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E.T. Jarvis, C. Linardich, and C.F. Valle

California Department of Fish and Game, Marine Region, Los Alamitos, CA 90720

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Abstract.—During the 1960s and 1990s, the California Department of Fish and Game tagged 8,634 barred sand bass in southern California, and 972 fish (11%) were recaptured. Tag returns suggest barred sand bass are transient aggregate spawners that form spawning aggregations consisting of both resident and migrant individuals. Spawning residency at a historic spawning location was estimated by the frequency of returns over time; most same-year returns (82%, n = 141) were recaptured within a 7 to 35-day period. The maximum recapture distance was 92 km. The average (± SD) non-spawning season recapture distance from peak spawning season tagging locations was 13 ± 8 km, and movement was generally northward. A positive relationship existed between fish size (TL) and migration distance to non-spawning season recapture locations. Fish tagged at a presumed non-spawning season residence were primarily recaptured south of the tagging location during peak and late spawning season; the average migration distance was 17 ± 15 km. Recaptures in subsequent years showed a high degree of spawning (80%, n = 135) and non-spawning (73%, n = 11) site fidelity. This is the first documentation of the spawning-related movements of barred sand bass and will be important for informing management decisions regarding this popular sport fish.

Introduction

Barred sand bass, *Paralabrax nebulifer*, continues to be a highly sought-after sport fish in southern California. In the early 1900s, barred sand bass was landed in both the commercial and recreational fisheries; however, due to limited demand in the commercial fishery and scarcity of the resource during the 1950s, commercial take was banned in 1953 and a 12-in (305 mm) minimum size limit was implemented for the recreational fishery in 1959 (Collyer 1949, Young 1969). Since the 1960s, barred sand bass ranked among the top 10 sport fish in the commercial passenger fishing vessel (CPFV) fleet in southern California, and total annual catches in the recreational fishery averaged nearly two million fish per year (Allen and Hovey, 2001; PSMFC 2010). From 2001 to 2005, "heavy annual landings" (e.g., ~700 tons) were also reported in the commercial fishery of Baja California, Mexico (Aburto-Oropeza et al. 2008).

Catch and effort in the southern California recreational fishery is highest during peak spawning season (June to August) when barred sand bass form large spawning aggregations over soft bottom habitat in depths of 20 to 40 m (Turner et al. 1969; Feder et al. 1974; Love et al. 1996a,b). Based on the exceptionally high landings of barred sand bass during summer months, it is possible these aggregations consist of thousands of fish, although underwater video documentation has never been reported. For decades, anglers have targeted well-known barred sand bass spawning aggregation sites including Ventura Flats, inner Santa Monica Bay, Huntington Flats, San Onofre, and Silver Strand

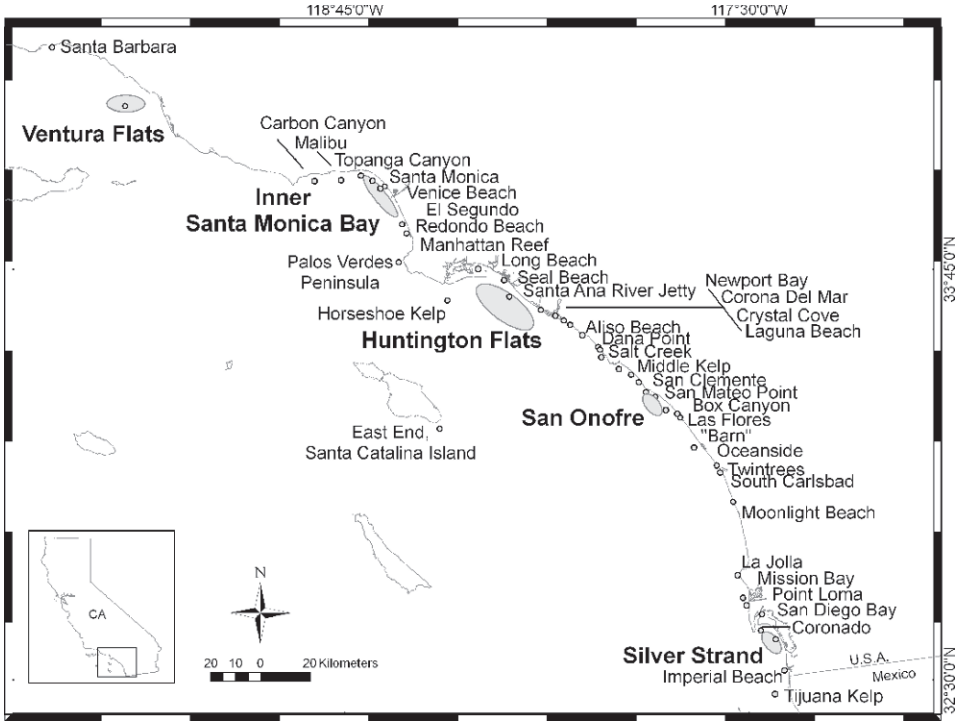

Fig. 1. Map of barred sand bass tagging locations in southern California, historical California Department of Fish and Game tagging project (1960s and 1990s). Shaded ellipses and bolded text identify historical barred sand bass spawning aggregation locations.

in San Diego (Love et al. 1996a; Figure 1). However, since the high in 2000, barred sand bass CPFV catch-per-unit-effort (CPUE) has declined by 65% (CDFG unpublished data) to below the 30-yr average, causing concern regarding the vulnerability of the population to future harvest impacts.

Fish species that are targeted during their spawning aggregations are especially susceptible to overexploitation because harvest effects may not be immediately evident (Sadovy and Domeier 2005). This is due to a condition of hyperstability, in which catch rates (and aggregation densities) remain deceptively high until the population reaches a critical minimum level. Once this occurs, spawning aggregations at historic sites may cease to exist, even after a population rebound (Domeier and Colin 1997; Sadovy and Domeier 2005). Commercial fishing on spawning aggregations in the Caribbean resulted in the disappearance of about one-third of historical spawning aggregations of the Nassau grouper, *Epinephelus striatus*, and a negative impact on the trophic levels of the surrounding ecosystem (Sadovy and Domeier 2005). It is unclear whether recent barred sand bass catch declines are indicative of an already exploited stock because no spawning biomass estimates exist. Nevertheless, a better understanding of barred sand bass spawning behavior and spawning movements will help to make informed management decisions.

Although the timing and location of barred sand bass spawning aggregations in southern California is well-documented, little else is known about their spawning-related movements. After peak spawning, considerably fewer barred sand bass are caught over

sand flats and catches typically resume inshore in bays or near low relief natural or artificial reefs, but not in such high numbers (Love et al. 1996a). Fishery-independent data also demonstrate seasonal differences in barred sand bass densities (Froeschke et al. 2005; Martin and Lowe 2010). These seasonal trends suggest barred sand bass exhibit transient spawning aggregation behavior, in which large aggregations form at specific, predictable locations at higher than average densities for a period of several weeks to months (Domeier and Colin 1997). Transient spawning aggregations are characterized by individuals that may (or may not) migrate relatively long distances, whereas resident spawning aggregations form near or within home ranges, occur year-round, and persist for only hours or days. Clearly, knowledge of the origins and destinations of barred sand bass spawning migrations and understanding the degree of site fidelity to historic aggregation locations will have important management implications for this species.

Throughout the 1960s and 1990s, biologists with the California Department of Fish and Game (CDFG) conducted tag and recapture studies of barred sand bass in southern California and Baja California, Mexico. The recapture information from these two time periods enables us to document the historical spawning-related movements of barred sand bass for the first time. Specifically, our objectives of this study are to examine these historical data for trends in 1) residency at spawning locations, 2) movement to and from spawning locations, and 3) spawning and non-spawning site fidelity.

Methods

Tagging Events

During the 1960s and 1990s, barred sand bass were tagged along the coast of southern California and at one location in Baja California, Mexico (Figure 1). Tagging locations included sand flats, reefs, and bay habitat. During both tagging periods, fish were captured by hook-and-line, measured to the nearest mm total length (TL), externally tagged with spaghetti or T-bar tags, and released. In the 1990s, fish were also captured by bottom trawl, and upon release, tagged fish suffering from barotrauma were recompressed to depth using weighted, inverted milk crates. Loran or GPS coordinates of the tagging sites were recorded (1990s); otherwise, a site name or geographic landmark was provided. In addition, depth (m) and release condition were recorded for some but not all fish. Rewards for recaptures of tagged fish were offered during both tagging periods. Recapture information included date, location, TL (mm), and tag ID number. In the 1990s, recapture depth (m) and Loran or GPS coordinates were also provided when available.

Analyses

All historical barred sand bass tag and recapture data were archived into a relational database. To standardize tagging effort across the two tagging periods, reported locations for all records were assigned a fishing site code based on historical southern California CPFV sport fish surveys (Ally et al. 1990). Site codes (N = 252) were inclusive of nearly every nearshore and coastal mainland and island area in southern California, enabling assignments of specific fishing sites even when only geographic landmarks were reported. Days at liberty, recapture distance (estimated or actual km), and general direction of movement were calculated and incorporated into the database. We used two-sample Kolmogorov-Smirnoff tests to compare distributions of tagged fish length structure, depth of capture of tagged fish, and days at liberty between the two tagging periods. Recapture distances were measured as linear distances between approximate or exact

tagging and recapture locations. The lack of high spatial resolution (e.g., GPS coordinates), especially in the 1960s, probably underestimates the actual linear distance between fish tag and recapture events. However, because our goal was to investigate large-scale movements between fishing sites (rather than fine-scale movements within fishing sites), this underestimate becomes negligible. Spawning season codes were also assigned to each tag and recapture record based on capture month (Nov.–Mar. = non-spawning season, Apr.–May = early spawning season, Jun.–Aug. = peak spawning season, Sept.–Oct. = late spawning season). Where noted, early and late spawning season recaptures were excluded from analyses to limit variability resulting from individuals that may not have been demonstrating spawning-related movements. In this paper we report *recapture* rates and *return* rates. Recapture rates refer to the number of fish recaptured at a given site divided by the total number of fish recaptures. Return rates refer to the number of fish recaptured at a given site divided by the total number of fish tagged at that site.

Spawning Season Residency

To investigate the residence time of individuals at spawning grounds, we selected fish tagged at Huntington Flats during peak spawning season and recaptured at Huntington Flats within the same year. This location was chosen because of the high return rate and because it is a well-known spawning aggregation location. We plotted the percent frequency of tag returns over days at liberty (in 7-day bins) for each group of fish tagged in June, July, and August, and overall. We assumed if spawning season residency of migrant fish did not vary widely among individuals, then the frequency of tag returns should drop off after a similar length of time, regardless of tagging month. This period of time was assumed to represent spawning residence time of migrant individuals and coincided with a drop in percent returns to less than 5%. We also reported the locations and recapture distances of fish that were recaptured away from Huntington Flats during the same peak spawning season.

Movement to Non-spawning Season Locations

Movement from peak spawning season tagging locations to non-spawning season recapture locations was assumed to be movement from spawning grounds to non-spawning season residences. To estimate the proximity of non-spawning season residences to spawning grounds, we grouped non-spawning season recapture distances for fish tagged during peak spawning season into 5-km bins. Average non-spawning season recapture distances were calculated for each tagging location to determine whether non-spawning season migration distances (= linear recapture distances) varied by spawning location. We then tested for a relationship between TL and migration distance using a Spearman Rho rank test.

Movement to Spawning Locations

We examined peak spawning season recaptures of fish tagged in Newport Bay during the non-spawning season to identify if and where Newport Bay residents migrate to spawn. This location was chosen due to the high return rate and because most non-spawning season tagging events were at this location. Spawning migration distances from Newport Bay to spawning grounds were reported and tested for a relationship with TL using a Spearman Rho rank test. We also looked for seasonal patterns in site fidelity to Newport Bay by creating a recapture plot of fish tagged in Newport Bay (Nov.–May) from the years 1964 to 1973.

Spawning and Non-spawning Season Site Fidelity

To investigate annual site fidelity of barred sand bass to specific peak spawning season tagging locations (i.e., presumed spawning grounds) we considered fish that were only tagged during peak spawning season and recaptured during subsequent peak spawning seasons. We constructed a matrix of the number of fish recaptured by tagging location and recapture location, with tag and recapture locations arranged from north (N) to south (S). A higher number of recaptures that occur along a series of corresponding tag/recapture locations within the matrix (i.e., where recapture location = tag location) indicated a higher degree of spawning site fidelity than an arrangement of non-corresponding tag/recapture locations or few corresponding tag/recapture locations within the matrix. To investigate non-spawning season site fidelity, we examined trends in percent site fidelity to Newport Bay (% returns to Newport Bay) across seasons and over subsequent non-spawning seasons. Again, we focused on this location due to the high return rate and because most non-spawning season tagging events were at this location.

Results

Tagging Effort

From 1962 to 1976 there were 4,687 barred sand bass tagged from Santa Barbara to San Diego Bay. Tagging was primarily at Huntington Flats (38%), Newport Bay (21%), Venice Beach (5%), San Onofre (5%), and El Segundo (4%; Table 2). Most fish were tagged during peak spawning season (72%) and non-spawning season (17%); early and late spawning season comprised 5 and 6% of tagged fish. Newport Bay accounted for 91% of the non- and early spawning season tagged fish (n = 737 and 179). Most fish at other locations were tagged during peak spawning season: Huntington Flats (98%), Venice Beach (100%), San Onofre (99%), and El Segundo (92%). Between 1989 and 1999, there were 3,947 barred sand bass tagged from Santa Barbara to Baja California, Mexico, including Santa Catalina Island. In the 1990s, 74% of fish were captured by hook-and-line. The distribution of tagging depths between line-caught and trawl-caught barred sand bass did not significantly differ ($D_{\max} = 0.310$, $p > 0.05$; Table 1). Fish in the 1990s were primarily tagged at Huntington Flats (32%), Horseshoe Kelp (12%), Manhattan Reef (10%), Ventura (9%), Tijuana Kelp (8%), Redondo Beach (6%), and San Diego Bay (6%; Table 2). Most fish were tagged during peak spawning season (76%) and non-spawning season (17%); early and late spawning season comprised 5 and 1% of tagged fish. Eighty-five percent of fish tagged during non-spawning season were tagged at Manhattan Reef (92%, n = 358) and Redondo Beach (97%, n = 198). Tagging effort (= mean fish tagged per day and mean tagging months per year) was similar between the two tagging periods (Table 1).

Ninety-one percent of tagged fish were of mature size (Table 1), and the average size of fish tagged at all sites was bigger than the size at 100% maturity (~ 270 mm TL; Figure 2). Sites with fewer than 80% mature tagged fish were San Onofre (64%), San Diego Bay (63%), and South Carlsbad (54%). Length frequency (LF) distributions of tagged fish significantly varied between the 1960s and 1990s ($D_{\max} = 0.310$, $p < 0.05$); most large fish were tagged in the 1990s at Ventura and Tijuana Kelp (Figure 2). There was a significant positive linear relationship between TL and depth of capture ($r^2 = 0.14$, $p = 0.001$).

Recaptures

There were 972 recaptures; 82% were from the 1960s (Table 1). Overall, 96% were of mature size (Table 1). In the 1960s, return rates ranged between 1 and 35% among sites

Table 1. Tag and recapture summary statistics for barred sand bass tagged in southern California, historical California Department of Fish and Game tagging project (1960s and 1990s).

Tag and recapture results	1960s	1990s
Tagged fish	4,687	3,947
Tagging effort		
days	174	153
Avg (±SD) fish/day	27 ± 32	26 ± 58
Avg (±SD) mo/yr	4 ± 3	6 ± 3
Capture method		
hook-and-line	100%	74%
bottom trawl	–	26%
Avg (±SD) capture depth (m)		
overall	–	15 ± 17
hook-and-line	–	22 ± 7
bottom trawl	–	25 ± 12
Avg (±SD) TL (mm)	306 ± 38	337 ± 72
% mature (≥ 270)	89%	93%
% legal size (≥ 305)	41%	70%
Recaptures	801	171
Recapture rate		
overall	17%	4%
hook-and-line	17%	5%
bottom trawl	–	3%
Avg (±SD) recapture depth (m)	–	23 ± 9
Avg (±SD) TL (mm)	326 ± 43	343 ± 46
% mature (≥ 270)	96%	98%
% legal size (≥ 305)	68%	86%
Days at liberty		
Avg (±SD)	200 ± 197	90 ± 187
Max	1,211	1,258
Recapture distance (km)		
Avg (±SD) - All fish	6 ± 12	7 ± 9
Avg (±SD) - Only movers	18 ± 15	10 ± 9
Max	92	76

with appreciable tagging effort (N ≥ 100 fish, average = 18 ± 11% SD; Table 2). Of these, percent returns were high (≥ 5%) with the exception of San Clemente (1%). Forty-five percent of all recaptures in the 1960s were caught at Huntington Flats and Newport Bay (Table 2). In the 1990s, return rates ranged between 1 and 6% among sites with appreciable tagging effort (average = 3 ± 2% SD); sites with the lowest percent returns were Redondo Beach, San Diego Bay, and Ventura (Table 2). Fifty-eight percent of recaptures in the 1990s were caught at Huntington Flats and Horseshoe Kelp (Table 2). Although the maximum days at liberty were similar between the two tagging periods (Table 1), there was a significant difference in the distribution of recaptures over time between the 1960s and the 1990s ($D_{max} = 0.310$, $p < 0.001$). The 1990s had fewer long term recaptures than the 1960s, with the majority of fish recaptures (75%, n = 128) caught within just 63 days at liberty compared with 315 days in the 1960s. Overall, the

maximum recapture distance was 92 km S (Los Alamitos to Oceanside). It is not clear how many recaptured fish were released versus how many were kept.

Spawning Season Residency

We identified 172 Huntington Flats same-year returns (1960s: n = 117, 1990s: n = 55). Overall, 82% of returns were recaptured within a 7 to 35-day period (Figure 3). Although the numbers of tagged fish were higher for fish tagged in July (n = 1,760) than fish tagged in June (n = 350) and August (n = 808), the return rate was highest for June-tagged fish (14%), compared to only 5% for July- and August-tagged fish. Regardless of tagging month, the frequency of tag returns decreased to less than 5% within a 35-day period, and there was an overall 75% decrease in tag returns between 35 and 42 days at liberty (Figure 3). At 28 days, we observed a peak in June- and August-tagged returns and an inflection in the decline of returns for fish tagged in July. After 35 days, the overall frequency of tag returns remained low (< 5%) with the exception of a second peak at 56 days (Figure 3). Maximum days at liberty was highest for August- (119 days) and June-tagged fish (77 days), compared to 56 days for July-tagged fish.

Fifteen fish tagged at Huntington Flats during peak spawning season were recaptured at a different location during the same peak spawning season; recapture locations for these migratory fish included Horseshoe Kelp (n = 9), Seal Beach (n = 1), Santa Ana River Jetty (n = 3), Corona Del Mar (n = 1), and Dana Point (n = 1). Most of these migratory fish (13 of 15) were tagged in July. Of these, eight were recaptured in July and seven were recaptured in August.

Movement to Non-spawning Season Locations

Non-spawning season recapture distances varied among and within sites. Fifty-nine barred sand bass were tagged during peak spawning season and recaptured during non-spawning season (1960s, n = 50; 1990s, n = 9). Sixty-four percent of fish were recaptured within 1 km of the tagging site; the rest showed a normal distribution around 15 km (Figure 4). In the 1960s, the overall average (±SD) non-spawning season recapture distance was 4 ± 7 km, but fish recaptured away from the tagging location had an average recapture distance of 13 ± 8 km. In the 1990s, eight of nine fish were recaptured away from the tag site; the average non-spawning season recapture distance was 19 ± 14 km. There was a positive relationship between fish size (TL) and migration distance to non-spawning season recapture locations ($r_s(57) = 0.31$, $p = 0.02$; Figure 5a).

Carlsbad and Huntington Flats tag locations had the highest number of tag returns during non-spawning season, but fish tagged at Huntington Flats showed higher variability in recapture distances (Table 3). The farthest movement between peak and non-spawning season was from Ventura to Carbon Canyon (40 km S) and from Tijuana, Mexico to La Jolla (35 km N). The farthest non-spawning season recapture location from Huntington Flats was the Palos Verdes Peninsula (29 km N). Most non-spawning season recapture locations were north of peak spawning season tagging locations (Table 3).

Movement to Spawning Locations

Fish tagged in a presumed non-spawning season residence (Newport Bay) during non-spawning season were primarily recaptured outside of Newport Bay during peak spawning season. We identified at least 16 different peak spawning season recapture sites that were typically located south of Newport Bay; the average (±SD) distance was 17 ± 15 km (Table 4, Figure 6). The farthest recapture location from Newport Bay was

Table 2. Numbers of barred sand bass tagged, percent of tags returned, numbers recaptured (= Recaps), and percent of total recaptures by site in southern California, historical California Department of Fish and Game tagging project (1960s and 1990s). Sites arranged north to south.

	1960s				1990s			
Site Name	Tags	% of Tags Returned	Recaps	% of Total Recaps	Tags	% of Tags Returned	Recaps	% of Total Recaps
Santa Barbara	2	50	1	<1	11	0	0	0
Ventura	–	–	–	–	350	1	1	1
Carbon Canyon	–	–	2	<1	11	9	1	1
Malibu	–	–	1	<1	42	5	1	1
Topanga Canyon	63	6	4	<1	18	0	0	0
Santa Monica	1	100	3	<1	18	0	2	1
Venice Beach	237	13	24	3	–	–	–	–
El Segundo	202	5	7	1	2	0	1	1
Manhattan Reef	–	–	2	<1	388	4	7	4
Redondo Beach	37	22	9	1	204	2	7	4
Torrance Beach	–	–	1	<1	–	–	–	–
Palos Verdes Peninsula	–	–	3	<1	4	0	0	0
Horseshoe Kelp	10	0	8	1	707	5	15	9
Long Beach	98	11	7	1	4	0	4	2
Seal Beach	–	–	2	<1	1	0	2	1
Huntington Flats	1,772	13	235	29	1,258	6	82	49
Santa Ana River Jetty	–	–	6	1	5	20	3	2
Newport Harbor	999	22	125	16	3	0	0	0
Corona Del Mar	1	0	5	1	1	0	1	1
Crystal Cove	7	14	4	<1	–	–	–	–
North Laguna Beach	33	15	19	2	–	–	–	–
South Laguna Beach	109	35	31	4	–	–	–	–
Aliso Beach	12	0	3	<1	–	–	–	–
Salt Creek	32	41	24	3	–	–	–	–
Dana Point	6	33	17	2	28	11	4	2
Capistrano Beach	–	–	1	<1	–	–	–	–
San Mateo Point	136	19	25	3	45	2	0	0
San Clemente	143	1	7	1	–	–	–	–
Middle Kelp	44	43	10	1	4	0	0	0
San Onofre Power Plant	229	28	61	8	7	0	1	1
Box Canyon	–	–	7	1	1	0	3	2
Barn Kelp	120	27	38	5	21	10	1	1
Las Flores	11	27	4	<1	17	18	0	0
Oceanside	157	8	5	1	17	0	3	2
South Carlsbad	104	31	44	3	–	–	–	–
Twintrees	106	14	12	1	–	–	–	–
Round Kelp	–	–	1	<1	–	–	–	–
Encinitas Pt.	–	–	1	<1	–	–	–	–
Moonlight Beach	7	14	0	0	–	–	–	–
La Jolla	1	0	0	0	–	–	–	–
Mission Bay	2	0	0	0	65	2	1	1
Point Loma	–	–	–	–	2	0	3	2
San Diego Bay	4	0	0	0	230	1	0	0
North Island/ Coronado Area	–	–	–	–	6	0	0	0
Silver Strand	–	–	–	–	63	6	4	2

Table 2. Continued.

	1960s				1990s			
Site Name	Tags	% of Tags Returned	Recaps	% of Total Recaps	Tags	% of Tags Returned	Recaps	% of Total Recaps
Imperial Beach	2	0	0	0	99	3	7	4
Santa Catalina Island	–	–	–	–	12	8	9	5
Tijuana Kelp	–	–	–	–	300	4	4	2

Oceanside (52 km S). In contrast to the results reported above (Figure 5a), no correlation was found between TL and spawning migration distance from Newport Bay ($r_s(71) = 0.23$, $p = 0.05$; Figure 5b).

Spawning and Non-spawning Site Fidelity

One-hundred sixty-nine fish were tagged during peak spawning season and recaptured during subsequent peak spawning seasons (1960s, n = 162; 1990s, n = 7). Eighty-nine percent were recaptured after 1 yr at liberty, 8% after 2 yr, and 2% after 3 yr. Overall, 80% were caught back at the same tagging location. The average recapture distance (±SD) for the 20% that were recaptured elsewhere was 18 ± 16 km. Overall, the recapture matrix plot identified a high degree of breeding site fidelity as indicated by the arrangement of recaptures along corresponding tag/recapture locations (Figure 7). Tagging locations with the highest measure of breeding site fidelity were Huntington Flats, Venice Beach, San Onofre, Carlsbad, and Twintrees. We also identified two fish that were twice recaptured in subsequent peak spawning seasons at the same locations (Twintrees and Huntington Flats, Table 5).

Of fish tagged in Newport Bay during non-spawning season, there were 170 tag returns. Two fish were recaptured twice at Newport Bay; once during the respective non-spawning tagging season and again during a subsequent non-spawning season (Table 5). Percent site fidelity was highest during non-spawning (86%, n = 36) and early spawning seasons (97%, n = 37) and lowest during peak (23%, n = 16) and late spawning (29%, n = 5) seasons. Including the two fish that were recaptured twice, there were 15 fish recaptured during subsequent non-spawning seasons. Of these, 73% were recaptured back at Newport Bay, and the other four fish were either recaptured at Laguna Beach (11 km S, n = 3) or San Clemente (31 km S, n = 1).

Discussion

Typical recapture rates using standard tag and recapture methods in the marine environment is 3 to 10% (Lowe and Bray 2006), making it difficult to attain fish movement information without significant spatial and temporal sampling effort. Even with adequate sampling coverage, spatial and temporal differences in fishing effort can potentially yield biased results. In this paper, we report an 11% overall recapture rate consisting of several hundred fish and, with few exceptions, we report relatively high return rates across sites (Table 2). Thus, although certain limitations are inherent in tag and recapture studies, we believe these historical data enabled us to provide an adequate characterization of the large-scale spawning-related movements of barred sand bass in southern California.

Our results indicate that barred sand bass individuals display a high degree of spawning site fidelity, may migrate up to tens of kilometers, and may reside at spawning

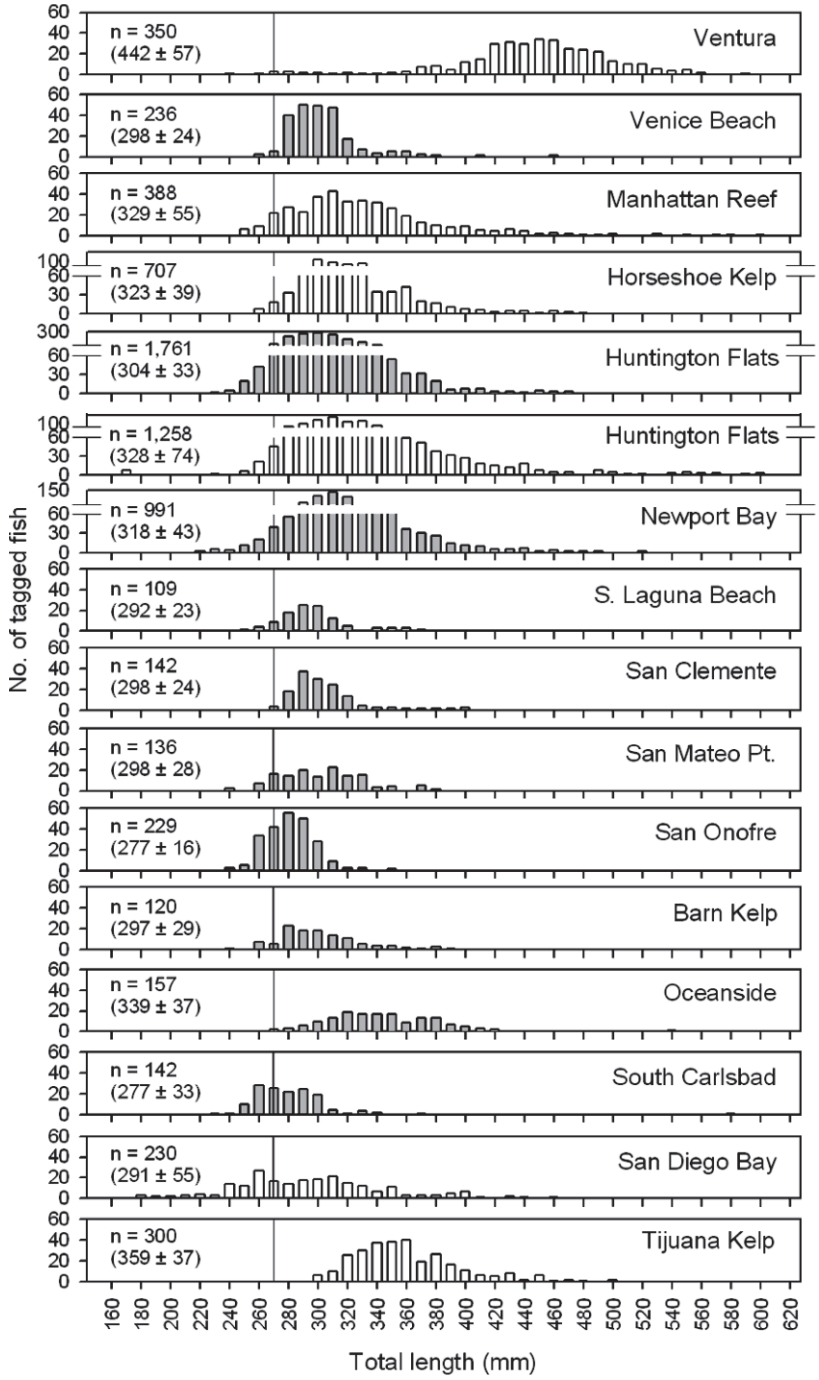

Fig. 2. Length-frequency distributions of barred sand bass by tagging location, historical California Department of Fish and Game tagging project (1960s and 1990s). 1960s and 1990s sites are represented by gray and white bars, respectively. Sites are arranged from north to south, and only locations with at least 100 tagged individuals are shown. Vertical lines represent size at 100% maturity (~270 mm), and numbers in parentheses represent mean total length ± SD.

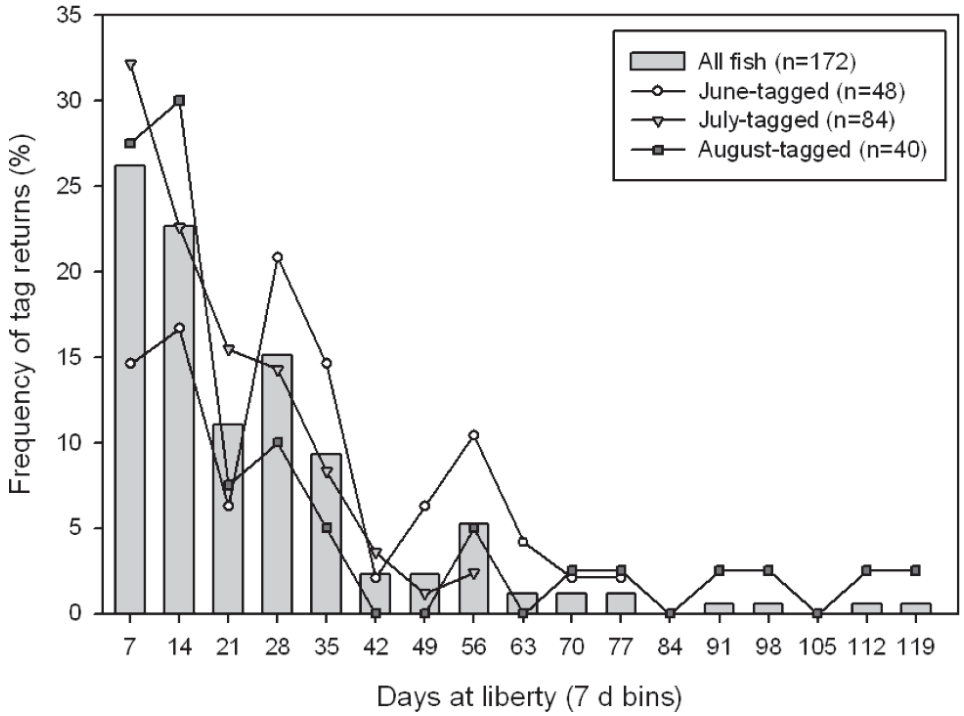

Fig. 3. Frequency of tag returns over time by peak spawning season tag month (lines with symbols) and all fish combined (gray bars) for fish that were tagged at Huntington Flats, CA and recaptured back at that location within the same year, historical California Department of Fish and Game tagging project (1960s and 1990s).

grounds for several weeks. These findings suggest barred sand bass, like other serranids, form transient spawning aggregations (Domeier and Colin 1997). Although more tagged fish displayed resident behavior, our results could potentially be biased toward fish resident to spawning grounds because other locations may not have been fished as intensely during non-spawning season. However, it is also possible that spawning movements were completely missed or that some fish were tagged in locations outside of spawning areas and did not migrate to spawn. Mason and Lowe (2010) reported that a portion of acoustically monitored adult barred sand bass at Santa Catalina Island, CA, showed year-round site fidelity to their home ranges, whereas others were not detected in these areas during spawning season. This type of "polymorphic movement behavior" has also been described for other transient aggregate spawners (Zeller 1998; Egli and Babcock 2004; Semmens et al. 2010).

Movement to and from Spawning Locations

Non-spawning residences were generally north of spawning grounds, implying migration directionality. Moreover, our data suggest spawning aggregations are not comprised of migrants from the same location. Indeed, fish tagged at Newport Bay did not migrate to the same (or to the nearest) spawning grounds. Zeller (1998) reported that coral trout, *Plectropomus leapardus*, showed differences in spawning migration distance, where fish with overlapping home ranges did not necessarily make excursions to the same spawning grounds. Red hind, *Epinephelus guttatus*, another serranid demonstrating

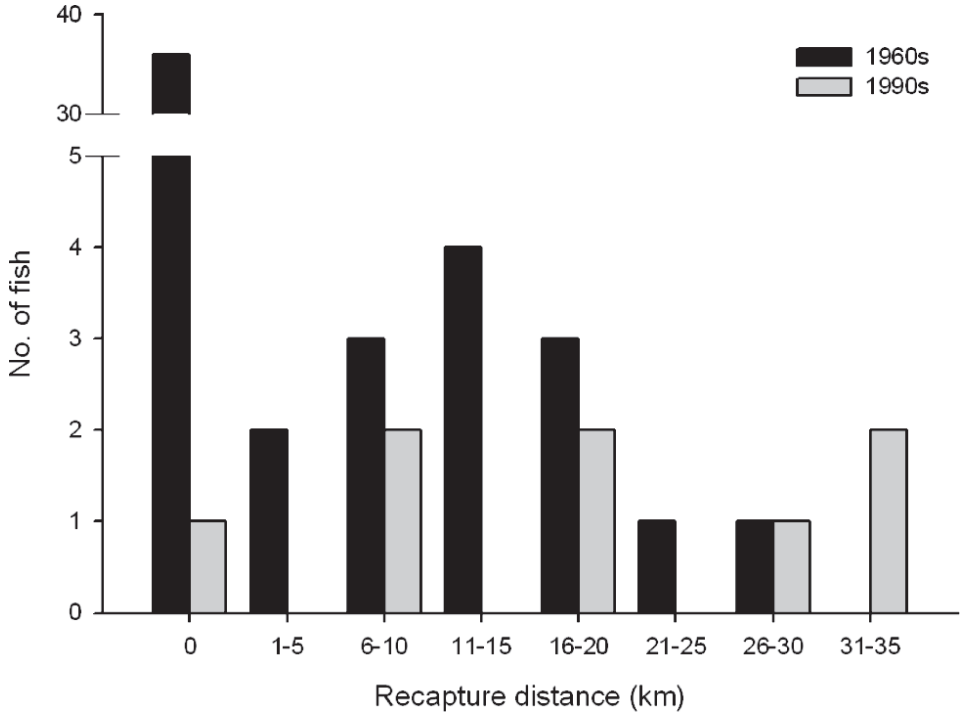

Fig. 4. Recapture distances for barred sand bass tagged during peak spawning season (Jun–Aug) and recaptured during non-spawning season (Nov–Mar), historical California Department of Fish and Game tagging project (1960s and 1990s). 1960s = dark bars, 1990s = gray bars.

transient spawning behavior, also showed variability in spawning migration distance (e.g., 1.8–32.3 km; Nemeth et al. 2007).

Spawning migration distance was related to body condition and size-at-age/maturity in Atlantic cod (*Gadus morhua*; Jørgensen et al. 2008), where fish that migrated longer distances were generally older, bigger fish with higher overall fitness. Although the relationship between barred sand bass TL and spawning migration distance was somewhat inconclusive, we cannot rule out bioenergetics as a possible explanation for individual variability in migration distance, as maturity and fitness were not determined for tagged fish.

Migration distance also varied by peak spawning season tagging location. This could be due to variability in the numbers of returns across sites or distinct differences among sites. Nemeth et al. (2007) attributed differences in migration distance and functional migration area (i.e., the area inclusive of home ranges and spawning ground) to differences in shelf area and fish length between spawning sites, where the site demonstrating a smaller functional migration area and shorter migration distances contained a smaller shelf area and aggregations of smaller fish.

Spawning Season Residency

Barred sand bass return rates at Huntington Flats suggested a spawning residence time within a 7 to 35-day period. Nemeth et al. (2007) reported a similar spawning residency period for tagged red hind recaptured on their spawning grounds (e.g., 7 d–2 mo); however, diver surveys of the same study indicated fish densities fluctuated during spawning season and were influenced by lunar phase and gender. We were unable to

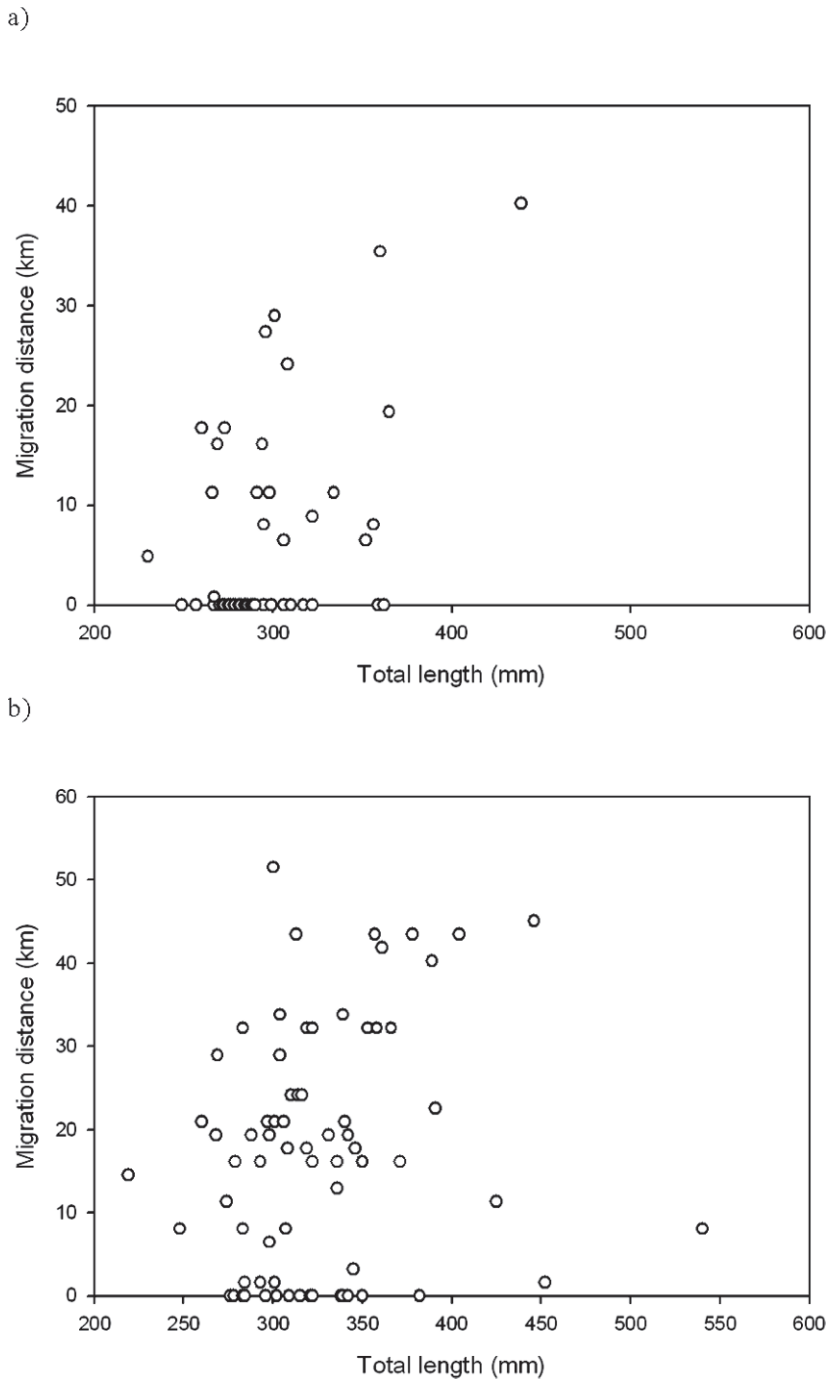

Fig. 5. Fish size (TL) versus (a) migration distance from peak spawning season (Jun–Aug) tagging locations to non-spawning season (Nov–Mar) recapture locations, and (b) migration distance from Newport Bay, CA to presumed spawning grounds. Only the relationship between TL and (a) was significant ($r_s(57) = 0.31$, $p = 0.02$).

Table 3. Recapture distances (= Recap Dist, km) of barred sand bass tagged during peak spawning season (Jun–Aug) and recaptured during non-spawning season (Nov–Mar), historical California Department of Fish and Game tagging project (1960s and 1990s). Dir. = direction of recapture location from tagging location (north versus south along the southern California coastline).

Peak Spawning Season Tag Location	N	Avg Recap Dist (km)	SD	Non-spawning Season Recapture Location	N	Distance from Tag Location (km)	Dir.
Ventura	1	40.0	–	Carbon Canyon	1	40.0	S
Santa Monica	1	–	–	Santa Monica	1	–	–
Venice Beach	2	7.5	10.6	Venice Beach	1	–	–
				Malibu	1	24.1	N
Redondo Beach	3	0.2	0.3	Redondo Beach	3	–	–
Horseshoe Kelp	2	27.0	–	Redondo Beach	1	27.0	N
				Unknown	1	–	–
Huntington Flats	14	5.1	8.7	Huntington Flats	8	0.0	–
				Long Beach	3	11.3–19.3	N
				Palos Verdes Peninsula	1	29.0	N
				Santa Ana River Jetty	1	8.0	S
				Unknown	1	–	–
Newport Bay	1	8.9	–	North Laguna Beach	1	8.9	S
Crystal Cove	1	–	–	Crystal Cove	1	–	–
South Laguna Beach	3	4.7	4.0	South Laguna Beach	1	–	–
				Dana Point	1	11.3	S
				Newport Bay	1	11.3	N
Salt Creek	1	–	–	Salt Creek	1	–	–
Dana Point	1	–	–	Dana Point	1	–	–
San Mateo Point	3	0.0	0.0	San Mateo Point	3	–	–
Middle Kelp	5	3.6	5.1	Middle Kelp	3	–	–
				Aliso Beach	1	11.3	N
				North Laguna Beach	1	17.7	N
San Onofre	7	3.3	5.2	San Onofre	4	–	–
				Salt Creek	2	16.1	N
				Unknown	1	–	–
Barn Kelp	1	–	–	Unknown	1	–	–

Table 3. Continued.

Peak Spawning Season Tag Location	N	Avg Recap Dist (km)	SD	Non-spawning Season Recapture Location	N	Distance from Tag Location (km)	Dir.
Carlsbad	11	0.6	1.4	Carlsbad	10	0.6	–
				Twintrees	1	4.8	S
Twintrees	1	–	–	Twintrees	1	0.0	–
San Diego Bay	1	–	–	San Diego Bay	1	–	–
Coronado	1	6.0	–	La Jolla	1	0.0	N
Imperial Beach	1	8.0	–	Point Loma	1	8.0	N
Tijuana Kelp	1	35.0	–	La Jolla	1	35.0	N

Table 4. Average recapture distances (= Recap Dist, km) of barred sand bass tagged in Newport Bay during non-spawning season (Nov–Mar) and recaptured during peak spawning season (Jun–Aug), historical California Department of Fish and Game tagging project (1960s). Dir. = direction of recapture location from tagging location (north versus south along the southern California coastline).

Peak Spawning Season Recapture Location	N	Avg Recap Dist (km)	SD	Dir.
Horseshoe Kelp	1	24.1	–	N
Huntington Flats	13	17.6	2.2	N
Santa Ana River Jetty	3	8.0	0.0	N
Newport Bay	19	0.5	1.5	–
Corona Del Mar	2	2.4	1.1	S
Crystal Cove	1	1.6	–	S
North Laguna Beach	3	10.2	1.9	S
South Laguna Beach	1	12.9	–	S
Salt Creek	2	18.5	1.1	S
Dana Point	6	20.4	1.3	S
Capistrano Beach	1	24.1	–	S
Middle Kelp	1	24.1	–	S
San Clemente	1	29.0	–	S
San Mateo Point	4	31.4	1.6	S
San Onofre	5	32.8	0.9	S
Barn Kelp	8	42.8	1.5	S
Oceanside	1	51.5	–	S

account for gender-specific movements or movement between tagging and recapture events. Nevertheless, we attribute the secondary peaks in spawning location tag returns at 28 and 54 days at liberty to pulses of immigration and emigration or pulses of aggregation formation, which may correspond with the 28-day lunar cycle. Spawning aggregations of coral trout and Nassau grouper occurred in pulses, and spawning

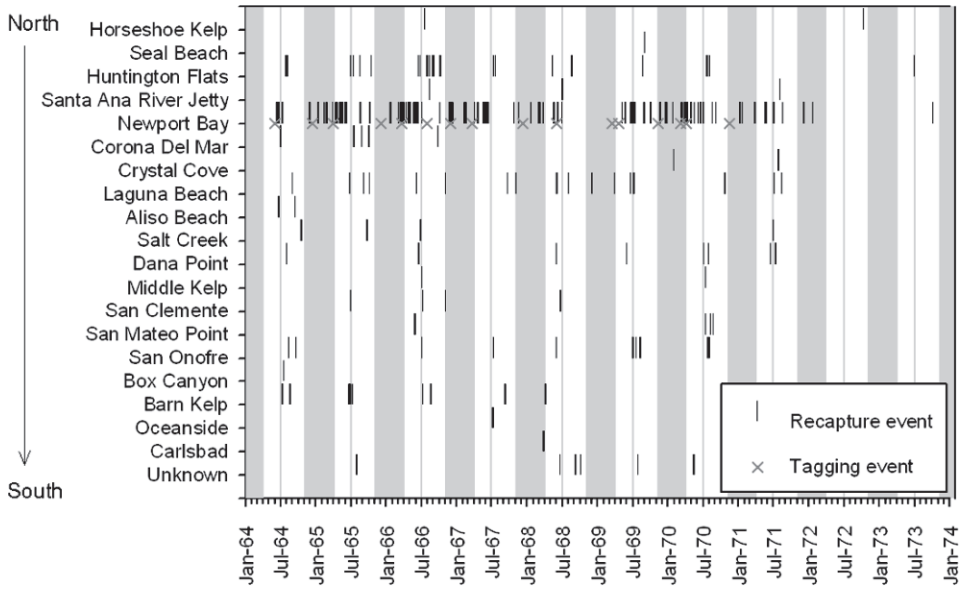

Fig. 6. Recapture plot of barred sand bass tagged in Newport Bay, California, historical California Department of Fish and Game tagging project (1960s). Shaded areas denote non-spawning season and the lines denote the middle of peak spawning season (July).

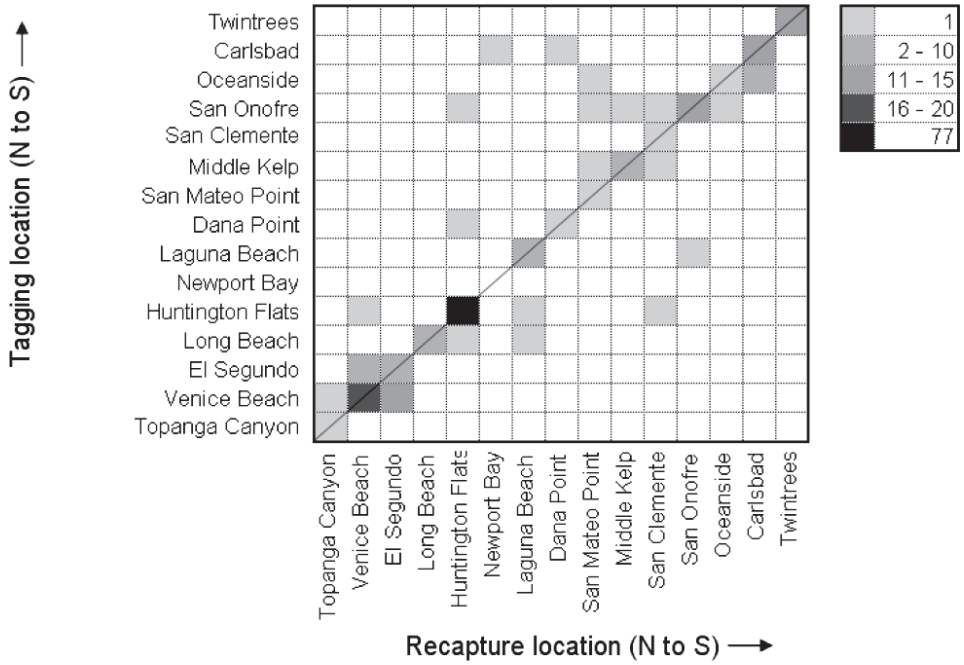

Fig. 7. Recapture matrix plot of barred sand bass tagged during peak spawning season and recaptured in subsequent peak spawning seasons, historical California Department of Fish and Game tagging project (1960s and 1990s). Shaded, darker boxes along the diagonal line indicate a higher degree of breeding site fidelity.

residence times at aggregation sites were relatively short (e.g., 4–14 d; Zeller 1998; Starr et al. 2007). For these tropical species, the pulses were related to specific monthly lunar phases, such as the full moon (Nassau grouper) or the new moon (coral trout). In contrast, spawning aggregation formations of dusky grouper, *E. marginatus*, a temperate serranid, pulsed at relatively longer intervals (e.g., 2–4 wk) without specific lunar synchronicity (Herue et al. 2006).

Fish tagged in June or August demonstrated longer-term residency (i.e., longer maximum days at liberty) at the spawning grounds than fish tagged in July, suggesting densities of migrant fish are highest in July. This timing is in agreement with seasonal trends in barred sand bass fishing effort and CPUE (CDFG unpublished data). Although the abbreviated residency time of July-tagged fish could be related to intense fishing pressure in July, our data indicate otherwise. First, the higher return rate of June-tagged fish relative to July-tagged fish indicated fish tagged in July were less available for recapture, despite there being many more fish tagged in July. Nemeth et al. (2007) reported a very similar pattern in monthly tag return rates of red hind at their spawning locations during spawning season. However, unlike this study, returns were only the result of sampling effort because spawning locations were closed to fishing during spawning season. Second, barred sand bass that were recaptured away from Huntington Flats during the same peak spawning season provided evidence of emigration from the spawning grounds.

Emigration during peak spawning season suggested barred sand bass may utilize multiple spawning locations during peak spawning season. Alternatively, peak spawning season emigrants may represent individuals that had already returned to their non-

Table 5. Tag and recapture dates and locations of barred sand bass recaptured on two separate occasions, historical California Department of Fish and Game tagging project (1960s).

Tagging location	Tag date	1st recapture location	1st recapture date	Recapture distance (km)	Days at liberty	2nd recapture location	2nd recapture date	Recapture distance (km)	Days since 1st recapture
Twintrees	7/26/1968	Twintrees	8/7/1969	0.0	376	Twintrees	9/2/1970	0.0	391
Newport Bay	12/13/1964	Newport Bay	5/15/1965	0.0	153	Newport Bay	11/10/1965	0.0	179
Newport Bay	12/13/1964	Newport Bay	2/27/1965	0.0	76	Newport Bay	5/19/1965	0.0	81
Laguna Beach	8/23/1968	Unknown*	10/8/1968	–	46	Laguna Beach	7/10/1969	12.9	275
Newport Bay	5/31/1964	Corona Del Mar	7/2/1964	1.6	33	Laguna Beach	9/30/1964	16.1	90
Middle Kelp	8/30/1968	Salt Creek*	9/21/1968	6.4	22	Newport Bay	9/29/1968	0.0	8
Laguna Beach	9/17/1968	Unknown*	10/8/1968	–	21	Newport Bay	2/10/1969	0.0	125
Huntington Flats	6/25/1968	Huntington Flats	6/28/1968	0.0	3	Huntington Flats	7/26/1968	0.0	28
Salt Creek	9/19/1968	Salt Creek*	9/21/1968	0.0	2	San Onofre	5/16/1969	35.4	237

* Asterisks denote fish that were released in Newport Bay following weigh-in at a fishing tournament.

spawning residences after spawning at Huntington Flats. With the exception of Horseshoe Kelp, the other emigration sites (e.g., Seal Beach, Santa Ana River Jetty, Dana Point) are not well-recognized as barred sand bass spawning aggregation locations. Fine-scale movement studies of other serranids report strong spawning site fidelity to a single spawning location (Zeller 1998; Starr et al. 2007).

Spawning and Non-spawning Season Site Fidelity

Most fish tagged during peak spawning season were recaptured at the same location during subsequent peak spawning seasons. These individuals may represent year-round residents or repeat migrants. In either case, the high percent of peak spawning returns that these fish comprised (80%) demonstrates a high degree of spawning site fidelity. The mere persistence of barred sand bass spawning aggregations over time (e.g., decades) also implies a strong degree of site fidelity. Tradition may play a primary role in spawning site selection over annual reassessment of resources, especially if resources are relatively unchanging from one year to the next (Warner 1988, 1990). Due to annual differences in tagging effort across tagging locations, it was not possible to accurately quantify long-term inter-annual variability in spawning site fidelity by tagging location. The few recaptures not displaying site fidelity may have reflected individual variability in the timing of spawning-related movements, movement among aggregation sites, or a degree of annual reassessment.

We also identified individuals that demonstrated non-spawning site fidelity to Newport Bay. Fish tagged and recaptured during non-spawning season in Newport Bay may have represented fish that remained there year-round or migrated to spawn and returned in the winter. Although barred sand bass prefer sand/rock ecotone habitat to 30 m depth (Feder et al. 1974; Johnson et al. 1994; Mason and Lowe 2010), adults have been shown to utilize bay habitat throughout the year (Pondella et al. 2006). Nevertheless, a portion of adult barred sand bass tagged in Newport Bay migrated to locations outside of the bay during spawning season. Although it is unknown whether these migrant recaptures would have returned to Newport Bay after peak spawning season, the seasonal pattern in site fidelity reported at this location is highly suggestive. Indeed, barred sand bass acoustically tracked and monitored at Catalina Island were shown to display home ranging behavior and an ability to home (Mason 2008; Mason and Lowe 2010). Coral trout and Nassau grouper have also demonstrated site fidelity to non-reproductive areas in addition to spawning site fidelity (Zeller 1998; Starr et al. 2007).

Recapture Rates

There was a striking difference in recapture rate between the 1960s (17%) and 1990s (4%). Given that tagging effort and numbers of tagged fish did not dramatically differ between the two tagging periods, recapture rates may have been influenced by changes in barred sand bass availability or the willingness of fishers to report tag returns. Generally, high recapture rates in open systems reflect relatively lower population sizes due to the higher probability of encountering the same fish at a later date. This may explain the higher number of long-term recaptures in the 1960s dataset. Barred sand bass were scarce during the 1950s (a cold water period) and encountered more frequently along the coast "in and subsequent to periods of warmer waters" (Young 1969; Feder et al. 1974). Indeed, CPFV barred sand bass catch values were nearly four times greater in the 1990s than in the 1960s despite only a doubling of fishing effort (CDFG unpublished data). Furthermore, kelp bass and barred sand bass larvae densities were also lower during the cool regime (1950s–1970s) and higher in the warm regime (1980s–1990s; Moser et al.

2001). Although it appeared that barred sand bass populations increased in the 1990s relative to the 1960s, barred sand bass stock-recruitment relationships and the effects on these relationships by natural and anthropogenic influences remain unknown.

Management Implications

Our data strongly suggest barred sand bass are transient aggregate spawners that show a high degree of spawning site fidelity. Thus, well-known spawning aggregation locations may comprise a large portion of the total annual reproductive output in southern California and enable spawning biomass estimates for stock assessment purposes. However, accurate biomass estimates at these locations may be difficult to attain without knowledge of whether barred sand bass aggregations flux with new or returning migrants over the course of the spawning season. In the midst of recent catch declines, a precautionary approach to management may be an important consideration until a harvest guideline can be developed. Measures taken to protect stocks of transient aggregation spawners include marine protected areas (MPAs), seasonal bans, and seasonal area closures (Sadovy and Domeier 2005). However, recent California MPA proposals for the south coast study region (i.e., Pt. Conception to the U.S./Mexico border) are not inclusive of known barred sand bass spawning aggregation locations (CDFG 2010), and seasonal bans or seasonal area closures may not be feasible to implement due to overlap among popular recreational fishing grounds. Alternatively, barred sand bass, which appears to have a relatively long spawning residency period (this study) and is capable of daily spawning (Oda et al. 1993), may benefit from a reduction in the current bag limit (10 fish). Further consideration of barred sand bass movement patterns, life history traits, and feasibility concerns will help to define additional management alternatives to protect the resource.

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