Specimens	Calcified	Spermatozoa
44.4 – 86.3	68.5	2.5 – 7	4.4	50	n	n
86.4 – 91.4	90.7	6.4 – 10.1	7.6	12	7	n
92.7 – 124.4	104.1	8.9 – 14.6	12.7	37	37	32

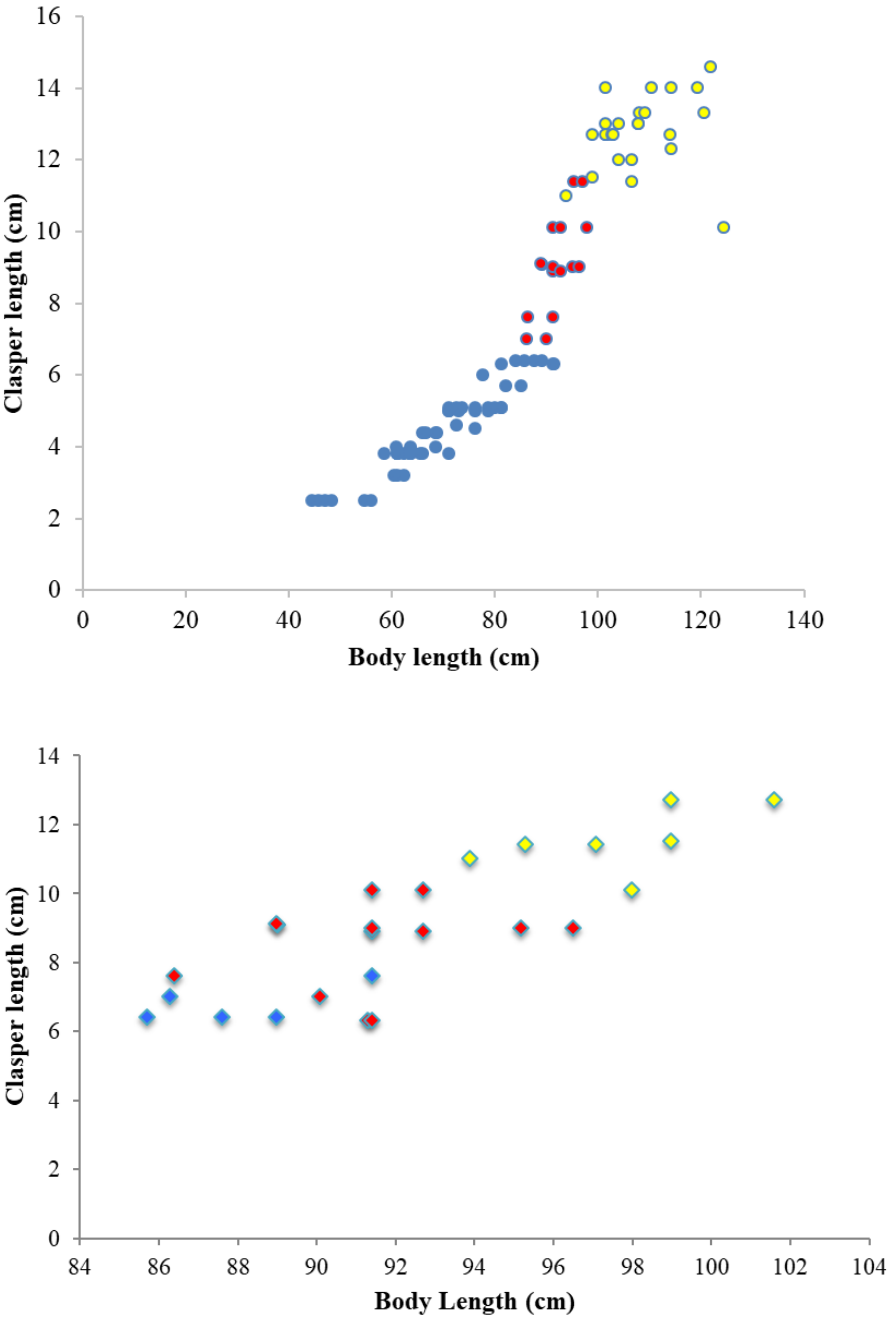


Figure 2. (a) Analysis of 99 male leopard sharks indicating the calcification of claspers (red) and the onset of spermatozoa with calcified claspers (yellow). (b) Analysis of 25 male leopard sharks from 85.7 cm to 101.6 cm TL indicating lengths at which calcification (red) and spermatozoa/calcification (yellow) occur. Blue indicates immature sharks without calcified claspers. Duplicate data points may be superimposed, one over another.

on clasper length, body length and testes weight, no study found or distinguished between the length at which calcification begins and the onset of spermatozoa production indicating any delay between the two episodes.

I conducted a separate analysis of 25 males, a subset of the larger sample of 99, ranging in TL from 85.7 cm (prior to calcification herein) to 101.6 cm (just beyond the 100% mature benchmark of 99 cm TL; Figure 2b). Here, claspers ranged from 6.3 to 12.7 cm long (9 cm MTL \pm 1.9 SD), including 7 (28%) juveniles along with 18 (72%) males with calcified claspers and only 8 (32%) of those possessing spermatozoa. These results showed that claspers grew rapidly until individuals approached >103 cm TL when growth slowed as maximum size limits in this study approached (124.4 cm TL), along with a delay in the production of spermatozoa between calcification at 86.4 cm and 93.9 cm TL when the first spermatozoa were found.

The first indication of calcification occurred at 86.4 cm TL (claspers at 7.6 cm long), which indicated that clasper length compared to body length was highly variable. For example, the largest specimen measured at 124.4 cm TL had claspers at 10.1 cm, which was equivalent to another male at 91.4 cm TL, a difference of 33 cm in TL length. Between 86.4 cm TL and 91.4 cm TL ($n = 12$), calcification was inconsistent appearing in only 7 (58.3%) males in this size range (Table 1). Claspers of males > 92.7 cm TL ($n = 35$, 106.7 cm MTL \pm 7.8 SD) had a median clasper length of 12.7 cm (\pm 1.4 SD) and were all calcified.

The production of spermatozoa was also inconsistent beginning at 93.9 cm TL and occurring among only 50% ($n = 3$) of the males between 93.9 cm TL and > 98.0 cm TL ($n = 6$) whereupon 100% of the males possessed spermatozoa. One male at 91.4 cm TL with 6.3 cm claspers represented the smallest claspers at which calcification occurred, yet it was still immature. The largest juvenile male with uncalcified claspers and no spermatozoa measured 91.4 cm TL. The smallest adult male with calcified claspers and spermatozoa was 93.9 cm TL.

Sexual maturity, as evidenced by presence of mature spermatozoa in seminal vesicles and sperm sacs as well as the coiled condition of the vas deferens, generally did not occur until males were > 93.9 cm TL with claspers at a minimum > 10.1 cm (Figure 2). Once calcification occurred there was a growth of 7.5 cm in body length combined with an increase in clasper length of 3.1 cm indicating a delay prior to sexual maturity as first reported here. Calcification and production of spermatozoa in this study occurred at a larger body length size (+16.4 cm) than the lower end "maturity" size (70 cm TL) given by Ebert (2003) but within his overall range. The range for sexual maturity in this study is relatively narrow (93.9 - 99 cm TL) compared to published estimates (100 - 105 cm TL [Kusher et al. 1992], 70 - 120 cm TL [Ebert 2003]) based on potential breeding locations, environmental conditions, changes in climate, and research methods. There is considerable variability in body length related to clasper length of individual leopard sharks possibly attributable to availability of food, parasites, general health, genetics and other environmental factors (Figure 2).

Based on data presented herein, sexual maturity cannot be inferred from length or the calcification of claspers alone in leopard sharks, given the potential variation in critical physical factors among individuals from one locality to another. Instead, clasper length and calcification in combination with presence of spermatozoa are the only reliable measure of sexual maturity for this species. Comparisons with male leopard sharks in other known breeding locations including an increased number of larger specimens should be made to refine our understanding of the reported 50 cm TL range for sexual maturity with leopard sharks, as well as factors that influence such differences.

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Habitat selection by bighorn sheep in a mesic ecosystem: the San Rafael Mountains, California, USA

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Bighorn sheep (*Ovis canadensis*) were extirpated from the San Rafael Mountains, Ventura County, California, about 1915, and remained so for 70 years. They were reintroduced to that range, which is near the western extreme of their historical distribution, in 1985 and 1987. We used aerial telemetry to investigate habitat selection by 18 bighorn sheep from 1985 to 1989. Resource selection showed some support for both sex and seasonal differences, but only seasonal variations appeared in the top model. Relative to availability, bighorn sheep selected locations clos-

er to water and farther from roads, with higher elevations, steeper slopes and increased terrain ruggedness, and areas that had burned recently, and had lower concentrations of xeric, mesic, and conifer habitat types during the summer. These results generally are consistent with observations of habitat use by bighorn sheep comprising the source population in the San Gabriel Mountains. Our results also support previous reports that burned areas, whether the result of natural or prescribed fire, are an important component of bighorn sheep habitat dominated by chaparral vegetation. Further, these results justify the use of prescribed fire to maintain high-quality habitat for bighorn sheep in the study area and elsewhere in the transverse range of California. The finding of seasonal differences in resource selection probabilities will facilitate development of an efficacious aerial survey strategy, and provide investigators with an objective method of assessing habitat for future reintroductions.

Key words: bighorn sheep, California, chaparral, fire history, habitat selection, *Ovis canadensis*, reintroduction, San Rafael Mountains, translocation

Bighorn sheep (*Ovis canadensis*) are among the most recognizable large mammals inhabiting North America. The geographic range of these iconic ungulates extends southward ~3,500 km from the northern Rocky Mountains in British Columbia, Canada (approximate latitude 54° N) to the Sierra de la Giganta, Baja California Sur, Mexico (approximate latitude 24° N). Historically, the distribution of bighorn sheep extended eastward from approximate longitude 127° W in British Columbia (Cowan 1940; Demarchi et al. 2000) to the badlands of North Dakota and South Dakota (approximate longitude 100° W), a distance of ~1,600 km. Thus, the distribution of bighorn sheep included parts of two provinces in Canada, portions of 15 American states, and ≥6 states in Mexico (Baker and Greer 1962; Monson 1980; Garcia-Mendoza and Lopez-Gonzalez 2013). The number of bighorn sheep that once inhabited the United States is open to question (Welles 1962; Valdez 1988), but there are far fewer individuals with a more restricted distribution than historically was the case (Buechner 1960). Bighorn sheep were extirpated from the San Rafael Mountains, Ventura County, California, near the westernmost extreme of their distribution in the continental United States (Buechner 1960), by about 1915 (Freel 1984). Factors contributing to this extirpation are unconfirmed, but likely include illegal hunting, diseases contracted from domestic sheep, and competition with domestic livestock (Buechner 1960; Freel 1984).

In 1971 and 1972, Richard A. Weaver of the California Department of Fish and Game (CDFG) conducted several overflights and on-the-ground evaluations of potential areas suitable for the reintroduction (*sensu* Hale and Koprowski 2018) of bighorn sheep to the San Rafael Mountains, near the western terminus of California's transverse range (Figure 1). Subsequent investigations by DeYoung (1975) and Fox (1983) led to the conclusion that San Rafael Peak and Cobblestone Mountain were suitable locations at which animals could be reestablished in that range (Freel 1984). As a result, bighorn sheep were reintroduced to the San Rafael Mountains in 1985 and 1987 (Peterson and Peterson 1987; Bleich et al. 1990). Our objectives are to explore habitat selection by bighorn sheep immediately following the reintroduction, develop models to provide an objective method of assessing

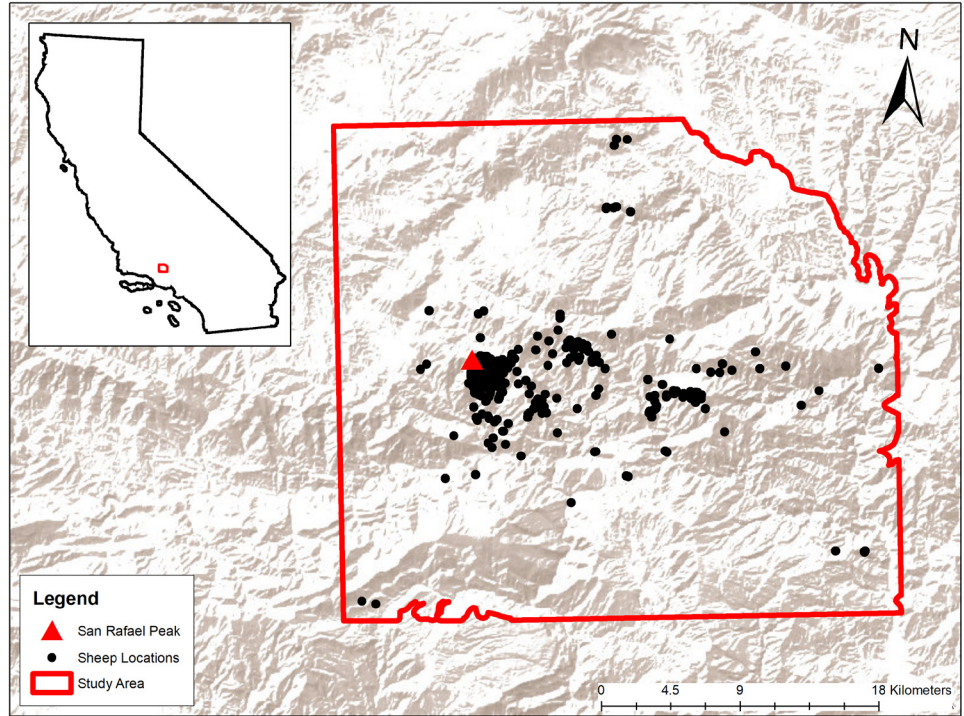


Figure 1. The study area, delineated by the red line in the San Rafael Mountains, Ventura County, is near the western terminus of California’s transverse range, which extends nearly 400 km from west to east in Santa Barbara, Ventura, Los Angeles, and San Bernardino counties, California, USA. The release site at San Rafael Peak, Ventura County, is shown for reference within the study area.

habitat suitability for future reintroductions, and to assist in development of an efficacious aerial survey strategy based on seasonal selection of habitat. We then use the results of those models to suggest habitat management options that likely will be of benefit to bighorn sheep conservation and are appropriate in that mesic environment.

METHODS

Study area

The transverse range in southern California extends nearly 400 km eastward from the Santa Ynez Mountains in Santa Barbara County to the Little San Bernardino Mountains, San Bernardino County. In the San Gabriel Mountains, the source of animals translocated to the San Rafael Mountains, the distribution of bighorn sheep ranges in elevation from approximately 300 m at the base of the cismontane side of the mountains to 3,350 m at Mt. San Antonio (Holl and Bleich 1983). Chaparral and coastal sage habitats are used heavily by mountain sheep and are widespread throughout the transverse range and are the dominant vegetation types on cismontane slopes in the San Gabriel Mountains below 1,800 m (Kuchler 1977; Holl and Bleich 1983).

Bighorn sheep occupy eight winter-spring seasonal ranges in the San Gabriel Mountains (Weaver et al. 1972; Holl and Bleich 1983), but habitat use is influenced strongly by periodic fire (Bleich et al. 2008; Holl and Bleich 2010; Holl et al. 2012). Habitat occupied by bighorn sheep in the San Gabriel Mountains has been described in detail elsewhere (Weaver et al. 1972; DeForge 1980; Holl and Bleich 1983, 2009, 2010; Bleich et al. 2008; Holl et al. 2012) and is similar to that in historically occupied areas of the San Rafael Mountains (DeYoung 1975; Fox 1983; Freel 1984). Further, the decision to use source stock from the San Gabriel Mountains was consistent with current recommendations for reintroductions, whereby ecological similarities between source and reintroduction locations should be a primary consideration (Wehausen 1989, Whiting et al. 2012; Brewer et al. 2014; Bleich et al. 2018; Coggins and Coggins 2018).

The San Rafael Mountains vary in elevation from about 75 m to 2,080 m. Vegetation consists predominately of chaparral and coastal sage scrub, with coniferous forests at upper elevations, riparian forests in canyon bottoms, and some grassy poteros scattered across the area (DeYoung 1975; Fox 1983; Freel 1984). Elsewhere, vegetation in the transverse range has been characterized in general terms as predominantly chaparral and coastal scrub with occasional woodlands, riparian communities, and grasslands (Soza et al. 2013).

Climate in the San Rafael and San Gabriel mountains is typical of Mediterranean ecosystems, with hot, dry summers and moist, mild winters (Bailey 1966). During winter, precipitation in both areas frequently occurs as snow at elevations above 1,500 m (Holl and Bleich 1983; Freel 1984). Except for grizzly bear (*Ursus arctos*; Storer and Tevis 1955), both mountain ranges support a full complement of native carnivores capable of preying on large ungulates, including bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), and coyote (*Canis latrans*; Freel 1984). Black bear (*Ursus americanus*) likely colonized the western part of the transverse range following extirpation of the grizzly bear (Grinnell et al. 1937), but were introduced (*sensu* Hale and Koprowski 2018) to the San Gabriel Mountains in 1933 (Burghdoff 1935).

In the early 1980s, >700 bighorn sheep inhabited the San Gabriel Mountains (Holl and Bleich 1983, 2009, 2010). That population has varied substantially in size over many decades (Holl et al. 2004), but evidence indicates it is isolated from other populations of bighorn sheep (Bleich et al. 1996; Buchalski et al. 2016). Mule deer (*Odocoileus hemionus*) are the only other native ungulate occupying the transverse range.

Reintroduction

In the early 1980s approximately 130 bighorn sheep occurred on the Cattle Canyon winter range in the San Gabriel Mountains (Holl and Bleich (1983). We used a drop-net to capture adult (≥ 1 year-of-age) bighorn sheep in Cattle Canyon (34.2555 N, 117.6842 W) in December 1985 and again in January 1987 (Kock et al. 1987; Bleich et al. 1990; Jessup et al. 2014). The drop-net was baited each morning with fermented apple pulp (Schmidt et al. 1978) and high-quality alfalfa hay, and after >1 month several dozen bighorn sheep were conditioned to the presence of a human and reliably coming to the trap site each day (Figure 2). A single drop of the net was sufficient to capture an adequate number of animals in 1985 and, again, in 1987.

Upon capture, animals were restrained physically, blindfolded, sedated with xylazine, and airlifted by helicopter to a nearby processing area (Jessup et al. 2014) where each was examined, biological samples were collected, ages were determined, and animals were fitted



Figure 2. Bighorn sheep were provided with high-quality alfalfa hay and fermented apple mash daily to ensure they would be ‘under the net’ when personnel arrived to implement the capture operation. Bill McIntyre, a volunteer representing the Society for the Conservation of Bighorn Sheep, carried out this critically important task in Cattle Canyon, San Gabriel Mountains, Los Angeles County, California, USA in 1985 and 1987 (photo © B. Moose Peterson).

with VHF telemetry collars incorporating a mortality sensor with a 6-hour delay (Mod 500, Telonics, Inc., Mesa, AZ, USA), or with individually identifiable marking collars. Animals then were placed in specially modified horse trailers and transported westward about 120 km to the San Rafael Mountains where they were held overnight in the trailers; alfalfa hay and water were provided *ad libitum* during confinement. During both years, we constructed a temporary corral at the release site proximate to San Rafael Peak in which animals would be held temporarily following aerial transport and, thereby, ensure all animals could be released simultaneously (Figure 3; Thompson et al. 2001).

Early in the morning following the 1985 capture event we used physical restraint to transfer each animal from the trailers to shipping crates ($0.5 \times 1.0 \times 1.5$ m) for aerial transport. Upon delivery to the release site, we transferred bighorn sheep to the corral where each was held for a short time ($\bar{x} = 4$ h; range 2–6 h) before all animals were released simultaneously (Figure 3). To minimize disturbance, the 8-person handling crew was not extracted for several hours following release of the animals, and the corral was not retrieved until several weeks later.

Bighorn sheep captured in 1987 again were held overnight, but high winds precluded early morning transport to the release site. Thus, we held animals in the trailers for an additional 6 hours, after which they were placed in crates and transported by truck to an alternative release site at MacDonald Peak, ~6 km east of San Rafael Peak. Weather conditions improved substantially during vehicular transport and, upon arrival at MacDonald Peak, the animals were flown to San Rafael Peak and transferred from the crates to the corral as in



Figure 3. Bighorn sheep were held in a special enclosure for up to 6 hours to ensure that animals would be released as a single group at San Rafael Peak, San Rafael Mountains, Ventura County, California, USA in 1985 and 1987 (photo © B. Moose Peterson).

1985. Animals were held in the corral (\bar{x} = 1.5 h; range 0.5–2.5 h) until the final individual was delivered, and then for an additional hour before being released simultaneously. Total time from capture to release in 1987 was ~ 7 h greater than in 1985.

Monitoring

We conducted telemetry flights from December 1985 to December 1989 at approximately 2-week intervals, weather permitting (\bar{x} = 14.7 days between flights). We used a fixed-wing aircraft with an H-type antenna on each wing strut and located animals in a manner adapted from that described by Krausman et al. (1984). We plotted the location of each telemetered individual on a 7.5' United States Geological Survey (USGS) topographic map and converted those locations to digital format. Safety concerns precluded visual confirmation of locations determined by aerial telemetry (Bleich et al. 2001), but telemetry error polygons in similar terrain elsewhere in the transverse range were small (\bar{x} = 0.098 km²; Nicholson et al. 1997) relative to home ranges of bighorn sheep in the San Rafael Mountains (\bar{x} = 25.24 \pm 6.84 [SE] km²).

Habitat modeling

We incorporated all locational data into a master file for further analysis. We used ArcGIS 10.4 (Environmental Systems Research Institute, Redlands, CA, USA) and multiple sources of digital data to project bighorn sheep locations and derive habitat features associ-

ated with each of those locations. We used Los Padres National Forest (LPNF) coverages of vegetation and fire history to derive habitat type and years since the most recent fire. Areas that had burned ≥ 30 years prior were treated as a single category given the uncertainty of what may represent a typical fire regime in the chaparral ecosystems of southern California (Keeley 2006). There is general agreement that fires historically were smaller than those that occur today and that most ignitions occurred during summer. Conflagrations occurring in the present, however, account for the bulk of the landscape affected by fire, and occur primarily during fall (Keeley and Fotheringham 2003). The historic fire regime likely involved several major fires per century that occurred at intervals of 30 to 40 years, and small fires have burned on winter-spring ranges used by bighorn sheep at fire return intervals of ≥ 20 years (Holl et al. 2012).

We removed habitat variables that did not appear in locations used by sheep, or that appeared very infrequently (inhibiting convergence of resource selection models). Habitat types removed were barren (0 used locations), lake (0 used locations), and urban land (0 used locations). Habitat types retained for analysis included conifer forest, xeric chaparral, mesic chaparral, coastal sage scrub, and oak woodland. We derived elevation, percent slope rise, and sine (-1 = due west and 1 = due east) and cosine of aspect (-1 = due south and 1 = due north) from a 10-m resolution USGS digital elevation model (<http://nationalmap.gov/viewer.html>). We used those data to calculate an index of terrain ruggedness (VRM; Sappington et al. 2007) and developed 3 such layers (neighborhood sizes of 3, 11, and 21) to account for multiple scales of ruggedness. We also created Euclidian distances from dirt roads or trails and from perennial streams using the LPNF coverages and the USGS National Hydrography Dataset (<https://nhd.usgs.gov/>).

Locations obtained with aerial telemetry were associated with larger errors than would have been the case with satellite collars incorporating GPS technology that have since become available, and complicated our ability to determine habitat type at each animal location. Therefore, we created a buffer of 0.098 km^2 around each location and calculated the percentage of each habitat type within those polygons (Bleich et al 2009). Additionally, we used those percentages to compute Shannon's diversity index for each location (Shannon 1948). Similarly, to address potential error with the topographic and distance layers (e.g., distance to water), we used the Zonal Statistics Tool in ArcGIS to compute average values across each buffered sheep location.

To represent resource units available to this translocated population, we generated 2 random locations for each animal location and used the same procedures to extract habitat attributes for each. These locations were drawn randomly from a defined study area that was delineated by creating a minimum convex hull around the used bighorn sheep locations and buffered by 1,000 m to account for potential movement by individuals (Bleich et al. 1997). The random and used locations were compiled into a single dataset for further analysis. No predictor variable was highly correlated ($r > |0.6|$) with any other, and we retained all of them for fitting resource selection models. We standardized all continuous predictor variables prior to calculating resource selection functions to facilitate comparison among variables.

We constructed resource selection models using mixed-effects logistic regression from the "glmmTMB" package in R 3.02 (Brooks et al. 2017). We first specified a full model that included all measured environmental covariates along with corresponding interactions with sex and season (Fall [September–November], Winter [December–February], Spring [March–May], and Summer [June–August]). Individual ID and year were included in the

model as random intercept terms. Since the full model (all measured covariates along with corresponding interactions with sex and season) would not converge, and because the habitat-class covariates (percent cover of oak, coastal sage scrub, xeric chaparral, mesic chaparral, and conifer) were subject to a unit-sum constraint, we selected one habitat-class covariate (coastal sage scrub) for exclusion from the full model; this model (full model without coastal sage scrub) converged, and we therefore considered it to be our 'global' model for further model selection (see below). We tested the adequacy of the model fit for the global model by visualizing scaled (quantile) residuals and performing diagnostic tests (uniformity across the range of predictions, presence of excessive outliers, and overdispersion) based on these residuals (Hartig 2019).

To determine which of the 3 different terrain ruggedness scales was most informative, we fitted the global model with each of the 3 ruggedness indices in turn and compared model fit using Akaike's Information Criterion (AIC). The largest-scale terrain ruggedness measure (Ruggedness21) strongly outperformed the other variables ($\Delta\text{AIC} = 6.4$), so this metric was used to represent ruggedness in the final model selection procedure. We then used a backward stepwise elimination procedure (implemented in the *buildmer* package in R, using AIC as the selection criterion; Voeten 2019) to select the best-fit model from all covariates and interaction terms included in the global model. This final model was used to generate partial-dependence plots and prediction maps, using the 'Raster Calculator' tool in ArcGIS 10.4, to aid in visualization of resource selection patterns across seasons.

To assess the predictive strength of our model, we used a modified form of leave-one-out cross-validation in which all telemetry locations from unique individual sheep were left out of model fitting in turn and subsequently were used for model validation (Shoemaker et al. 2018). In this cross-validation scheme, model performance was assessed using the area under the curve (AUC) metric from a Receiver Operating Characteristic analysis (Boyce et al. 2002).

RESULTS

We captured 21 bighorn sheep (16 ♀, 5 ♂) in December 1985 in Cattle Canyon, Los Angeles County, and released them at San Rafael Peak (34.6236 N, 119.0017 W) in the San Rafael Mountains, Ventura County (Figure 1). In January 1987 we again captured bighorn sheep in Cattle Canyon and released 15 (11 ♀, 4 ♂) at the same location. We used aerial telemetry locations ($n = 757$) from 4 ♂ and 14 ♀ individual bighorn sheep in our analyses ($\bar{x} = 42$ locations, $SD = 15.8$, $Range = 11\text{--}63$).

Best performing model

We found little support for sex-based resource selection in that interactions between sex and environmental gradients were not present in the final model. We did, however, find variation in selection coefficients across seasons (Table 1; Figures 4 and 5). Bighorn sheep (males and females combined) selected higher elevations, steeper slopes (not significant during summer months), and more rugged terrain than were available across the landscape (Figure 4). Additionally, individuals selected areas closer to water (indicated by a negative regression coefficient) and areas further from roads across the landscape (Figure 4). Bighorn sheep also selected habitat patches that were burned more recently across all seasons (albeit

Table 1. Results from the top mixed-effects logistic regression model for bighorn sheep reintroduced to the San Rafael Mountains, Ventura County, California, 1985–1989. Beta estimates, standard errors, and *P*-values are reported to highlight population-level selection by bighorn sheep. Positive values denote selection and negative values indicate avoidance of continuous variables across the landscape. This relationship is reversed, however, for “distance to” variables (i.e., “Distance to Road” and “Distance to Water”). In addition, negative values for “Years Since Fire” indicate selection for areas that have burned more recently.

Habitat Variable	β	Standard Error	<i>P</i> -Value
Intercept	-1.54057	0.43137	< 0.001
Elevation	2.03356	0.14899	< 0.001
Slope	0.24706	0.17033	> 0.05
Ruggedness	0.45620	0.11609	< 0.001
Cos Aspect	-0.51838	0.11050	< 0.001
Sin Aspect	0.41345	0.08044	< 0.001
Distance to Road	0.34120	0.09090	< 0.001
Distance to Water	-0.59932	0.10983	< 0.001
Years Since Fire	-0.74212	0.13916	< 0.001
Conifer Forest	-1.15560	0.24510	< 0.001
Mesic Chaparral	-0.86246	0.21021	< 0.001
Xeric Chaparral	-0.60986	0.24576	< 0.05
Oak Woodland	-0.46081	0.10859	< 0.001
Slope:Winter	1.06979	0.27220	< 0.001
Slope:Spring	1.41257	0.30904	< 0.001
Slope:Fall	1.39987	0.33289	< 0.001
Fire:Winter	-0.40370	0.26175	> 0.05
Fire:Spring	-0.42629	0.27578	< 0.05
Fire:Fall	-1.05857	0.36822	< 0.01
Cos Aspect:Winter	0.24510	0.20415	> 0.05
Cos Aspect:Spring	0.71919	0.244410	< 0.01
Cos Aspect:Fall	0.20676	0.27810	> 0.05
Conifer:Winter	-0.08958	0.39389	> 0.05
Conifer:Spring	-0.06702	0.37636	> 0.05
Conifer:Fall	1.40517	0.52815	< 0.01
Xeric:Winter	-0.03937	0.39734	> 0.05
Xeric:Spring	-0.50633	0.40006	> 0.05
Xeric:Fall	1.14301	0.55355	< 0.05
Mesic:Winter	-0.13534	0.34901	> 0.05
Mesic:Spring	-0.27615	0.35380	> 0.05
Mesic:Fall	1.05927	0.46650	< 0.05

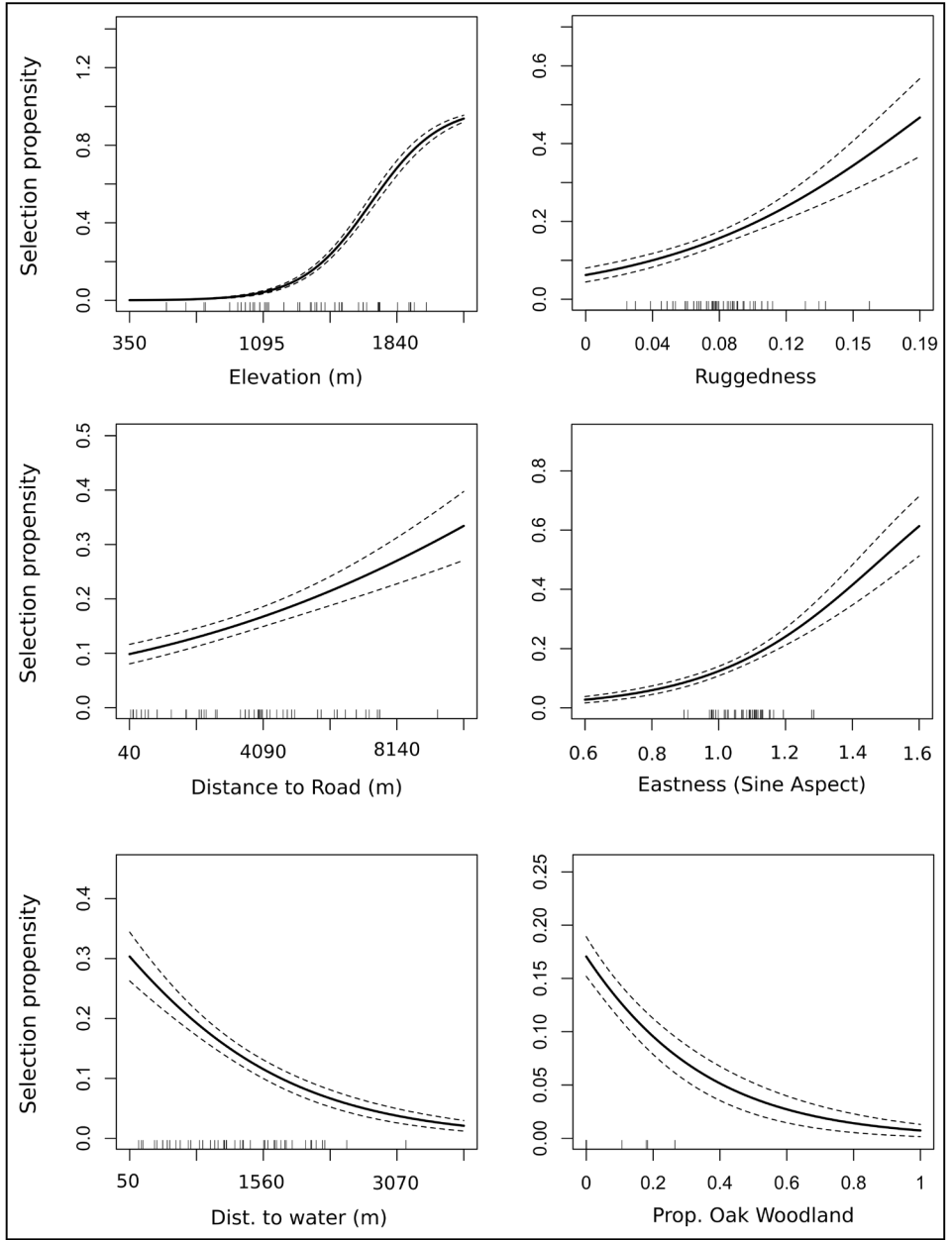


Figure 4. Partial dependence plots illustrating seasonally independent responses of bighorn sheep to environmental gradients in the San Rafael Mountains, California. Each panel represents a different environmental gradient, and each curve represents predictions from our best-performing resource selection model across each environmental gradient, with all other covariates held at mean values. Our best-performing resource selection model indicated little or no evidence for seasonal variation in selection propensity for all environmental gradients depicted in this figure. Dashed lines denote 95% confidence intervals.

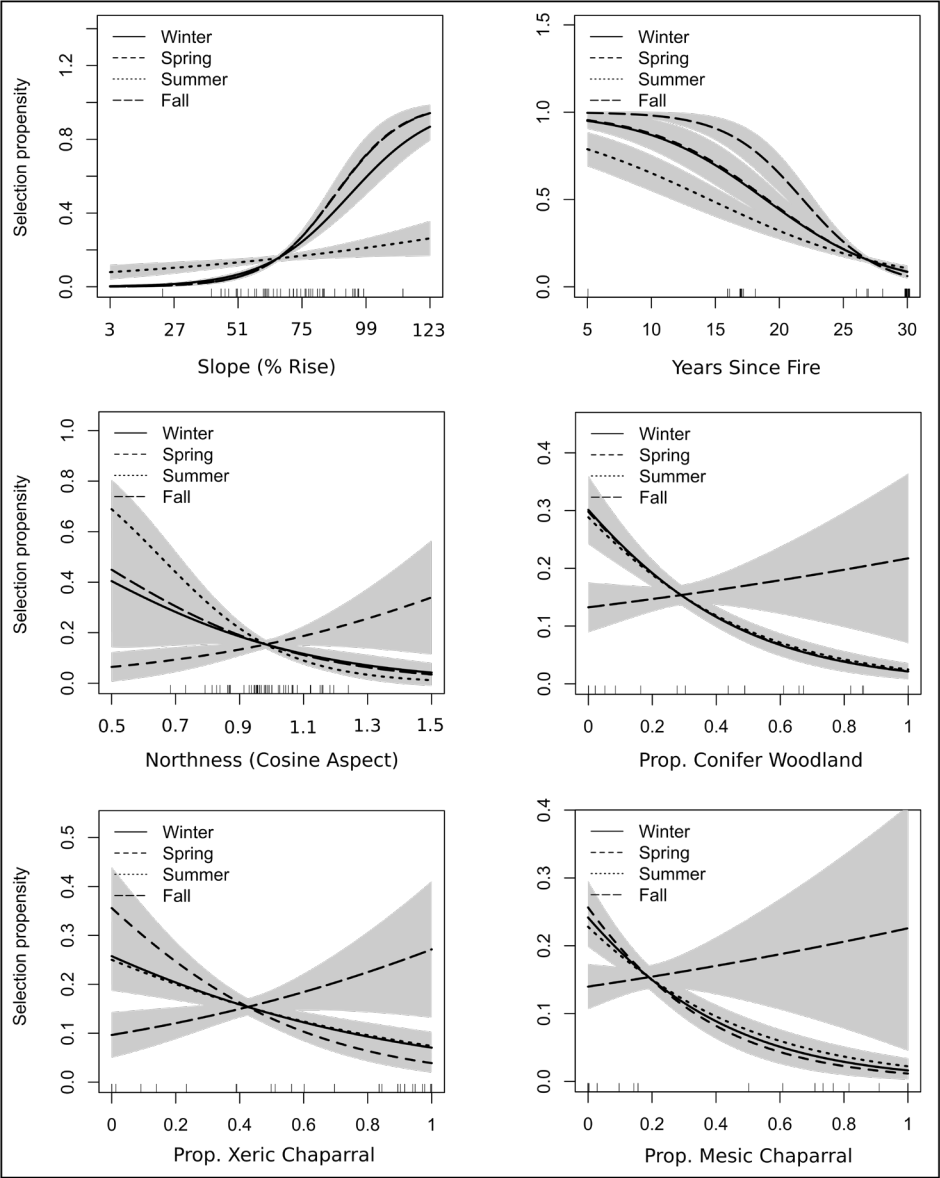


Figure 5. Partial dependence plots illustrating seasonally dependent responses of bighorn sheep to environmental gradients in the San Rafael Mountains, California. Each panel represents a different environmental gradient, and each curve represents season-specific predictions from our best-performing resource selection model across each environmental gradient, with all other covariates held at mean values. Our best-performing resource selection model included a seasonal interaction term for all environmental gradients depicted in this figure. Shaded areas denote 95% confidence intervals.

not significant during winter months; Figure 5). Magnitude of selection or avoidance varied by season in addition to some variables shifting between negative and positive effects on selection. Bighorn sheep selected southeastern slopes during summer and more northeastern slopes during spring, while fall and winter interaction terms were not significant (Table 1).

Although selection for topographic variables generally was consistent across seasons, selection for specific habitat types was less pronounced (Table 1). Seasonal variation in selection for habitat-classes was most pronounced in fall and summer. During fall, bighorn sheep selected areas with greater percentages of conifer cover, xeric chaparral, and mesic chaparral compared to summer, but selected for areas with lower concentrations of oak woodland, conifer cover, mesic chaparral, and xeric chaparral during summer. Additionally, the habitat diversity variable did not appear in any seasonal model, indicating that individuals did not select areas having a higher diversity of habitat types over areas with high percentages of specific habitats. Our cross validation returned an AUC value of 0.85, indicating strong predictive ability for our top resource selection model. Finally, we used the regression coefficients from the top model to predict bighorn sheep habitat use during each season (Figure 6).

DISCUSSION

Reintroductions have played an important role in the restoration of bighorn sheep to historically occupied areas (Brewer et al. 2014). Although post-translocation assessments are expensive and labor-intensive, such information is important for informing future management decisions (Thompson et al. 2001; Brewer et al. 2014; Tetzlaff et al. 2019). Nonetheless, increasing responsibilities among wildlife biologists working in state or federal agencies (Meine et al. 2006), declining operating budgets (Hutchins et al. 2009), and shifting priorities within management agencies (Capen 1989) often have precluded the timely assessment, analysis, or publication of results despite what appear to have been successful management actions, and such has been the case with bighorn sheep reintroduced to the San Rafael Mountains.

In our study, habitat selection was similar to that described by Holl and Bleich (1983) for bighorn sheep comprising the source population in the San Gabriel Mountains. The absence of sex as an interaction term, however, was surprising given that males generally range more widely than do females, but with females characteristically using areas most likely to enhance safety for themselves and offspring, and males seeking areas in which to maximize nutrient intake to be competitive during the mating season (Bleich et al. 1997).

The absence of a sex-interaction in the top model may be explained by several factors, among which are a lack of familiarity with the reintroduction site in that monitoring occurred for a period of time inadequate to allow segregation by habitat (Bowyer 2004) to develop into a regular pattern, an extended period of exploratory movements by bighorn sheep as they adapted to the new location (Thompson et al. 2001), small sample size of males, or the level of precision associated with telemetry data. If additional research on habitat selection in the San Rafael Mountains occurs, we anticipate that the long-term presence of this population in that range, combined with telemetry collars employing geographic positioning system technology will yield intersexual differences in habitat selection, a behavioral trait of polygynous ungulates that characteristically segregate by sex during their annual cycle (Bowyer 2004).

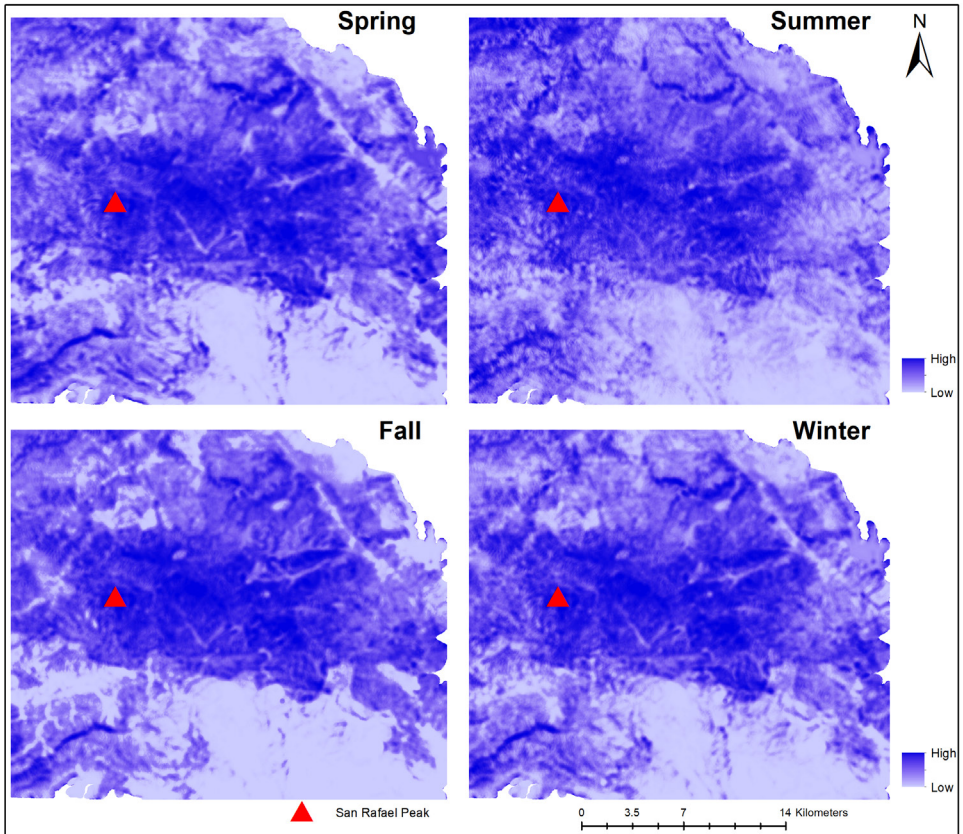


Figure 6. Prediction maps of resource selection during spring, summer, fall and winter seasons for a translocated population of bighorn sheep in the San Rafael Mountains, Ventura County, California, USA. Darker areas represent locations with higher selection probability, while lighter areas represent locations with lower selection probability based on seasonal resource selection functions, 1985–1989. For reference, the release site at San Rafael Peak is indicated on the maps.

Bighorn sheep demonstrated differential selection of habitat types on a seasonal basis, and prediction maps indicated areas of highest prediction probabilities were smaller in size during fall and summer when compared to winter or spring (Figure 6), results that may have occurred because we subdivided chaparral into subcategories rather than treating it as a single vegetation type. Nevertheless, bighorn sheep did select areas that had burned more recently than were available across the landscape, consistent with results from the San Gabriel Mountains (Bleich et al. 2008), and there was a strong seasonal effect during winter, spring and fall consistent with habitat use by herbivores dependent on open terrain and the best available forage (Risenhoover and Bailey 1980, 1985; Holl 1982; Bleich and Holl 1982; Etchberger et al. 1989). Chaparral is a fire-adapted plant community and bighorn sheep rely on recently burned areas both for nutritious forage and for openness, the latter being a key factor in detecting and evading predators (Bleich and Holl 1982; Holl and Bleich 1983, 2010; Bleich et al. 1997, 2008; Holl et al. 2012).

Terrain characteristics, such as slope, aspect, or ruggedness, are important attributes of bighorn sheep habitat (McCarty and Bailey 1994). Bighorn sheep selected higher elevations

and more rugged terrain, but steepness of slope was important only during winter, spring, and summer (Table 1). Steepness of slope alone does not necessarily imply ruggedness, but still may enhance the ability of bighorn sheep to evade predation (Bleich et al. 1997). These results are consistent with those for bighorn sheep elsewhere in the transverse range (Bleich et al. 2009; Anderson et al. 2017; Anderson 2018) as well as bighorn sheep in general (McCarty and Bailey 1994; Bleich et al. 1997).

Bighorn sheep selected east-facing aspects during spring and fall, and south-facing slopes were selected during summer, but aspect did not appear in the winter model. Bleich et al. (1997), who also used aerial telemetry in their investigation of habitat selection by bighorn sheep in the Mojave Desert, did not include aspect in their analyses because of its sensitivity to resolution associated with the small size of aspect polygons relative to potential location error. Further, there was no selection for aspect by bighorn sheep in the Sonoran Desert when hot and cool seasons were compared, but females did avoid 'level' terrain (Andrew et al. 1999). Similarly, bighorn sheep in the San Bernardino Mountains demonstrated no significant selection for aspect (Bleich et al. 2009). Given the confounding nature of locational error and the absence of selection for aspect reported by others, we suggest investigators view selection of aspect reported here with some level of caution.

Overall, bighorn sheep in the San Rafael Mountains selected for areas closer to water and further from roads during all seasons, consistent with bighorn sheep inhabiting the Sonoran and Mojave deserts elsewhere in California (Bleich et al. 1997; Andrew et al. 1999). Our index to habitat diversity, however, failed to enter our models. This was somewhat surprising because an increase in precipitation occurs with elevation in the Mediterranean climate (Aschmann 1973) typical of the San Rafael Mountains and diversity of vegetation can enhance forage quality in some systems (Wehausen and Jaeger 2016). The absence of a diversity effect reported here may be explained by the short duration over which monitoring was carried out, extensive exploratory movements by reintroduced bighorn sheep, or other factors that are yet unrecognized.

Management Implications

Collectively, bighorn sheep selected areas closer to water when compared to random points and selected recently burned areas during all seasons, and the importance of topographic attributes is clear. These results are consistent with reports from elsewhere in the transverse range and provide useful information with which to evaluate the suitability of additional areas for reintroductions therein (Holl 1982). Moreover, seasonal effects on habitat selection and resulting selection probabilities (Figure 6) have important implications for the design or timing of aerial surveys, or interpretation of aerial survey data (Schaller and Junräng 1988; Bleich et al. 1997; Rubin and Bleich 2005; Wehausen and Bleich 2007).

Our results clearly demonstrate the importance of the role of fire to bighorn sheep in the San Rafael Mountains, and provide a platform upon which future investigators can base more complex models. Managing for habitat burned at intervals of ≤ 15 years and that is selected by bighorn sheep elsewhere in the transverse ranges (Bleich et al. 2008) is inconsistent, however, with the natural variation in fire-return intervals in coastal chaparral systems. Moreover, fires occurring at < 15 -year intervals increase the spread of exotic herbaceous plants (Keeley and Fotheringham 2003). The careful application of prescribed fire to simulate a more natural fire regime will, however, enhance habitat for bighorn sheep

(Holl et al. 2012) and must receive serious consideration for the population to remain viable.

Legislation (U.S. Congress 1994) enacted since the reintroduction currently presents serious obstacles to the application of prescribed fire in wilderness (Bleich 2016). As a result, administrators now must consider actions necessary to maintain a tangible resource and a near-intact ecosystem relative to the sociological (Spurr 1966), intangible (Larsen 1997; Fredrickson and Anderson 1999; Tin 2012), or sociopolitical (Corliss 2019) aspects of wilderness. Current fire management strategies and the constraints imposed by Congress may jeopardize the ability to manage habitat for the benefit of bighorn sheep and other species dependent upon early successional stages of chaparral vegetation.

This population also may provide a refugium for bighorn sheep adapted specifically to the relatively mesic habitats typical of the western transverse range, and could be a source of reintroduction stock should an outbreak of respiratory disease among bighorn sheep inhabiting the San Gabriel or San Bernardino mountains result in a catastrophic loss (Schommer and Woolever 2008; Clifford et al. 2009). In the absence of a strategy to restore a natural fire regime, however, the utility of the San Rafael Mountains as a refugium for a unique ecotype of bighorn sheep is in question.

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Author Contributions

Conceived and designed the study: VCB, SAH

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Performed analyses of the data: MEB, KTS, VCB, DS

Authored the manuscript: VCB, MEB, KTS

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Observations of the spawning ecology of the imperiled Clear Lake Hitch

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Migrations for the purposes of reproduction are widely documented across the animal kingdom and are particularly common in fishes and other aquatic organisms (Dingle 2014). One important migration strategy in fishes is potamodromy, which is the movement from one location to another entirely within freshwater (Morais and Daverat 2016). Thurow (2016) estimated that worldwide there are approximately 13,000 potamodromous fish species. Potamodromous migratory behavior is thought to arise from spatial, seasonal, and ontogenetic separation of optimal habitats for growth, survival, and reproduction (Northcote 1984). Potamodromous species as a group are also relatively imperiled, owing to the loss or destruction of the diversity of habitats often required for successful reproduction and recruitment (Thurow 2016).

The Clear Lake Hitch *Lavinia exilicauda chi* is an imperiled potamodromous cyprinid that is endemic to a single freshwater lake: Clear Lake, Lake County, California, USA. It was originally described as a unique subspecies of *Lavinia exilicauda* (Hopkirk 1973) but has recently been proposed as a distinct population segment (Baumsteiger et al. 2019). The species lives to approximately six years of age and attains a maximum size of approximately 350 mm fork length. As juveniles and adults, it feeds primarily on macroinvertebrates, including insects and zooplankton (Geary and Moyle 1980). Formerly highly abundant and a staple food for the Pomo tribes of the Clear Lake region, Clear Lake Hitch abundance is believed to have declined substantially from historical levels (CDFW 2014). Presently, Clear Lake Hitch is listed as threatened under the California Endangered Species Act and has been petitioned for listing under the U.S. Endangered Species Act.

The Clear Lake Hitch exhibits a potamodromous life cycle, whereby adults ascend Clear Lake's ephemeral tributaries during the spring to spawn. Adult migration, spawning, embryo incubation, larval development, and juvenile emigration all occur during a short temporal window during the spring season when dry stream beds become temporarily inundated from seasonal rains. Some spawning has been observed along the shoreline of Clear Lake (Kimsey 1960), but within-lake spawning is not presently known to be a significant

source of Clear Lake Hitch production and recruitment. Anthropogenic modification and loss of stream spawning habitat are thought to be important elements driving the decline of Clear Lake Hitch (CDFW 2014).

Clear Lake Hitch have been observed in streams during periods of migration and spawning (e.g., <http://lakelive.info/chicouncil/>). However, aside from Kimsey's (1960) description of spawning along the Clear Lake shoreline, descriptions of spawning behavior and habitat use within streams have been relatively limited in scope (Moyle 2002; Macedo 1994; Murphy 1948). For example, spawning habitat has long been characterized as clean gravel substrate at water temperatures of approximately 14–18 °C. The purpose of this paper is to document fortuitous observations of Clear Lake Hitch spawning and holding in stream habitat to generate baseline information that is needed to manage the species. The observations facilitated addressing the following questions (1) under what water temperature and flow conditions does spawning occur? (2) what are the major habitat features where spawning takes place? (3) what are the fundamental aspects of spawning behavior? (4) what is the immediate fate of eggs deposited during spawning? and (5) when not engaged in spawning, what type of stream habitat is used by Clear Lake Hitch and do they actively feed?

Clear Lake is in Central California, approximately 100-km north of San Francisco Bay. It is the largest natural freshwater lake completely within California (Goldman and Wetzel 1963). At full capacity, it has a surface area of approximately 17,700 ha and a total volume of approximately 1.4 billion m³. I conducted visual observations of Clear Lake Hitch in Kelsey Creek, a primary tributary to Clear Lake, during daylight hours on 01 April 2018. I observed spawning and holding behavior at sites located approximately 6.3 km and 4.6 km upstream of the confluence of Kelsey Creek and Clear Lake, respectively (Figure 1). I obtained water temperature data from a logger (ONSET HOBO Model U20L-002) deployed approximately 2.6 km upstream of the confluence of Kelsey Creek and Clear Lake. The water temperature data are available at <https://doi.org/10.5066/P9L3TXNK> (Feyrer 2019). I obtained flow data from a gauge operated by the California Department of Water Resources located 0.5 km upstream from the temperature logger. The flow data are available at: http://cdec.water.ca.gov/dynamicapp/staMeta?station_id=KCK.

I observed spawning behavior in shallow, low-velocity run habitat encompassing an area of approximately 5 m in length, 3 m in width and 0.25 m in depth which encompassed approximately 50% of the width of the creek. The other approximate 50% of the channel was deeper (up to approximately 1.5 m) and accommodated most of the flow. I measured water surface velocity in the shallow and deep sections of the run using an improvised float method by recording the time it took a floating object to travel 2 m five separate times at three locations along the cross section of the stream, two sites in the shallow section and one site in the deep section. I observed Clear Lake Hitch spawning in the run directly overhead from a position on the Merritt Road bridge which crossed approximately 6 m over the stream. I documented approximately 120 minutes of observation conducted in the afternoon under a bright, clear sky with photographs and video taken with a Nikon D5300 digital camera.

I observed and recorded holding behavior in pool that was approximately 6 m long, 5 m wide and 1.5 m deep that was situated at the head of a short, shallow run. I documented observations using a video camera (SOOCOO S100Pro) positioned underwater on the stream bed at the head of the pool. The video camera was oriented to face in a downstream direction to observe 10–15 Clear Lake Hitch which were holding in the pool and facing into the current. The video camera was secured in place with rocks from the streambed; All

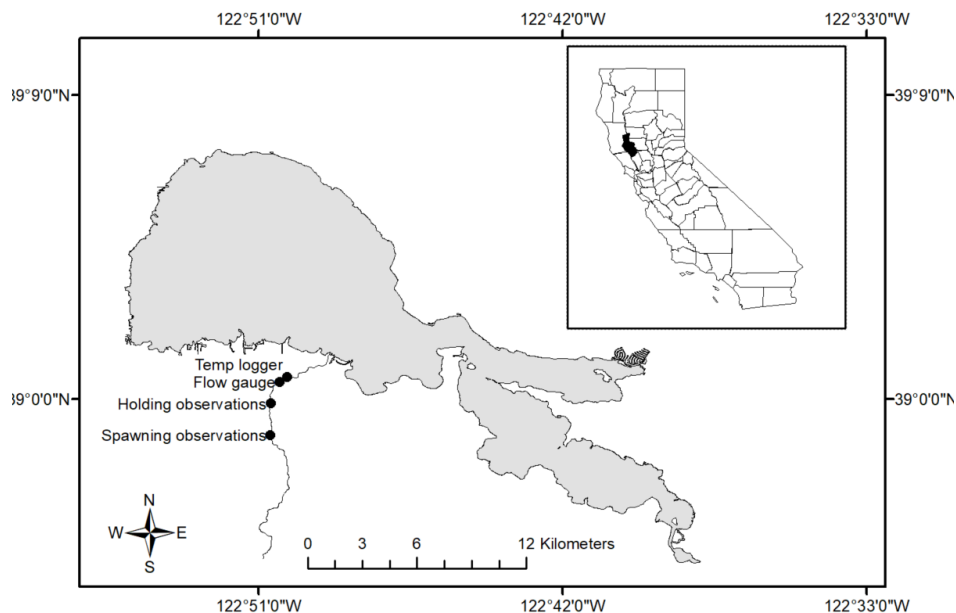


Figure 1. Map of the study area showing the location of the streamflow gauge, water temperature logger, and fish observation sites. The inset is a map of the counties of California with Lake County highlighted as the filled polygon.

observational data, in the form of representative photographs and video clips, are archived in the U.S. Geological Survey's ScienceBase catalogue and are available at <https://doi.org/10.5066/P90BNFFL> (Feyrer 2018).

Average daily water temperature on the date when spawning was observed was 13°C (Figure 2). Average daily flow was 3 m³/sec (Figure 2). This was on a relatively steady yet descending limb of the hydrograph following a peak flow of approximately 40 m³/sec on March 22 (Figure 2).

Average surface velocity was 0.36 m/sec in the run where spawning took place and 0.77 m/sec in the adjacent main channel (individual measured velocity values were as follows: run transect 1: 0.36, 0.41, 0.42, 0.29, 0.37; run transect 2: 0.29, 0.36, 0.33, 0.41, 0.39; main channel transect: 0.95, 0.81, 0.85, 0.78, 0.77). The substrate where spawning was observed was comprised of a mix of irregular-shaped cobble and gravel overlaying a bed of fine pebbles that was clear of sediment (Figure 3). Substrate in the rest of the channel of the immediate area was similar and also included a few larger cobbles and small boulders. Average water depth in the run was not measured but was estimated to be approximately 0.25 m. There was no riparian vegetation in the area other than a few small, isolated unidentified bushes that appeared to be of no significance to the fish or their activity.

The run in which fish were spawning was actively occupied by numerous (10-15+) individual adult Clear Lake Hitch milling in the area. Spawning activity consisted of groups of 2-6 individuals occasionally clustering tightly together and engaging in relatively short but very active and conspicuous spawning bursts (Figure 4). The spawning bursts consisted of one or more males gathering alongside a female and rigorously quivering, rotating and burst swimming with the female in attempt to fertilize eggs broadcast by the female. The

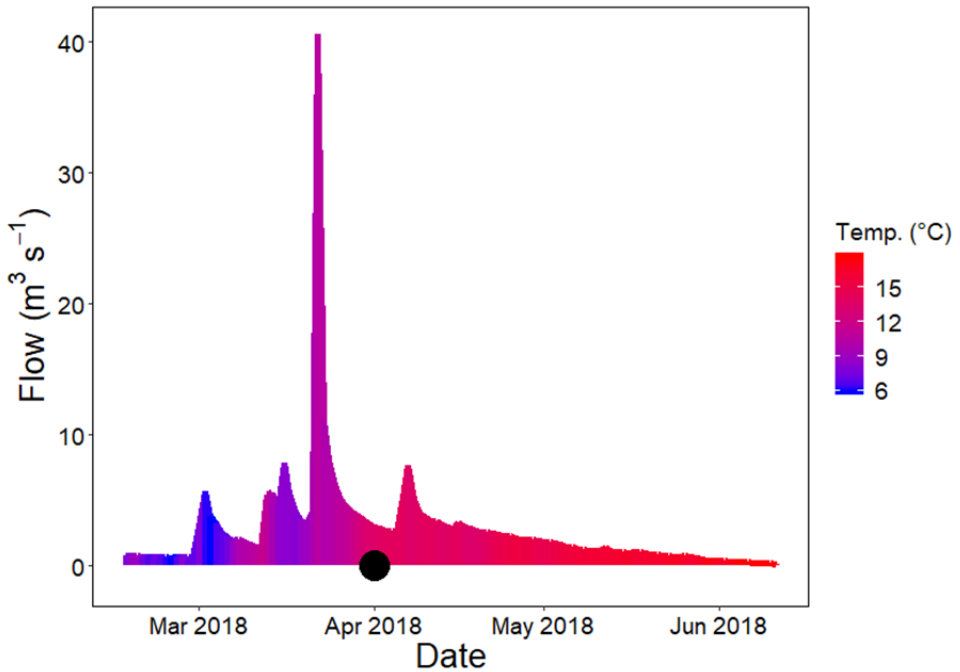


Figure 2. Hydrograph and water temperature of Kelsey Creek, 16 February – 11 June 2018. Flow data were from the California Department of Water Resources, and temperature data were from an ONSET HOBO Model U20L-002 logger deployed for this study. The black marker denotes the date when fish observations occurred.

behavior occurred in very shallow water, often shallower than the body depth of the fish, such that individuals were often observed squirming over rocks with a majority of their bodies exposed to the air. Spawning bursts occurred at seemingly random times and locations within the confines of the run. Concurrently, dozens of non-spawning Clear Lake Hitch were holding in low-velocity sections of an adjacent pool. I could not assess the movements of individuals between the pool and the run. One or more males fertilized eggs broadcast by a female during the spawning bursts. The negatively buoyant eggs quickly settled into crevices of the rocky substrate (Figure 3).

Individual fish not actively engaged in spawning held together in schools in relatively low-velocity pool or margin habitat in various areas throughout the stream. Individuals in the pool habitat monitored with the video camera held in a tight school milling near the bed in the lowest velocity-sections. Individual fish were occasionally observed to quickly dart up in the water column and then return to their original position, giving the appearance of feeding on invertebrate drift.

Clear Lake Hitch release eggs and sperm over unprepared substrate and can therefore be characterized as broadcast spawners, the most common and primitive form among the eight proposed functional categories of spawning modes of North American minnows; the other seven forms being crevice spawning, pit building, pit-ridge building, saucer building, mound building, egg clumping and egg clustering (Johnston 1999). Johnston (1999) noted that over 60% of North American minnows are broadcast spawners. Somewhat unique to extant broadcast-spawning minnows, as well as many other fishes in general, Clear Lake



Figure 3. Representative photographs of negatively buoyant Clear Lake Hitch eggs and the irregular rocky substrate into which they settled. For reference, fertilized egg diameters were approximately 1.0–2.0 mm (Swift 1965).



Figure 4. Two representative examples of Clear Lake Hitch spawning behavior. Top panel: Two smaller males positioned alongside a single larger female immediately prior to a spawning burst. Bottom panel: Typical spawning burst behavior whereby several males are attempting to fertilize eggs broadcast by a female. Additional photographs and video documenting behavior are available at <https://doi.org/10.5066/P90BNFFL>

Hitch undergo potamodromous migrations from lakes to spawn in lotic habitats which are typically dry for much of the year.

Potamodromous migrations in fishes are thought to have evolved as a means to optimize fitness through enhanced growth and/or survival (Northcote 1984). In the case of Clear Lake Hitch, stream spawning must have provided evolutionary fitness benefits to the population, otherwise there would be little reason for it to persist as a dominant trait. Why this trait developed and has persisted, especially given that spawning in permanently wetted lake habitat is possible (Kimsey 1960), is not clearly understood but it is postulated as a means to improve fitness of offspring via optimal environmental conditions and/or refugia from predation. The overall fitness benefits are apparently sufficient to offset a presumed high risk of survival for eggs and larvae. Clear Lake Hitch observed in this study, and anecdotally by others, deposited eggs in extremely shallow water on the descending limb of the hydrograph. Such circumstances risk, and have sometimes been observed to result in, either desiccation of eggs before embryos can develop and hatch or stranding of larvae or juveniles. Interestingly, potamodromy at Clear Lake is not unique to Clear Lake Hitch as Sacramento Sucker *Catostomus occidentalis* and the extinct Clear Lake Splittail *Pogonichthys ciscooides* also have/had similar life history strategies, suggesting broad, generalized benefits to migrating out of Clear Lake for reproduction (Moyle 2002).

Imperilment of broadcast-spawning North American minnows is broadly associated with loss or degradation of spawning habitat, especially through siltation of spawning substrates (Johnston 1999). Spawning habitats of Clear Lake Hitch are vulnerable to similar problems. While flushing flows from seasonal rains likely wash spawning substrate clean of debris accumulated during the dry season, human activities that extract or disturb substrate (e.g., mining or off-road vehicle recreation) in dry stream beds can alter or impair the quantity and quality of instream habitat used for holding, spawning and rearing.

Effective conservation of imperiled species fundamentally requires knowledge of the habitats which contribute to production. The fundamental aspects of the spawning habitat and behavior of the Clear Lake Hitch described in this study will be useful for resource managers tasked with the conservation of this imperiled species. This study expands upon previous limited descriptions of spawning by documenting specific aspects of stream habitat, substrate, temperature, velocity and flow conditions occupied by actively spawning individuals. However, the results are based on relatively few observations. Further study is needed to more fully understand the stream ecology of Clear Lake Hitch. For example, basic information is lacking on the conditions which trigger the migration of Clear Lake Hitch into streams, whether the species exhibits philopatry, and the full range of flow, velocity, temperature, substrate and other habitat features used for holding and spawning. Such information will help resource managers further refine strategies to conserve the Clear Lake Hitch.

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Comparing video and visual survey techniques for Barred Sand Bass in rocky reef ecotone habitats

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Fishery-independent data contribute estimates of the distribution and abundance of marine species that are valuable to fishery management. Here, we compared two fishery-independent survey methods: underwater visual census (UVC) and baited remote underwater videos (BRUVs) to determine the best design for a long term monitoring study of Barred Sand Bass (*Paralabrax nebulifer*) at the edges (ecotone) of inshore natural and artificial reefs in southern California. Both methods were effective at detecting Barred Sand Bass, which were significantly more abundant at artificial compared to natural reefs. Seasonal effects on Barred Sand Bass abundance were observed on UVC but not on BRUV. BRUVs detected Barred Sand Bass more frequently than UVC surveys (83% vs 46%, respectively), and a power analysis estimated that BRUVs required substantially fewer samples than UVC to detect a 100% change in the relative abundance of Barred Sand Bass over time (19 vs 52 samples, respectively). However, Barred Sand Bass exhibited territorial behavior around the bait and BRUV data were quite conservative, suggesting that UVC will perform better at generating estimates of total abundance. UVC only detected three unique species, while BRUVs detected 23, many of which were cryptic or transient and predatory. So a combination of UVC and BRUV surveys may be ideal, depending on the monitoring objective and available resources.

Key words: artificial reef, BRUV, fishery-independent, *Paralabrax nebulifer*, UVC

Reliable, long-term estimates of fish abundance are vital to fishery management. Fishery-dependent data (e.g., landings and catch-per-unit-effort) help characterize catch trends across regional and temporal scales, but they can give inaccurate estimates of fish abundance (Koslow and Davison 2016). Fishery-dependent data can be confounded by factors such as changes in angler interest, regulations, technological advancements, weather, bait availability or species behavior (Harley et al. 2001; Bishop 2006; Johnson and van Densen 2007). Alternatively, fishery-independent monitoring provides important estimates of fish abundance and biomass that can control for some of those confounding variables (Rotherham et al. 2007). Many fishery-independent survey methods such as diver surveys using underwater visual census (UVC) and netting (e.g., seining, trawling, trapping, and gillnetting) have been applied to coastal fisheries for decades but advances in video technology offer new and potentially complementary methods for fishery monitoring.

Diver surveys using UVC has been the most common non-extractive method used for subtidal surveys of fish in nearshore waters since the 1950s (Brock 1954). These surveys provide standardized estimates of fish abundance and biomass and it is an effective method for a range of habitats and species (Murphy and Jenkins 2010). However, diver surveys are labor intensive, subject to inter-observer error (depending on each diver's experience level; Bernard et al. 2013), require relatively calm, non-turbid conditions and are often depth limited. Moreover, UVC may be confounded by the response of fishes to diver presence (Dickens et al. 2011).

Video-based surveys of fish abundance, or baited remote underwater videos (BRUVs), were first used in the 1990's (Ellis and DeMartini 1995) and have since been used extensively, including on temperate rocky reefs (Whitmarsh et al. 2017). Like UVC, BRUVs offer an estimate of the relative abundance of fishes, although the sample area can vary depending on the size of the bait plume (Taylor et al. 2013) and estimates of total biomass or abundance may be conservative since BRUV counts are limited to the maximum number of fish observed at one time to avoid duplicates. Despite these factors BRUVs have proven effective for measuring changes in fish abundance over time and between locations (Hill et al. 2014; Bornt et al. 2015; Malcolm et al. 2015). In the field, BRUVs can be more time and cost-efficient since multiple BRUV units can be deployed simultaneously over a large area. They can be configured to capture more precise size and behavior data (Cappo et al. 2006) and can produce better estimates of abundance for generalist carnivores and species that are diver-averse (Colton and Swearer 2010; Langlois et al. 2010; Lowry et al. 2012). BRUVs can also replace or supplement UVC in areas that are ill-suited for diving due to depth, high currents, or high turbidity (Gilby et al. 2016; Watson and Huntington 2016). These attributes make BRUVs useful in long-term monitoring plans for fishery species (Bornt et al. 2015; Starr et al. 2016). However, their application must be considered on a species-specific basis since the effectiveness of BRUVs varies among feeding guilds (Bernard and Götz 2012).

In southern California, UVC is the primary non-destructive method for long-term monitoring of reef fish populations (Stephens, Jr. et al. 1994; Hamilton et al. 2010; Kushner et al. 2013). Although few studies have used BRUVs in this region, underwater cameras have successfully been used to monitor federally and state managed fisheries in other parts of the USA since the 1990s (Somerton and Glendhill 2005). Exploratory baited video surveys of rockfish in central California suggest this is a promising method for quantifying the abundance of carnivorous fishes in deep, high relief habitats (Starr et al. 2016).

Multiple researchers in southern California run long-term fishery-independent surveys

in kelp forest habitats (Caselle et al. 2010; Kushner et al. 2013; Caselle et al. 2015) but few monitor fishes in the transition area between the reef slope and the seafloor, or ecotone. The Barred Sand Bass (*Paralabrax nebulifer*) is a focal species in southern California's recreational fishery that is resident to ecotone habitats. This species forms large, predictable, annual spawning aggregations that are extremely vulnerable to overfishing (Jarvis et al. 2014; Miller and Erisman 2014). Peak spawning season for Barred Sand Bass has historically occurred during the summer months of July through August (Jarvis et al. 2014), when fish leave their home reefs to aggregate over inshore sand flats throughout southern California (Jarvis et al. 2010), however these aggregations have been absent since 2013 (Bellquist et al. 2017). Fishery-dependent data failed to flag substantial declines in Barred Sand Bass abundance in the early 2000's because of their spawning behavior. Catch rates remained artificially high when anglers targeted spawning aggregations, while the relative abundance of Barred Sand Bass was declining (Erisman et al. 2011). Thus, fishery-independent surveys of relative abundance will be fundamental to the successful management of this species in the future.

Here we compared two survey techniques (BRUVs and UVC) for assessing the abundance of Barred Sand Bass at the ecotone of nearshore reefs in southern California. Our main objectives were to (1) assess and compare the efficiency (based on lowest variance and labor required) of the two methodologies for surveying the abundance of Barred Sand Bass and other fish species over reef ecotone habitat and (2) to identify differences in Barred Sand Bass abundance related to reef type (artificial vs natural) and sampling season (summer vs fall) to help develop a long-term monitoring strategy.

METHODS

Sampling location

Barred Sand Bass are typically found in low densities outside of spawning aggregations (Anderson et al. 1989; Semmens and Parnell 2014). Therefore, we considered a stratified sampling design ineffective. Instead, we chose survey locations where Barred Sand Bass have been observed consistently in past UVC surveys (California Department of Fish and Wildlife and Occidental College's Vantuna Research Group, unpublished data). We sampled six sites in Los Angeles County monthly between June and October 2017 (Figure 1, Table 1). Summer and fall sampling were done because these months offer the best conditions for survey field work (calm weather combined with adequate visibility), and historical fishing knowledge suggests large numbers of Barred Sand Bass are found on reefs in the early fall (Bedford 2001). Three sites consisted of artificial boulder reef, and three were natural rocky reefs. Based on previous research, Barred Sand Bass are most commonly observed on artificial reefs (Martin and Lowe 2010, McKinzie et al. 2014), but natural reefs were included to test this assumption.

The survey sites at the artificial reef were located along the exposed western, middle and eastern sections of the Los Angeles and Long Beach Harbor Breakwater (Figure 1). The breakwater is exposed to west and south swells and is composed of large granite boulders, descending vertically to a gently sloping sand and silt seafloor at ~15 m. There was a narrow canopy of giant kelp (*Macrocystis pyrifera*) in ~6 meters depth along the edge of the wall, but most of the deep reef substrate was covered in sessile invertebrates (e.g., golden gorgonians [*Muricea californica*], tunicates [*Styela montereyensis*], bryozoa spp.). The two natural reef sites along the Palos Verdes Peninsula are rock and boulder reefs with giant

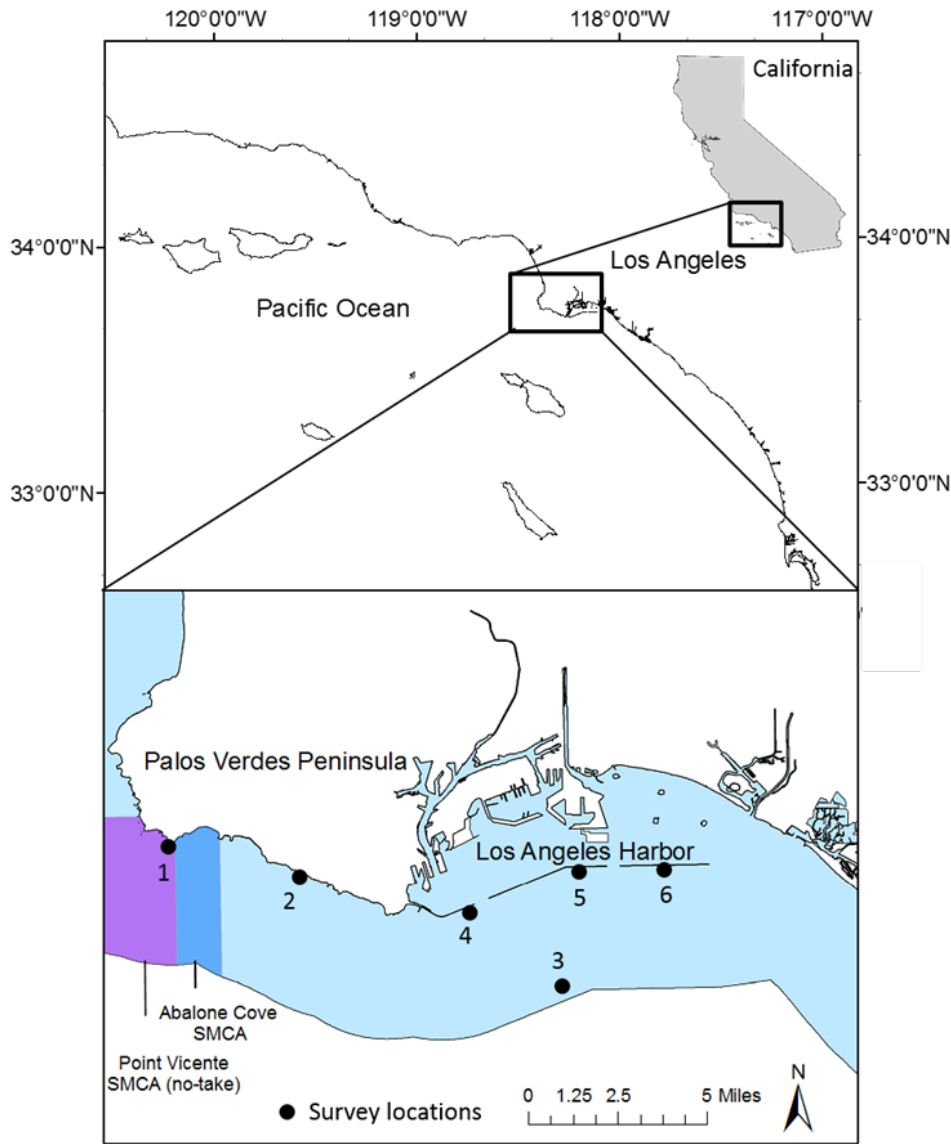


Figure 1. Survey sites in Los Angeles County at natural reefs near Palos Verdes Peninsula (1-3), and artificial reefs at the Los Angeles Breakwater (4-6). SMCA = State Marine Conservation Area.

kelp canopies bordering a sand edge in ~15 m of water. The westernmost reef site is located within a no-take marine conservation area, but protection was not expected to have a major effect on Barred Sand Bass abundance since they are most vulnerable to fishing over sand flats during summer spawning aggregations. The third natural reef site, Horseshoe Kelp, is an isolated patch reef of low relief rock fingers covered in low canopy kelps (e.g. *Laminaria farlowii* and *Pterygophera californica*) at ~20 m depth.

BRUV surveys

We constructed three replicate BRUV frames out of PVC pipe (Figure 2). Each unit stood 0.5 m off the seafloor with a single GoPro Hero 4 camera mounted to an aluminum crossbar inside the frame. We weighted the frames with 6 kg of dive weights and rebar and attached a 1.5 m bait arm with a black plastic mesh bait pocket that extended in front of the camera, level with the substrate. A small subsurface buoy was attached to the surface rope just above the frame with a longline snap to prevent the floating line from obstructing the camera's frame of view.

At each site, we baited the BRUVs with 500 grams of chopped Pacific mackerel (*Scomber japonicus*) and dropped them within 3 meters of the reef edge for 60 minutes. We felt a 60-minute soak time would be conservative since studies in other temperate environments found soak times between 30 and 60 minutes were effective for achieving MaxN (Whitmarsh et al. 2017). We deployed the BRUVs by hand, with the camera facing the reef, from the deck of a research vessel. Each BRUV was marked with a surface buoy and collected using a pot puller. We tested Pacific Sardine (*Sardinops sagax*), Market Squid (*Loligo opalescens*) and Red Sea Urchins (*Strongylocentrotus franciscanus*) as baits in pilot surveys but Pacific Mackerel was the most effective attractant since few to no fishes approached the camera when other baits were used. At each site the first BRUV was deployed at a specific coordinate, while the second two units were deployed along the reef at 200-m intervals following the same depth contour. We completed all video deployments between 0700 and 1300 hours on days with slack high tides in the morning to reduce potential variability in bait plume size and fish behavior related to diel and tidal cycles. The number of BRUV replicates varied among sample days depending on deployment success since frames occasionally landed too far out over the sand away from the reef ecotone or the frame of view was blocked by kelp or boulders (Table 1).

UVC surveys.—At each study site, conditions permitting, SCUBA divers did six replicate 30 m x 2 m x 2 m UVC belt transects (transect area = 60 m² or 120 m³) to count and estimate the length of all fish to the nearest 5 cm. Three transects ran parallel to the reef along the ecotone and three transects ran perpendicular to the reef across the sand (sand transects were ultimately discarded from analysis due to high zero counts). Transects began at a designated GPS point identical to the coordinate used for the BRUVs and the diver teams swam in opposite directions along the depth contour. Typically, two diver teams surveyed each site (i.e. totaling six ecotone transects per site); however, if time allowed, we completed extra transects. One diver swam forward continuously just above the seafloor and recorded fish counts and size classes while a second diver swam side-by-side deploying the transect tape and maintaining the compass heading. At the end of each transect, divers moved forward 2 meters before beginning the next survey to ensure independent areas of reef were sampled. The same divers recorded fish counts on all surveys to reduce inter-observer error. UVC transects were done during the same days and timeframes as the BRUV deployments if visibility remained >3 m. We completed replicate BRUV and SCUBA surveys within a four-day period each month, with sampling occurring on at least three of the four days, to control for temporal variability, except when we rescheduled due to adverse weather conditions on two occasions. UVC surveys were rarely done after a BRUV deployment, but if so, they were done >2 hours later to eliminate any effect of bait plumes on survey results.

Although each reef site was visited monthly from June through October, field conditions dictated the final sampling effort (Table 1). UVC surveys were not done at some sites

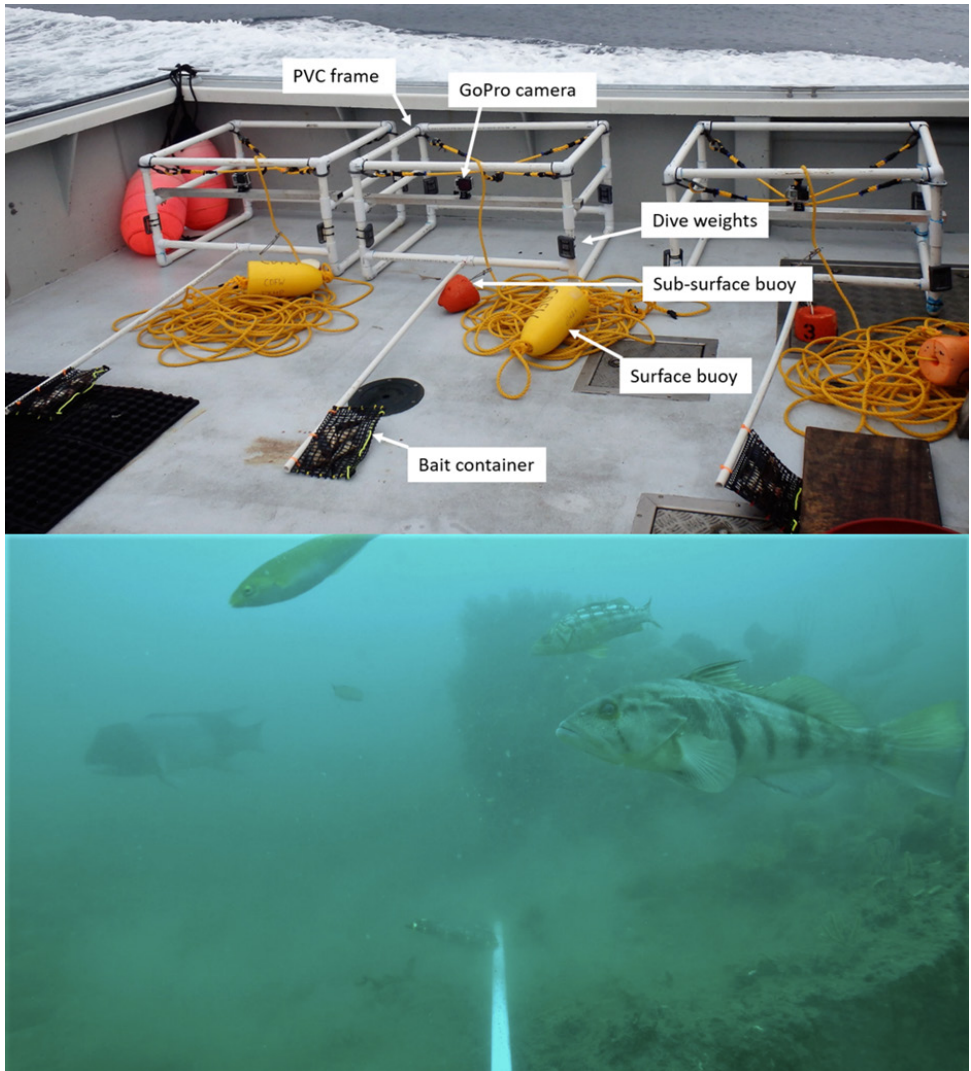


Figure 2. (a) Baited remote underwater video stations (BRUVs) used in this study and (b) a still image from a BRUV showing a Barred Sand Bass, Kelp Bass, Señorita and California Sheephead over ecotone habitat at the Los Angeles Breakwater.

during July and August due to adverse diving conditions (high surge, visibility <3 m). Also, fewer UVC replicates were done on some sample days due to reduced visibility on different parts of the reef.

Data processing

We transferred BRUV video files from cameras to external hard drives and reviewed the first 60 minutes in full, using standard video editing software (e.g., VLC media player). To ensure accuracy and precision, we only evaluated files where the bait pocket was visible throughout the entire recording, and only recorded fish that passed ~ 2 m from the camera

Table 1. Average depth (m) and structure of survey sites in Los Angeles County and the number (n) of replicate BRUV and UVC surveys completed at the reef ecotone each month over a four-day sampling window.

Site	Location	Reef type	Depth (m)	BRUV Surveys (n)					UVC Surveys (n)				
				Jun	Jul	Aug	Sep	Oct	Jun	Jul	Aug	Sep	Oct
1	3 Palms West - PV	Natural	18	1	3	3	3	3	10	9	6	6	4
2	Long Point - PV	Natural	17	3	2	3	3	3	3	4		3	3
3	Horseshoe Kelp	Natural	20	5	3	3	3	3	2		2	5	5
4	LA Breakwater WEST	Artificial	15	2	3	2	3		3	6	3	3	3
5	LA Breakwater MIDDLE	Artificial	15	1	3	3	3	3	2	7		3	3
6	LA Breakwater EAST	Artificial	18	2	2	2	2	3	2			3	3

(within 0.5 m from the end of the bait arm). The 2 m distance was estimated by the technician, but usually only included fish actively visiting the bait and excluded fishes passing by further from the camera. We did not include surveys in the analysis if the frame of view was obscured for more than a minute at a time during the 60-minute deployment (by boulders/kelp/poor visibility), excluding periodic obstruction by waving kelp. Surveys from BRUVs that landed upside down or facing away from the reef (toward the sand) were also discarded. We used a measure of MaxN (the maximum number of individuals present in the field of view at any one time throughout the one-hour deployment) to assess the abundance of all species. MaxN is the most accepted measure of abundance for video surveys because it prevents the same fish from being counted multiple times during a given deployment (Willis et al. 2000; Harvey et al. 2012).

Statistical analysis: UVC data.—Divers observed very few fish on UVC transects over sand habitat, so only data from ecotone habitat were considered in the analysis. We converted the observed lengths of individual fish to estimates of biomass from UVC survey data (cm) using the published length-weight relationship for Barred Sand Bass (Williams et al. 2013). We converted biomass and abundance estimates to fish density (observed per 100 m²) for ease of comparison with similar studies.

To find the best areas and timeframe for UVC surveys of Barred Sand Bass, we tested the effect of the factors “reef type” (fixed, artificial vs natural), and “season” (fixed, summer [June–August] and fall [September–October]) on fish abundance using a hurdle regression model in the ‘pscl’ package (Zeileis et al. 2008, Jackman et al. 2015) in R Version 3.5.2 (R Development Core Team, 2018). We used a hurdle model because the UVC count data had more zeros than would be expected from pure count data (Poisson distribution) (Barry and Welsh 2002). Hurdle models use a two-step procedure or delta approach (Serafy et al. 2007) where presence-absence data are modelled first using a binomial distribution, followed by a truncated negative binomial model which is applied only to the samples with positive counts (Zeileis et al. 2008). The negative binomial distribution allows for overdispersion in the dataset. To assess the effect of “reef type” and “season” on fish biomass density we ran a linear model on log(x+1) transformed biomass density. Assumptions of normality and homogeneity of variance were confirmed by plotting the residuals from the models.

Statistical analysis: BRUV data.—We tested the relationship between the abundance

(MaxN) of Barred Sand Bass with the same factors as UVC using a general linear model (glm) in R to assess the best areas and timeframe for BRUV surveys. A hurdle model was unnecessary since the BRUV data had few zero counts. We modeled the data with a Poisson distribution, to account for overdispersion and generated P-values using a chi-square test.

Statistical analysis: method comparison.—We ran a power analysis to assess the number of replicates required for each survey method to detect a 50% and 100% change in the number of Barred Sand Bass over time using a two-sample paired t-test with two levels (before and after) in the program “pwr” (R Core Team 2018). We pooled the mean and variance of Barred Sand Bass abundance for each survey method for sites, reef types and seasons to calculate the effect size.

To compare the fish community observed between methods and reef types, we calculated the Shannon Weaver diversity index (H) (Shannon and Weaver 1963). We also ran a Permutational Analysis of Variance PERMANOVA (PERMANOVA+ version 1.0.3) with the fixed factors “method,” “reef type,” and “season” and the random factor “site” on presence/absence transformed abundance data and a Sorenson resemblance matrix. The Sorensen index is recommended for binary data (Clarke et al. 2006). We included a dummy variable of 1 for all samples to calculate the resemblance for transects where no fish were counted (Clarke et al. 2006). We also tested the homogeneity of multivariate dispersions (PERMDISP) using the same design to assess whether differences observed in the PERMANOVA analysis could be attributed to differences in the dispersion of the data. We visualized the species responsible for observed differences using a PCO plot with vectors to illustrate the strength of the relationship for species with Pearson correlations > 0.6 and we tested the strength of these relationships using Dufrene-Legendre indicator species analysis using the ‘labdsv’ package in R (Dufrene and Legendre 1997; Roberts 2014). Only species with significant ($P < 0.05$) indicator values ≥ 40 are presented.

RESULTS

Fish community summary

Divers completed 103 UVC transects and observed 25 different fish species from 13 families. On average, 3.9 ± 1.9 species were observed on each UVC transect. We completed a total of 78 BRUV deployments and observed 45 fish species from 26 families while reviewing the 4,680 minutes of footage. The average number of species observed on each BRUV was 8.6 ± 3.3 (mean \pm SD). Fish diversity differed between reef type and survey method, with more diverse communities observed on artificial reefs than natural reefs ($H = 1.55$ vs. 1.04 , respectively), and a higher diversity detected by BRUVs ($H = 1.66$) than UVC ($H = 0.95$). Of the 48 species recorded during the study, 22 were seen on both survey methods (46 %). All but three species observed on UVC transects were also observed on BRUVs (Table 2). However, 23 species were observed on BRUVs but not on UVC, including rockfishes, Giant Sea Bass (*Stereolepis gigas*), and elasmobranchs (Table 2). The species observed most frequently on both survey methods was California Sheephead (*Semicossyphus pulcher*), which was present in 100% of BRUV and 93% of UVC surveys, followed by Kelp Bass (*Paralabrax clathratus*) which was observed 95% and 71% of the time, respectively (Table 2).

The time of first arrival for any fish species typically occurred within the first minute of the BRUV reaching the bottom. The average time until the maximum number of spe-

cies was observed on each BRUV was 37 ± 14 min, and ~40% of cameras did not detect the maximum number of species until the last 15 minutes of recording (Figure 3a). The maximum number of species occurred earlier for more BRUV units on natural reefs (after 20 minutes) than artificial reefs (most reached a maximum species count after 35 minutes). The average time until the first Barred Sand Bass arrived at each BRUV unit was 5.6 ± 5.6 min at artificial reefs and 19.0 ± 17.4 min at natural reefs. There was a bimodal distribution of MaxN counts for Barred Sand Bass on both natural and artificial reefs where 20 to 40% of surveys recorded MaxNs in the first 10 minutes, while most of the remaining surveys did not achieve MaxN until after 35 minutes (Figure 3B).

PERMANOVA results (based on presence/absence data) showed the fish community differed significantly between reef types and between survey methods, with no main effect of season (Table 3). There was a significant interaction between sampling method and reef type but not with season (Table 3, Figure 6) and post-hoc tests suggested fish community structure differed between reef types on UVC surveys ($t = 3.0$, $p = 0.025$) but not on BRUVs ($t = 1.7$, $p = 0.07$). However, PERMDISP analysis showed there was also a difference in dispersion between reef types, with more variability in species composition or beta diversity among surveys at natural reefs than at artificial reefs ($F_{1,179} = 27.45$, $p < 0.001$). This pattern was visible in the PCO plot and therefore, differences between reef types for UVC were probably due to differences in the variability of the data rather than community structure (i.e., more variability among samples on natural reefs). There was no significant difference in dispersion between survey methods (PERMDISP, $F_{1,179} = 0.85$, $p = 0.41$). Both PCO plots and Dufrene Legendre indicator species (IndVal) analysis suggested that differences in community structure between survey methods were driven by more frequent occurrence of Señorita (*Oxyjulis californicus*), kelp bass, California sheephead and Barred Sand Bass on BRUV surveys (Figure 4, Table 4). IndVal analysis suggested rock wrasse (*Halichoeres semicinctus*) were also responsible for the observed differences (Table 4).

Barred Sand Bass abundance.—We observed Barred Sand Bass consistently using both survey methods, though they were observed in nearly double the number of BRUV drops compared to UVC, on 46% of all UVC surveys and on 83% of BRUV surveys. They were present five times more often on UVC transects at artificial reefs than on natural reefs ($\chi^2_{1,102} = 61.0$, $p < 0.001$) and appeared 1.5 times more often during the fall compared to the summer months on UVC ($\chi^2_{1,102} = 11.4$, $p < 0.001$) (hurdle model on presence absence data) (Figure 5a and b). When present on UVC transects, Barred Sand Bass were also three times more abundant at artificial reefs than on natural reefs ($\chi^2_{1,46} = 15.4$, $p < 0.001$) and nearly three times more abundant during the fall than during the summer months ($\chi^2_{1,46} = 35.2$, $p < 0.001$) (hurdle model on count data, Figure 5c and d). Additionally, when Barred Sand Bass were present, five times more biomass was observed on artificial reefs than on natural reefs ($F_{1,32} = 12.87$, $p < 0.01$) and four times more biomass was observed during the fall months compared to the summer months ($F_{1,32} = 11.98$, $p < 0.01$; Figure 5e and f). In BRUV surveys, Barred Sand Bass were nearly twice as abundant on artificial reefs compared to natural reefs ($\chi^2_{1,76} = 14.3$, $p < 0.001$), but there was no significant difference in the number observed during summer and fall sampling events ($\chi^2_{1,76} = 3.8$, $p = 0.05$; Figure 5g and h).

BRUV surveys had more statistical power than UVC to detect a change in the abundance of Barred Sand Bass (Figure 6). At least 52 UVC surveys are required to detect a 100% change in abundance and at least 206 UVC surveys are required to detect a 50% change with a power of 0.8. In comparison, only 19 BRUV surveys are needed to detect a 100%

Table 2. Frequency of occurrence of the most common fishes observed on UVC and BRUV surveys over ecotone habitat, listed in order from most to least frequently observed on BRUVs.

Family	Scientific name	Common name	BRUV	UVC
Labridae	<i>Semicossyphus pulcher</i>	California Sheephead	100	93
Serranidae	<i>Paralabrax clathratus</i>	Kelp Bass	95	71
Serranidae	<i>Paralabrax nebulifer</i>	Barred Sand Bass	83	46
Labridae	<i>Halichoeres semicinctus</i>	Rock Wrasse	78	31
Labridae	<i>Oxyjulis californica</i>	Señorita	59	27
Pomacentridae	<i>Chromis punctipinnis</i>	Blacksmith	50	53
Embiotcidae	<i>Embiotica jacksoni</i>	Black Surfperch	42	20
Malacanthidae	<i>Caulolatilus princeps</i>	Ocean Whitefish	36	3
Pomacentridae	<i>Hypsypops rubicundus</i>	Garibaldi	33	14
Kyphosidae	<i>Medialuna californiensis</i>	Halfmoon	26	4
Embiotcidae	<i>Rhacocholis vacca</i>	Pile Perch	24	3
Kyphosidae	<i>Girella nigricans</i>	Opaleye	24	2
Scorphaenidae	<i>Scorpaena guttata</i>	California Scorpionfish	24	1
Sebastidae	<i>Sebastes auriculatus</i>	Brown Rockfish	24	0
Sebastidae	<i>Sebastes carnatus</i>	Gopher Rockfish	18	0
Embiotcidae	<i>Rhacocholis toxotes</i>	Rubberlip Perch	15	4
Sebastidae	<i>Sebastes atrovirens</i>	Kelp Rockfish	12	2
Sebastidae	<i>Sebastes serranoides</i>	Olive Rockfish	12	3
Embiotcidae	<i>Hypsurus caryi</i>	Rainbow Perch	10	3
Haemulidae	<i>Anisotremus davisonii</i>	Sargo	10	8
Sebastidae	<i>Sebastes serripes</i>	Treefish	10	1
Myliobatidae	<i>Myliobatis californica</i>	Bat Ray	9	0
Polyprionidae	<i>Stereolepis gigas</i>	Giant Sea Bass	8	0
Hexagrammidae	<i>Oxylebius pictus</i>	Painted Greenling	6	1
Sebastidae	<i>Sebastes mystinus</i>	Blue Rockfish	6	3
Carangidae	<i>Seriola lalandi</i>	Yellowtail Amberjack	5	0
Embiotcidae	<i>Phanerodon furcatus</i>	White Seaperch	5	0
Sciaenidae	<i>Atractoscion nobilis</i>	White Seabass	5	0
Paralichthyidae	<i>Paralichthys californicus</i>	California Halibut	4	0
Scianidae	<i>Cheilotrema saturnum</i>	Black Croaker	4	0
Embiotcidae	<i>Brachyistius frenatus</i>	Kelp perch	3	0
Gobiidae	<i>Rhinogobiops nicholsii</i>	Blackeye Goby	3	0
Muraenidae	<i>Gymnothorax mordax</i>	California Moray	3	0
Sphyrnidae	<i>Sphyrna argentea</i>	Pacific Barracuda	3	0
Triakidae	<i>Triakis semifasciata</i>	Leopard Shark	3	0
Bathymasteridae	<i>Rathbunella hypoplecta</i>	Stripedfin Ronquil	1	0

Table 2 - continued.

Family	Scientific name	Common name	BRUV	UVC
Carangidae	<i>Trachurus symmetricus</i>	Pacific Jack Mackerel	1	0
Clinidae	<i>Heterostichus rostratus</i>	Giant Kelpfish	1	1
Cottidae	<i>Scorpaenichthys marmoratus</i>	Cabazon	1	0
Heterodontiae	<i>Heterodontus francisci</i>	Horn Shark	1	0
Hexanchidae	<i>Notorynchus cepedianus</i>	Broadnose Sevengill Shark	1	0
Paralichthyidae	<i>Citharichthys stigmaeus</i>	Speckled Sanddab	1	0
Pleuronectidae	<i>Pleuronichthys ritteri</i>	Spotted Turbot	1	0
Pleuronectidae	<i>Pleuronichthys coenosus</i>	C-O Sole	1	0
Sebastidae	<i>Sebastes dallii</i>	Calico Rockfish	1	0
Haemulidae	<i>Xenistius californiensis</i>	California Salema	0	3
Kyphosidae	<i>Hermosilla azurea</i>	Zebra Perch	0	4
Rhinobatidae	<i>Rhinobatos productus</i>	Shovelnose Guitarfish	0	1

change in abundance while 72 BRUV surveys are needed to detect a 50% change with a power of 0.8. Surveys using BRUVs required around three hours per survey unit (including data collection, video review, and data entry) while each UVC survey only required around one hour in total (including data collection and data entry).

DISCUSSION

This study offers the first comparison of video (BRUV) and diver surveys (UVC) for assessing fish abundance over the ecotone of rocky reefs in California. Both methods were capable of detecting Barred Sand Bass and the results indicate that fall surveys at artificial reefs would detect the largest aggregations. Surveys using BRUVs had greater power to detect changes in the abundance of Barred Sand Bass since the data were less variable and frequency of occurrence was higher. But BRUVs were also substantially more labor intensive than UVC due to processing time and the data were less reliable for making estimates of total abundance since they were conservative and affected by fish behavior. Targeted fishery species were observed more frequently on BRUV than UVC and BRUVs sampled a higher species richness by detecting more cryptic and transient predatory species.

While nearly half of all species observed during this study were detected by both BRUV and UVC, the most commonly targeted fishery species (Kelp Bass, California Sheephead, and Barred Sand Bass) were detected more frequently on BRUVs. This pattern is consistent with previous studies that found UVC surveys are less effective at detecting highly mobile, recreationally fished species (Lowry et al. 2011) and this may be attributed to biases in the survey method. For example, BRUVs may detect these fishes more often simply because they sample a larger area than UVC due to the size of the bait plume and the longer survey time (Willis et al. 2000). The sampling area for each BRUV can only be calculated if simultaneous estimates of current velocity and direction are collected (Taylor et al. 2013) and this varies temporally due to changes in tidal and sea state, but BRUVs could easily sample five times the area of a UVC transect, even if the radius of the bait plume were only 10 m.

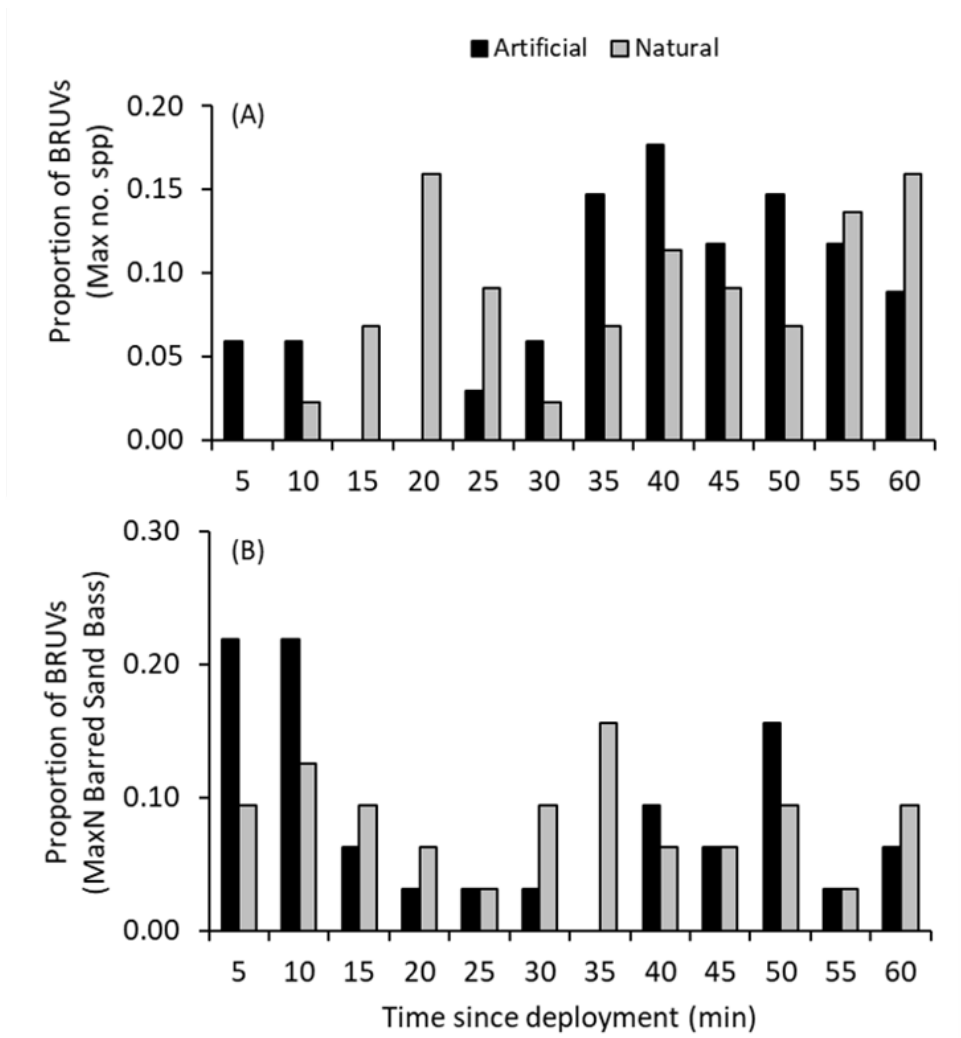


Figure 3. The proportion of BRUV survey units that reached (a) the maximum species richness and (b) the MaxN count for Barred Sand Bass summed by 5-minute bins across the 60-minute deployment.

Additionally, species-specific biases may influence the frequency that a particular species is observed on each method. For example, clear declines in the abundance of targeted fishery species have been observed in relation to diver presence (Dickens et al. 2011), but not in relation to the presence of BRUVs (Whitmarsh et al. 2018).

BRUVs detected more species than UVC, including four elasmobranchs (Leopard Shark, Sevengill Shark, Horn Shark, and Bat Ray) and four transient pelagic species (White Seabass, Yellowtail, Pacific Barracuda, and Pacific Jack Mackerel). Several species of cryptic, reef-associated predators were also observed solely on BRUV including California Moray and three species of rockfish (Calico, Brown, and Gopher Rockfish). These results agree with previous studies that found BRUVs are better than UVC at detecting invertebrate carnivores, generalist carnivores and cartilaginous fishes (Colton and Swearer 2010; Langlois

Table 3. Results of a comparison of all fish species observed using presence/absence data and a Sorenson resemblance matrix in PERMANOVA for the fixed factors reef type, method and season.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Reef Type	1	15,293	15,293	5.2	0.015	719
Season	1	1,492	1,492	0.8	0.578	9,953
Method	1	22,164	22,164	16.8	0.003	9,958
Reef Type*Season	1	1,964	1,964	1.1	0.418	9,956
Reef Type*Method	1	5,472	5,472	4.1	0.026	9,944
Season*Method	1	1,080	1,080	2.1	0.150	9,960
Reef Type*Season*Method	1	1,437	1,437	2.8	0.104	9,964

et al. 2010; Bernard and Götz 2012) since these fishes are known to display diver-averse behavior (Watson and Harvey 2007). On the other hand, prior studies found UVC surveys detect a higher species richness since divers are more effective at counting cryptic species (Colton and Swearer 2010; Lowry et al. 2011). Yet this was not observed in our study as BRUVs recorded both more predators and more species overall than UVC, including cryptic rockfishes. It is surprising that BRUVs detected more rockfish since UVC surveys using similar methods were more effective than BRUVs for these species in Canada (Burke 2018). Divers in this study may have missed cryptic species since they swam continuous transects and did not use dive lights or spend time looking under boulders, especially at the artificial reef where high relief boulders and deep crevices offered substantial shelter. Both cryptic and transient predatory species contributed considerably to species richness in our surveys, making BRUV a better method for characterizing species richness and diversity in southern California's reef ecotone habitats.

We found more variability in UVC fish community structure data on natural reefs when compared to UVC surveys on artificial reefs, perhaps due to the inherent variability associated with a natural benthos. Natural reef sites were widely dispersed and had differing benthic structure and protection status, while artificial reef sites were located along a single breakwater with similar benthic communities and high relief habitat. However, this trend was not observed for BRUVs, suggesting UVC surveys may be less efficient at sampling the whole fish community at each site. Data from UVC surveys may also be inherently more variable than BRUV data due to the greater heterogeneity of habitats sampled along diver transects (Langlois et al. 2010).

Trends in Barred Sand Bass abundance from BRUV and UVC showed that fall monitoring surveys on artificial reefs would detect the highest frequency of occurrence. The higher abundance and biomass of Barred Sand Bass on artificial reefs was expected based on their habitat preference and foraging strategy. Barred Sand Bass are benthic carnivores that benefit from hunting in turbid, high-sediment habitats such as the LA Breakwater (Anderson et al. 1989; Teesdale et al. 2015). The fact that arrival times for Barred Sand Bass were much shorter on average at artificial reefs compared to natural reefs was probably a function of higher density. Moreover, Barred Sand Bass may occur in higher densities during fall surveys when transient fish return from summer (June – August) spawning grounds

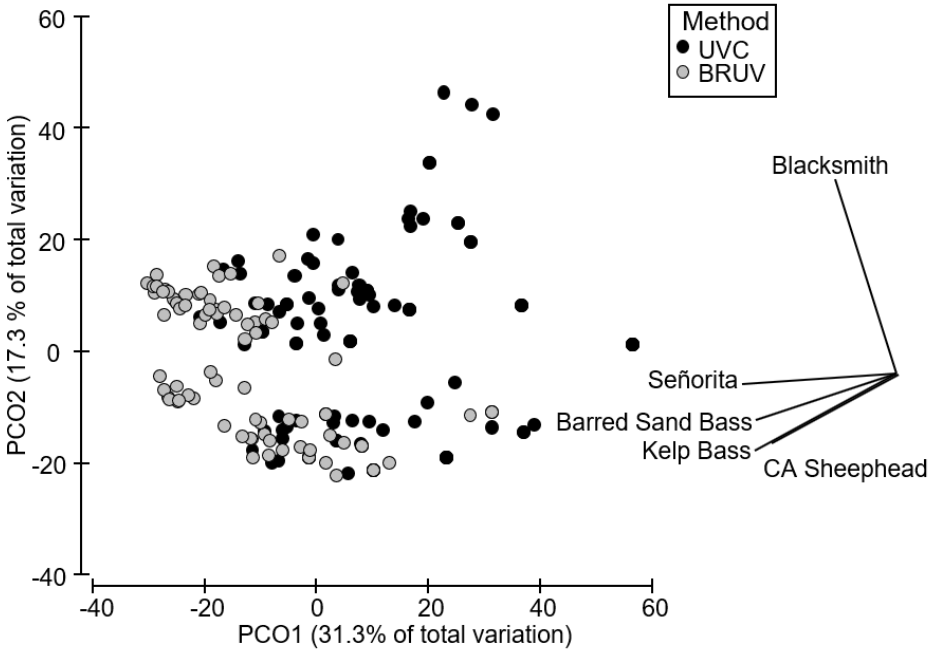


Figure 4. PCO plot comparison of the fish assemblage (presence/absence) seen on UVC versus BRUV surveys over ecotone habitat. Vectors represent species with Pearson correlations > 0.6 and longer vectors indicate stronger relationships.

(Jarvis et al. 2010; McKinzie et al. 2014). Historical observations by California Department of Fish and Wildlife divers and anglers suggest large aggregations of Barred Sand Bass are common on artificial reefs in southern California in early fall (Bedford 2001). BRUVs failed to detect a seasonal effect, potentially due to changes in fish behavior. For example, visibility was often better on fall transects (4.7 m vs 3.9 m on average) and fish may have been more wary of approaching the bait pouch, especially to avoid competitive interactions if other fish were already present.

Barred Sand Bass were detected more frequently on BRUVs, while UVC detected higher counts per transect when they were present. Although density counts are not directly comparable between the two methods since BRUVs do not sample a standardized area, it is still surprising because BRUVs have the potential to sample a much greater area than UVC. The low counts on BRUVs may be a limitation of the MaxN count method used for BRUVs, a result of territoriality of Barred Sand Bass around the bait, or a combination of these factors. Using MaxN prevents fish from being counted twice in a single survey, but it also results in a very conservative estimate of relative abundance, which can underestimate population trends (Conn 2011). This issue may be particularly problematic for an aggregative spawning fish like Barred Sand Bass. Barred Sand Bass did exhibit territorial behavior around the bait bags, often only allowing one or two fish to feed at a time. Therefore, combining BRUV and UVC data may be critical to future monitoring.

Table 4. Indicator values and significance level for species driving differences in presence/absence community structure over ecotone habitat between survey methods. Species listed were more frequently observed on BRUVs.

Species	IndVal	P-value
Rock Wrasse	0.56	0.005
Kelp Bass	0.54	0.005
California Sheephead	0.54	0.007
Barred Sand Bass	0.53	0.005
Señorita	0.40	0.005

BRUV data were less variable and therefore had a greater power to detect changes in fish abundance than UVC. This pattern should be considered with respect to the methodology however, since it may be driven by differences in the characteristics of the abundance metrics used. MaxN counts may be less variable since they are inherently conservative. They may be affected by fish behavior and can reach saturation at high counts when limited by the frame of view. Whereas UVC counts are probably better at detecting true changes in density, and are therefore more variable, and have lower power. Thus, while UVC data were more variable and require more samples to detect change, they will likely be a more sensitive metric to observing changes in total population abundance over time, which is important for fishery monitoring. Data from BRUVs on the other hand may be better suited to detecting the presence/absence of Barred Sand Bass with potential application for detecting range shifts associated with increasing biomass, climate change scenarios or settlement on new artificial reefs. Video surveys would also be useful for confirming the presence of Barred Sand Bass in deepwater habitats, outside the normal scope of diver surveys.

We found there were caveats to each survey method that are important to consider when designing a monitoring study. BRUV and UVC data differ both temporally and spatially since BRUVs sample over a longer time period, but UVC surveys cover a greater physical distance. Soak times of 30 minutes or less have been effective for BRUV surveys of fish on rocky reefs in other areas (Harasti et al. 2015; Watson and Huntington 2016) but our study found at least a 60 minute soak time was required since MaxN counts and species richness often did not peak until well past 30 minutes. The bimodal distribution of the MaxN data suggest that the cameras reaching MaxN early landed directly by the fish, while the remaining cameras probably depended on the bait as an attractant, requiring soak times of at least 35 minutes. Future surveys may consider trialing soak times longer than 60 minutes, however this would be logistically inefficient, since fewer sites could be sampled per day. UVC surveys take less time than BRUVs to complete, sample a standardized area enabling estimation of density, and data entry is simple, compared to the hours of video review required for BRUVs and the limitation of using MaxN—a conservative estimator of relative abundance. On the other hand, BRUVs require less staff expertise to implement in the field (e.g., scientific divers), are effective in low visibility conditions, and provide a permanent record that can be reviewed.

Fish stocks in California are subject to environmental instability (Koslow et al. 2015) and heavy fishing pressure (Zellmer et al. 2018). Those that form spawning aggregations, like Barred Sand Bass, are especially vulnerable to overexploitation. Long term, fishery-independent datasets are essential for detecting and predicting changes in fishery health

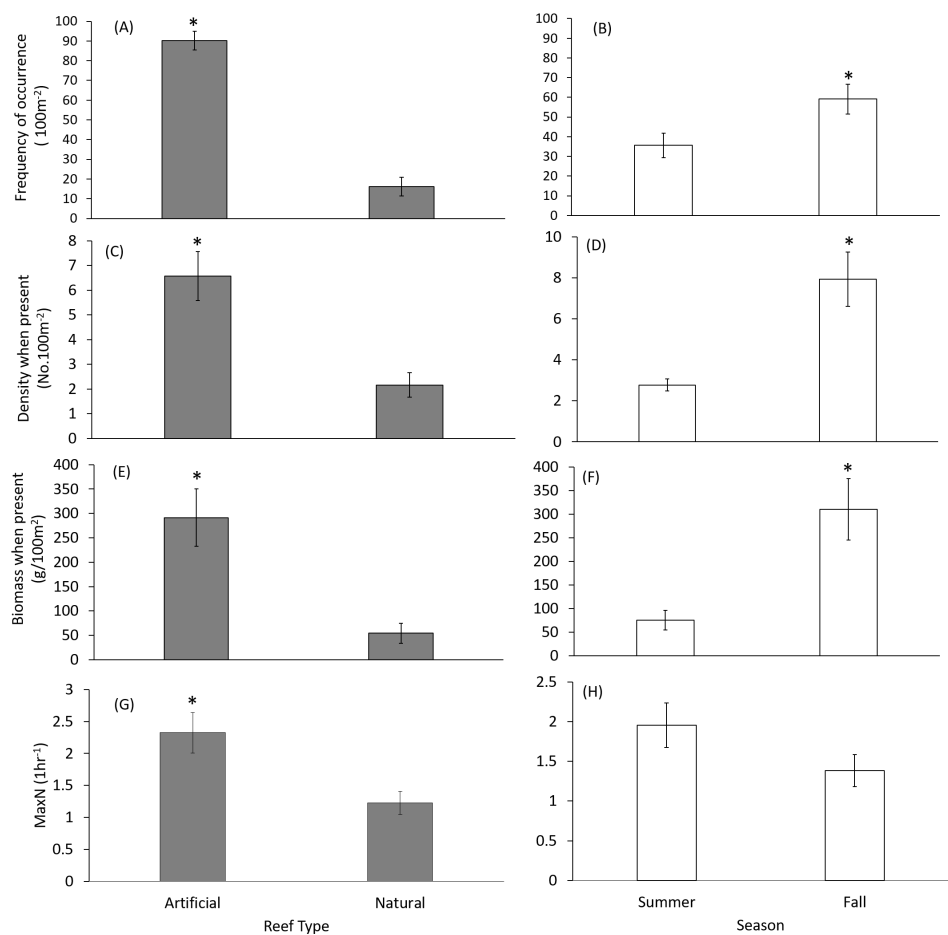


Figure 5. Abundance of Barred Sand Bass by reef type and season from UVC (a-f) and BRUV (g-h) surveys. Error bars = ±1 SE. * = significant effect ($p < 0.05$).

for these species. Both UVC and BRUV methodologies are valuable tools for monitoring Barred Sand Bass over reef ecotone habitats, and each method has strengths and weaknesses that should be considered in relation to monitoring objectives and available resources. In addition to BRUV and UVC, other survey methods should be explored if the resources are available. For example, split beam sonar can be used to estimate the size of spawning aggregations, and it may offer a useful method for estimating spawning stock biomass, a key parameter for fishery management (Won 2018). Although these methods should be tested temporally over more sites across southern California before being adopted as part of a long-term monitoring strategy. Our results also suggest future studies should consider the applicability of BRUVs for monitoring other common fishery species in southern California, such as California sheephead and kelp bass.

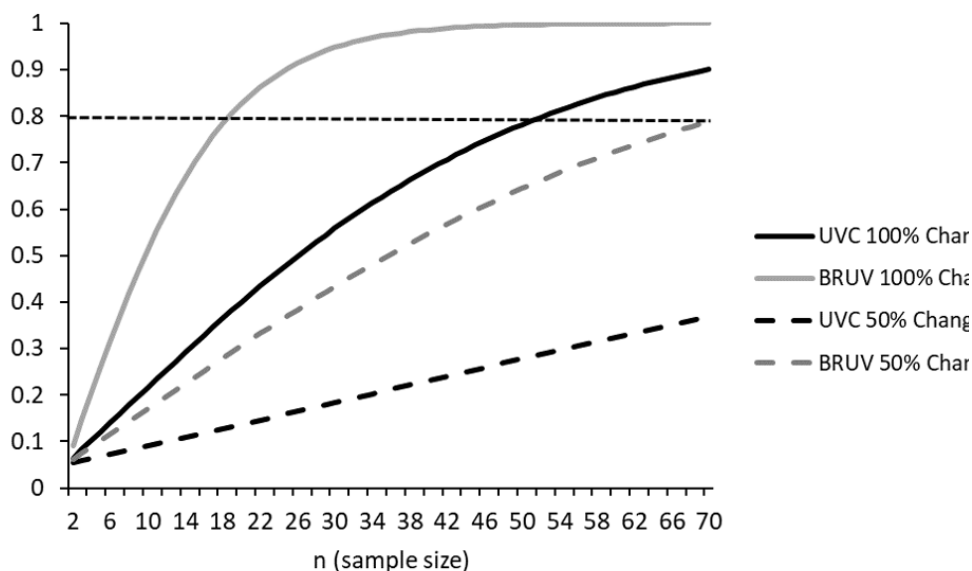


Figure 6. Power curves generated to estimate the sample size required to detect a statistically significant ($p < 0.05$) 50% and 100% change in the abundance of Barred Sand Bass sampled by UVC (black lines) and BRUV (grey lines).

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Author Contributions

Conceived and designed the study (JD, CV, MH, HG)

Collected the data (JD, MH, HG)

Performed the analysis of the data (JD)

Authored the manuscript (JD)

Provided critical revision of the manuscript (JD, CV, MH, HG)

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INFORMATION FOR AUTHORS

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Front.—Bighorn sheep (*Ovis canadensis*). Photo by Lorraine Elrod © California Academy of Sciences.

Back.—Clear Lake Hitch (*Lavinia exilicauda chi*). CDFW file photo.



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