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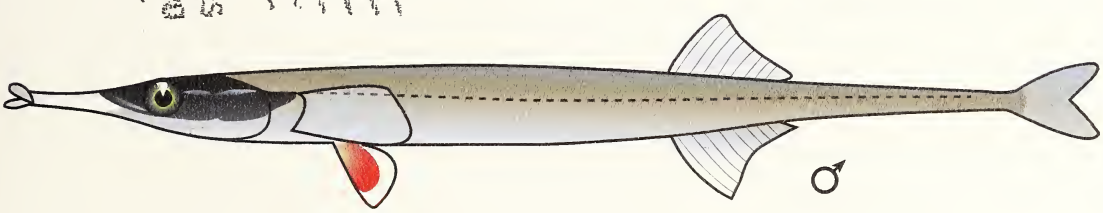

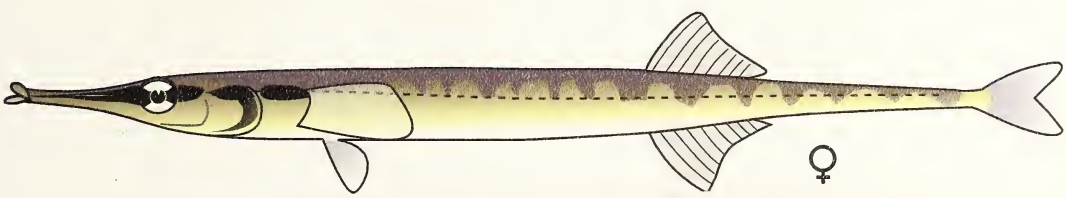

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Expansion of the Non-native Mississippi Silverside, *Menidia audens* (Pisces, Atherinopsidae), into Fresh and Marine Waters of Coastal Southern California

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Abstract.—Mississippi Silversides, *Menidia audens*, were first recorded in southern California reservoirs and nearby outflows in the late 1980s and early 1990s. In 1997–2000 they were taken in King Harbor, Redondo Beach, and in 2000 in the Santa Ana River. By 2005–2006 they were found in several other coastal drainages from the San Gabriel River in Orange and Los Angeles counties northward to Arroyo Burro, Santa Barbara County. Initial invasion was via the California Aqueduct in the late 1980s and early 1990s and more recently dispersal has taken place along the southern California coast. The records from King Harbor occurred for a relatively short period, mid-1997-mid-2000 (mostly 1997 and 1998) before they were established in coastal drainages. Their impact on native species is not known but on some occasions Mississippi Silversides have outnumbered native Topsmelt, *Atherinops affinis*, in small coastal lagoons estuaries. Mississippi Silversides are known to prey on eggs and larvae of other fishes and could be increasing predation on small native animals as well as serving as prey for larger piscivores like steelhead and terns.

In the fall of 1967 the Mississippi Silverside, *Mendia audens* (Hay 1882), (Atherinopsidae), was introduced into Blue and Clear lakes, Lake County, northern California to control larvae of a non-biting midge, a cosmetic nuisance in the region (Dill and Cordone 1997). Fish dispersed downstream into the Sacramento and San Joaquin rivers and became widespread in the greater San Francisco Bay Delta (Bennett and Moyle 1996; DeLeon 1999; Fuller et al. 1999). By the late 1980s and early 1990s they were taken in some southern California reservoirs at the southern terminus of the California Aqueduct (Aqueduct). The Aqueduct has conveyed Delta water to southern California since the early 1970s (Swift et al. 1993; Dill and 1997; Moyle 2002). A few were taken farther downstream in the Santa Clara River near the mouth of Piru Creek below both Pyramid Reservoir and Lake Piru on the creek. These fish were thought to have come down Piru Creek through these intervening reservoirs. Otherwise they were not detected until 1997 when larvae were taken in the marine habitat at King Harbor, Redondo Beach,

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Los Angeles County and in 2000 when they began to be recorded at several freshwater and estuarine localities. Swift et al. (1993) and Schroeter and Moyle (2006) predicted this expansion and its progress is presented here.

The mostly freshwater Mississippi Silverside is native to the lower Mississippi River and Gulf of Mexico drainages east to the Pearl River, Mississippi and west to the Sabine River, Louisiana and Texas (Suttkus and Thompson 2002; Suttkus et al. 2005). It was synonymized with the coastal brackish-water Inland Silverside, *M. beryllina*, by Chernoff et al. (1981) and was again elevated as a distinct species by Suttkus and Thompson (2002), Suttkus et al. (2005), and Page et al. (2013). A third similar species, the Tidewater Silverside, *M. peninsulae*, also occurs in more marine coastal areas of the Gulf of Mexico (Suttkus and Mettee 1998). Suttkus and coauthors provided convincing evidence of the morphological distinctions between these three taxa. However, Johnson (1975) and Fuker, et al. (2011) found fewer genetic distinctions in allozymes and mtDNA, respectively, between the Mississippi and Inland Silversides than between the Inland Silverside and the Tidewater Silverside.

Methods and Materials

Live specimens were collected with small seines or dip nets and occasional dead specimens were taken by hand. King Harbor material was taken in monthly surface hauls of a one-meter conical plankton net of 333 μm mesh from 1974 through the present (Stephens et al. 1994, Stephens and Pondella 2002, Pondella et al. 2012). Voucher specimens deposited in the Fish Collection of the Natural History Museum of Los Angeles County (LACM) and some were originally preserved in ethyl alcohol for potential DNA study. The King Harbor larval collections are Moore Laboratory of Zoology, Occidental College. Below LACM catalogue numbers are followed by the number of specimens and range in standard length (SL) in brackets. To distinguish the Mississippi silversides from the local native atherinopsids and to confirm their specific identity in the genus *Menidia,* scale and gill raker counts were taken according to Hubbs and Lagler (2004) with the following clarification for lateral line scale counts. Suttkus and Mettee (1998) followed Hubbs and Lagler (1958) in presenting predorsal scale counts for species of *Mendia*. Suttkus and Thompson (2002) and Suttkus et al. (2005) provided lateral scale counts also. The posterior two-thirds or so of the pored or grooved scales of the lateral line in *Menidia* lies below the lateral midline. The anterior one-quarter to one-third lies above with a vertical gap of two to three unpored scale rows. Hubbs and Lagler (1958, 2004) define the lateral scale count as from the base of the caudal fin to the first scale touching the shoulder girdle and if some scales are not pored, "...the number of scales along the line in the position that would normally be occupied by a typical lateral line scale." A count from the caudal base along the lower pored lateral line segment, continuing forward on unpored scales ends at a narrow fleshy unscaled area just behind the pectoral base, not reaching the pectoral girdle itself; counting posteriorly from the shoulder girdle above the pectoral fin base on the upper, shorter anterior pored segment results in a complete count to the caudal base as defined, but bypasses the majority of the pored scales in the lower lateral line. The lower count is 2–4 scales less than the upper count. We present the upper counts here as Chernoff et al. (1981) described as "The lateral scale series was that row immediately above the lateral stripe, originating at the junction of the head and the dorsal margin of the pectoral girdle and terminating at the caudal base." Presumably this was methodology of Suttkus et al. (2005). Counts were taken on 50 fish as follows: Santa Clara River (58125-

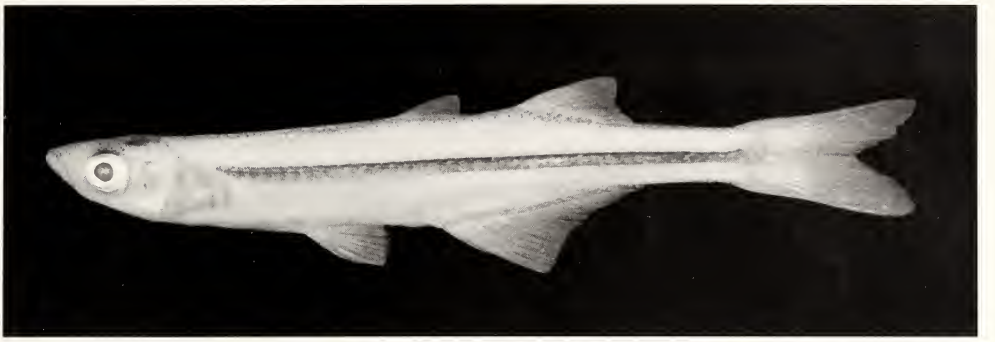

Fig. 1. Specimen of *Menidia audens*, 47.8 mm SL, Los Angeles County, Malibu Lagoon, 17 November 2006, from LACM 58123-1, pectoral fin removed to show lateral pigmentation. Photo by Camm Swift

2, 10[53–85]), Malibu Lagoon (58123-1, 20[47–58]), and the Santa Ana River (58117-1, 20[55–72]). Three Malibu fish had anomalous gaps in the gill raker spacing near the lower end of the row and were excluded from those counts. Three other Malibu specimens had one or a few distinctly foreshortened gill rakers otherwise in normal position and were included in the counts.

Identification

The Mississippi Silverside's slender shape and pale, semi-translucent and yellowish or light greenish color differs from all other freshwater fishes currently in coastal southern California (Fig. 1). In the estuarine areas it can be confused with small Topsmelt, Jacksmelt, *Atherinopsis californiensis*, and California Grunion, *Leuresthes tenuis*. In southern California estuaries Topsmelt are often common. Jacksmelt and California Grunion, typically more marine, are usually uncommon in lower salinity zones of coastal lagoons but occur in larger tidal bays and estuaries. The dorsal, anal, and pectoral fins are larger and longer in Mississippi Silversides, the depressed pectoral fin extends back 90% or more of the distance to the vent whereas it extends 50% or less of this distance in the three native atherinopsids. The first unbranched pectoral ray in the Mississippi Silverside is 90% or more the length of the second, or first branched ray vs. 60–70% of that ray in the native atherinopsids. The pectoral fin base is almost vertical, sloping slightly posteroventrally on the Mississippi Silverside and is strongly sloped backward and downward about 45° in the native species. Mississippi Silversides also have a much finer and reticulated melanophore pattern on dorsolateral scales consisting of a single row of finely divided melanophores bordering each scale in contrast to several rows of darker concentrated cells in the native species. The background color in Mississippi Silversides is pale yellowish, greenish, or tan in life rather than bluish or grayish as in the three native species. The Mississippi Silverside reaches about 100 mm SL compared to ≥150 mm for Topsmelt, Jacksmelt, and California Grunion. Finally meristic counts are all fewer than in the native atherinopsids with little or no overlap: dorsal spines, Mississippi silversides, IV–VI vs. V–IX; dorsal rays i +8–9 vs. i + 8–14; anal rays, i + 15–19 vs. i + 19–26; total gill rakers on first arch 23 or fewer vs. more than 30; lateral scales, 34–45 vs 60–80; predorsal scales 18–22 vs. more than 25; and scales between the dorsal fin 4–6 vs. 7–12 in the three native atherinopsid species.

Key to California Species of Atherinopsidae

1a. Depressed pectoral fin extends posteriorly 80–90% of distance to vent or cloaca; pectoral fin base almost vertical or only slightly sloped backward; scales large and outlined with one row of very finely divided pigment cells; lateral scales 35–45; gill rakers on first left arch 23 or fewer, size ≤ 100 mm SL (4 inches) . . . . . .Mississippi Silverside. *Menidia audens*

1b. Depressed pectoral fin extends only 50–60% of distance to vent; pectoral fin base slopes backward at about a 45° angle; lateral scales more than 50; gill rakers more than 30; size often greater than 100 mm SL and up to about 380 mm SL (17.5 inches TL) 2

2a. Ten to 12 scales between the dorsal fin bases; anal fin origin posterior to a vertical through posterior end (insertion) of the first (spinous) dorsal fin base; teeth in multiple rows with single points (unicuspid) at all sizes. . . . . .Jacksmelt, *Atherinopsis californiensis*

2b. Five to nine scales between the dorsal fin bases; anal origin below a vertical through some portion of the first (spinous) dorsal fin base; teeth absent or in one row (uniserial) and bifid (forked) in fish over about 50 mm SL, with single points on teeth in smaller fish 3

3a. Teeth distinctly developed, in a single row and forked in fish over about 50 mm SL; Five to eight scales between the dorsal fins; protruded upper jaw (premaxillary bones) extends forward rather than downward; body deeper, depth 4 to 6 times in SL . . . . . .Topsmelt, *Atherinops affinis*

3b. Teeth lacking or minute, difficult to detect even in adults; seven to nine scales between dorsal fin bases; mouth protrudes forward and downward; body slender, greatest depth 6 to 8 times in SL . . . . .Grunion, *Leuresthes tenuis*

Other Potential *Mendia* Invasions

Consideration of two additional similar species of *Menidia* is important because of the potential for them to be introduced into California waters. Toxicity testing of various natural and waste waters utilizes live two to seven or eight day old fish called Inland Silversides. These are laboratory cultured and widely distributed to testing laboratories and stocks originate in the coastal Gulf of Mexico and Atlantic coast of Florida or from domesticated stocks cultured specifically for water testing. Thus, depending on where they were taken either Inland (*M. beryllina*) or Tidewater (*M. peninsulae*) Silversides could be captured and utilized. Laboratory populations from widely separated areas might have unique genetic or morphological features from wild populations and could add to the non-native silverside mix in California.

The three similar, widespread species of *Menidia* (*peninsulae, beryllina*, and *audens*) are difficult to distinguish. Suttkus and Mettee (1998) found the ratio of pre-anal length to standard length is less than 0.7 *M. beryllina* and usually more in *M. peninsulae*. Otherwise these two species to be almost identical in meristics and morphometrics except for total gill rakers on the first left gill arch; *M. beryllina* usually 22–23, *M. peninsulae* usually 25–26, and *Menidia audens* usually has 21 or fewer. The largely brackish *M. beryllina* is separated from the largely freshwater *M. audens* since the latter is slimmer with lower head, body, and caudal peduncle depth compared to *M. beryllina*. In addition an index adding the predorsal and lateral line scale counts together separates these two species 98.4% of the time with *audens* having 58 or more and *beryllina* 57 or less (Suttkus et al. 2005). The counts for 50 southern California fish noted above (47 for gill rakers) follow: lateral line scales (see

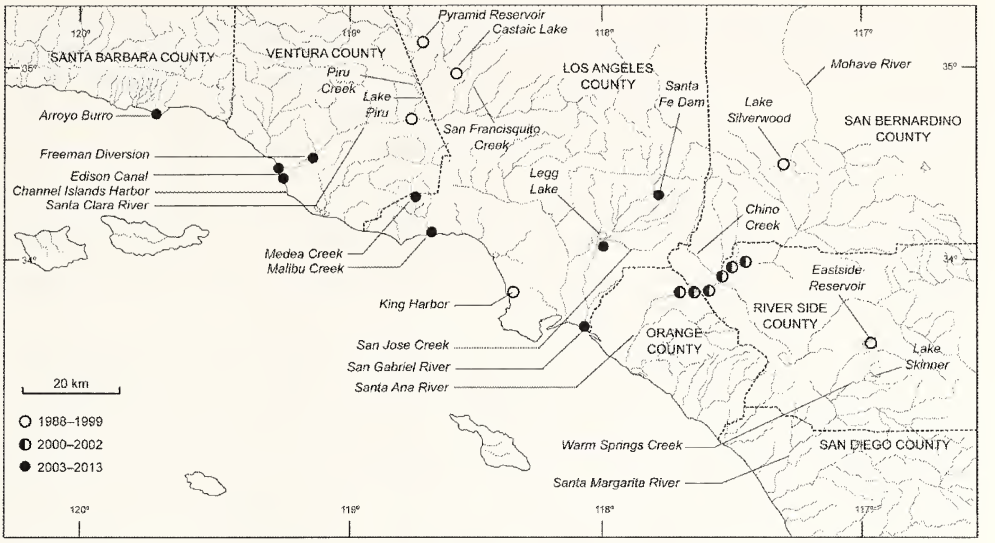

Fig. 2. Coastal southern California with locality records of Mississippi silversides. All except King Harbor and Arroyo Burro are considered established populations either because they are known to directly or indirectly receive unfiltered California Aqueduct water or have been observed continuously over several years. Lake Cachuma is the lake north of Arroyo Burro on the Santa Ynez River.

methods) X = 41.56, (SD = 1.1457); predorsal scales, X = 22.2549, SD = 2.0961; total of lateral line and predorsal scales, X = 63.76, SD = 2.5117; and gill rakers, X = 19.1667, SD = 1.118. These three counts are diagnostic for *Menidia audens* as shown by Suttkus et al. 2005) with gill rakers lower and scale counts higher than in *M. beryllina* and *M. peninsulae*.

Records (North to South, Fig. 2)

Arroyo Burro Lagoon, Santa Barbara City and County: On June 2, 2004, two individuals were taken by ECORP biologists (58119-1, 2[69–92]). No more have been taken in repeated sampling in the next 10 years at this site or at the larger Mission Creek lagoon about 5.5 km to the east.

Santa Clara River drainage, Ventura and Los Angeles counties: Records of California Department of Fish and Wildlife biologists in 1988 and 1992 were documented by Swift et al. (1993) from Pyramid (45701-4, 6[60–105]) and Castaic reservoirs. In 1993 about 10 small individuals were observed in the River within a kilometer of the mouth of Piru Creek (45698-1; 45792-1; 58110-1; 58111-1), and two small specimens were taken in this same vicinity in 1999 (45715-1, 2[50–53]). On 24 August and the first week of September 2006 a few specimens were photographed from the Freeman Diversion on the river 16.8 km upstream of the ocean. On October 24, 2006 three specimens were kept (58120-1, 3[49–55]) and on November 17, 2007 another 15 were taken (58144-1). They were also seen in or near diversion impoundments near Santa Paula about 20 km upstream of the Freeman Diversion. Mississippi Silversides entered the diversion canal at the Freeman Diversion through a 3/16 mesh wedge wire intake screen designed to exclude steelhead. The silversides have established a population within the canal and pond system. Hundreds were observed in the canals in 2007 through 2009 and remain present but rare since.

The lagoon at the mouth of the river was sampled two to three times a year from 1999 onward, and the first Mississippi Silversides were taken on 23 October 2007 (58125-1).

About sixty juveniles to adults were taken on 14 October 2008 and about 20 were observed on September 17, 2010. They have been repeatedly taken through 2012. On January 9, 2008 two individuals (58126-1, 2[37–51]) were taken in a small separate beach pond along the open coast just south of the southern extent of the lagoon and near the cooling water outfall of the Southern California Edison (now Reliant Energy) Mandalay Power Generating Station.

Channnel Islands Harbor, Edison Canal, Ventura County: Also on January 9, 2008, one (58126-1, 1 [38]) was taken in the Edison Canal within 100 m of the Mandalay Station intake. This canal carries marine water for 3 km northwest from upper end of Channel Islands Harbor to the Power Plant.

Malibu Creek Lagoon and Creek, Los Angeles County: Malibu Lagoon was sampled a few times per year from the 1970s onward with high school student classes and from 1991 onward to monitor the introduced population of the federally endangered Tidewater Goby, *Eucyclogobius newberryi*. The first Mississippi Silversides (56403-1, 18[33–68]) were taken on November 2, 2005. They were taken subsequently on 17 November 2006 and greatly outnumbered Topsmelt, *Atherinops affinis*. They continue to be taken in the lagoon, most recently on January 8, 2012 and August 5, 2013 (Rosi Dagit, Topanga-Las Virgenes Resource Conservation District, personal communication, including photographs). On June 13, 2007 Manna Warburton and Brian Zitt (ECORP Consulting, Inc., personal communications) took about 20 Mississippi Silversides in Medea Creek (tributary of Malibu Creek) near the crossing of the 101 Freeway. This site is upstream of both Rindge Dam and Malibu Lake reservoirs on Malibu Creek.

King Harbor, Redondo Beach, Los Angeles County: Early larvae with large yolk sacs still evident were taken in sixteen monthly plankton hauls from mid-1997 to mid-2001. Fourteen were taken as one or two individuals almost monthly from June, 1997 to July 1998 with one in June, 2000 and another in June, 2001. These are the only records during this continuous monthly sampling from 1974 to present (Vantuna Research Group collections, Occidental College). King Harbor is a coastal marine harbor site with marine salinities and warming influence of the adjacent AES Redondo Beach generating station.

San Gabriel River, Los Angeles and Orange counties: On October 12, 2006 two individuals (58121-1, 2[78–80]) were taken with Topsmelt in the tidal and channelized San Gabriel River at the lower end of the concrete-lined channel just downstream of the mouth of Coyote Creek. They were among at least 150 similar sized atherinopsids moving in with the rising tide. Upstream at the mouth of San Jose Creek they were common on 17 August 2007, with about 100 observed (58124-1, 31 [20–48]). Earlier on 11 October 2006 and later on 20 August 2008 none were taken at this site. The river had been very low and possibly dried out within a few weeks before the 2008 visit. On October 13, 2006 one specimen (58122-1, 1[38]) was taken in the Santa Fe Dam Recreation fishing lake, part of the flood control basin for the San Gabriel River.

Santa Ana River, Riverside and Orange counties: On March 26 and 27, 2000, several small, silvery fish were observed escaping fyke traps in a diversion channel about 200 m downstream of the River Road bridge in Norco. These were likely Mississippi silversides since ten days later, April 6th one (58113-1, 1[44]) was taken about 8 km upstream near the south end of California Avenue and the outlet of a channel draining Hidden Valley Regional Park. In the next few months individuals were taken from the mouth of Evans Lake Drain at Mission Road, City of Riverside, to about 50 km downstream at the Imperial Highway crossing (58114-1, 58116-1, 58118, and others). They became common in the lower gradient parts of the Santa Ana River from about the Interstate 15 crossing

downstream to Imperial Hwy until the heavy winter of 2004–2005 when they became uncommon. They continue to be recorded through 2012 and have clearly become established (Kerwin Russell, Riverside-Corona Resource Conservation District, Bonnie Johnson, Orange County Water District, personal communications, 12–14 January 2013).

Santa Margarita River, San Diego and Riverside counties: Mississippi silversides entered the East Side Reservoir, just south of Hemet in Riverside County, in late 1999 or 2000 as the reservoir filled with water from the California Aqueduct and Colorado River (Michael Guisti, personal communication). This reservoir lies in the Santa Margarita River drainage but does not directly release water. Water is transferred from this reservoir to Lake Skinner and then occasionally released into Warm Springs Creek, a northern tributary to the Santa Margarita River (Michael Guisti, personal communication). This creek is usually intermittent or dry but provides a potential avenue of invasion into the Santa Margarita River drainage.

Mojave River Drainage, San Bernardino County: On 2 October 1993 about 300 Mississippi Silversides were seen at the boat launch ramp area on the southern edge of Lake Silverwood and 24 were kept (58112-1, [33–46]. No other collections are known but they likely still inhabit the lake since it receives Aqueduct water, which can be released down the Mojave River.

Discussion

The introduction of second non-native species very similar to one in the same genus already established has precedents in California. The initial putative spread of Chameleon Goby, *Tridentiger trigonocephalus*, into the low salinity Delta region of San Francisco Bay was due to the arrival and spread of a second, very similar brackish water species, the Shimofuri Goby, *Tridentiger bifasicatus* (Matern and Fleming 1995), described in Japan by Akihito and Sakamoto (1989). Markle and Simon (1997) found that Fathead Minnows in Klamath Lakes (Oregon-California border) were morphologically the northern subspecies, *Pimephales promelas promelas*, a form utilized for water testing, rather than the commonly cultured bait fish, *P. p. confertus*, the southern subspecies, introduced into the southwestern United States from Texas (Dill and Cordone 1997). These species pairs are in addition to the known introductions of more than one geographically distinct population of game fishes like Largemouth Bass, *Micropterus* salmoides, Spotted Bass, *M. punctulatus*, Bluegill, *Lepomis macrochirus*, and Black Crappie, *Pomoxis nigromaculatus*, now recognized as separate species or subspecies in their native regions (Warren 2009).

Clearly the distribution of water via the California Aqueduct has led to the establishment of Mississippi Silversides in several coastal southern California localities and the species will likely spread farther to the north and south with dispersal along the coast. Coastal streams and brackish estuaries provide adequate habitat for this fish and it can tolerate higher salinities (Hubbs et al. 1971). It feeds on larval fishes and could impact the native fishes in freshwater streams and coastal lagoons (Luttrell et al. 1999; Baerwald, et al 2012). While initial entry into southern California was via the California Aqueduct, the coastal sites like Malibu Lagoon and Arroyo Burro do not directly receive unfiltered Aqueduct water and the populations at these sites may require different explanations. Dispersal may take place during the wet season when runoff makes coastal waters fresher for short periods, but *Menidia audens* from Lake Texoma, OK were found to be tolerant of marine or near marine salinities for at least two days (Hubbs et al. 1971). The presence of Mississippi Silversides in Medea Creek, tributary to

Malibu Creek, suggests anglers or others may have introduced them and then dispersed downstream. Medea Creek receives Aqueduct water but it has been subjected to chloramination and filtration before entering the drainage so silversides could not have arrived via this route (Randal Orton, Jan Dougall, Las Virgenes Water Conservation District, personal communications). Arroyo Burro can indirectly receive Aqueduct water via flush valves in a pipeline of unfiltered water from Lake Cachuma. However, the Aqueduct water is also chloraminated and filtered before entering Lake Cachuma (Rosemary Thompson, Cardno ENTRIX, Santa Barbara, personal communication). Thus Mississippi Silversides would have to have been independently introduced into Lake Cachuma to be transferred to Arroyo Burro. Possibly they occur in Lake Cachuma and have been undetected to date. Both freshwater and coastal marine dispersal have been factors in the Mississippi silverside dispersal in southern California and it is likely they will become more widespread.

Swift et al. (1993) noted four other fish established outside the receiving reservoirs after likely arrival in Aqueduct water. In the late 1980s a population of Blackfish, *Orthodon microlepidotus*, was present in the Santa Ana River below Prado Dam but disappeared in the late 1990s. The inland form of Prickly Sculpin, *Cottus asper*, became established in the Santa Clara and Mohave rivers in the early 1990s and persists. Specimens of Prickly Sculpin have been observed in a diversion and associated groundwater infiltration basins of the Santa Margarita River near Lake O'Neill on Marine Corps Base Camp Pendleton every year from 2008 to 2012 (Michael Rouse, Manna Warburton, personal communication). They may be more widespread in the drainage, which occasionally receives water from Lake Skinner as noted above. This indicates the Mississippi Silverside is to be expected in the Santa Margarita River. Finescale Logperch, *Percina microlepida*, were present in Irvine Lake in the Santa Ana River drainage the early 1990s. Then one was taken downstream in the Santa Ana River in Burris Basin, adjacent to the river in Anaheim on June 30, 2012 (Bonnie Johnson, Orange County Water District, personal communication with photo). A population of Hitch, *Lavinia exilicauda*, (Cyprinidae) has been recently documented in the Mohave River downstream of Lake Silverwood where they have hybridized with Arroyo Chub, *Gila orcutti,* (Jeffrey Seigel, LACM, personal communication, LACM specimens; Chen et al. 2013). The Arroyo Chub were introduced long ago (Swift et al. 1993) in upper tributaries of the Mohave River. Other reservoir species from the Central Valley of California like the native Tule Perch, *Hysterocarpus traski*, and non-native species like Striped Bass, *Morone saxitilis*, and Shimofuri Goby, *Tridentiger bifasciatus*, had not become established downstream of Aqueduct reservoirs like Pyramid, Castaic, Silverwood, and East Side. However, a few shimofuri gobies have recently been discovered in Piru Creek below San Felicia Dam and in the Freeman Diversion (Ventura County) in late 2013 and early 2014 (Howard, personnal observations). In some cases these occurrences may be repeated invasions via the same routes rather than established populations but the prickly sculpin, finescale logperch, and Mississippi silversides have been established for ten or more years. In the case of the logperch and sculpin, more than twenty years in the Santa Ana and Santa Clara rivers, respectively. Stephen et al. (2007) and Foss et al. (2007) note several mechanisms of coastal movement/transport of non-indigenous aquatic organisms in California without considering the inland movement with water deliveries, clearly an important avenue with subsequent local coastal movement.

The Santa Clara River was extensively sampled from Santa Clarita to the ocean by a variety of biologists after the few Mississippi silversides were taken in 1993 near the

mouth of Piru Creek and before the two that were taken in 1999. This included annual monitoring for steelhead at the Freeman Diversion. Apparently they were absent or rare and relatively unsuccessful from 1993 until they appeared in 2006 and became established. They arrived either 1) via Piru Creek from Pyramid Reservoir to Lake Piru and over San Felicia Dam, 2) from releases of California Aqueduct Water from Castaic Reservoir down Castaic Creek into the Santa Clara, or 3) via San Francisquito Creek from Metropolitan Water District pipeline maintenance releases. These latter releases occur about every five years and Castaic releases occur occasionally related to demand by water users downstream. Apparently conditions were not satisfactory for establishment for the species in the Santa Clara River as they were in the Santa Ana River. However in 2006 increasing numbers of Mississippi silversides became apparent and at least thousands were found in the estuarine mouth of the Santa Clara River in October of 2007 and in the settling ponds below the Freeman Diversion. Based on collections at the Freeman Diversion after the 2005 floods these fish became widely distributed after spills from reservoirs. They continue to be present in the system through 2012 but in smaller numbers at the Freeman Diversion and no spills over the Santa Clara River reservoirs have occurred since 2005.

The Santa Ana River was also extensively sampled beginning in 1997 leading up to the appearance of the silversides in early 2000. The river receives water from Aqueduct sources via its tributary, Chino Creek. Presumably this was the source of the silversides. The San Gabriel River was not extensively collected before or since the sampling in 2006, 2007, and 2008 and it is not known if the populations are persisting. At least two lakes in the system, Santa Fe Dam and Legg Lake, receive Aqueduct water. Small numbers of these fish probably leak through the system occasionally, sometimes find conditions favorable to expand their populations, and if conditions change, disappear as described for other introduced fish species in the lower Colorado River (Minckley 1982; Minckley and Marsh 2009).

As noted above Malibu Creek does not directly receive aqueduct water and the presence of fish in Medea Creek upstream of two dams in the system requires artificial introduction. The sources of these introductions are not known and were possibly to provide forage for game fish in Malibu Lake downstream. It would be impossible for fish from the lagoon to move upstream over these two dams on Malibu Creek. Thus fish may have invaded Malibu Lagoon from upstream rather than having moved along the coast in the ocean from the Santa Clara River or elsewhere.

The relatively brief period of larval records at King Harbor (1997–2000) from an almost 40 year monthly times series is exceptional, requiring local spawning or long distance dispersal of late stage larvae from unknown sites. Our records indicate no southern California source populations were present north of King Harbor in those years. Transport south from as far north as San Francisco Bay seems very unlikely, even in the strong freshwater runoff and warm conditions of the 1997–1998 El Niño event, particularly for late stage larvae which presumably resulted from spawning within the local area. Otherwise they would have to have come from the southern sites like the San Gabriel or Santa Ana rivers where they were not recorded until at least 2000. Coastal longshore movement of water is largely from north to south and the source presumably was to the north where other records in the lower Santa Clara River and Malibu Creek lagoons did not occur until 2005 or 2006. Otherwise only occasional rare individuals were taken in the early 1990s and 1999 as noted above for the Santa Clara River, and well upstream.

Mississippi silversides spawn from April to September in San Francisco Bay (Moyle 2002) and the presence of late larvae at King Harbor in several winter months is surprising also. In 1997–1998 the warmer El Niño ocean temperatures combined with the artificial warming by power plant outflows may have supported a population of *Menidia* but possibly not *M. audens* since low salinity environment is lacking. The source of this brief pulse of *Mendia* at King Harbor remains speculative and may have involved some kind of locally introduced fish. The nearby Hyperion Wastewater Plant utilized 7–11 day old *Menidia* larvae for testing from December 1994 to July 2005 when they were discontinued in favor of larval Topsmelt. At this age the fish are much larger than yolk sac larvae and the testing protocols requires disposal of all test organisms and none were released (Gerald McGowan, retired, City of Los Angeles, personal communication).

Mississippi Silversides may compete with Topsmelt, a species it overlaps with ecologically in southern California bays and estuaries. Particularly in Malibu Lagoon and the Santa Clara River lagoon the Mississippi Silversides were more common than Topsmelt in some collections. Most of the other sites were not sampled on a regular basis to determine relative abundance and it is not known if the Mississippi Silversides have spread to the lower estuarine areas of the Santa Ana River. It is less likely competition will occur with the more marine California Grunion and Jacksmelt but juveniles of these species utilize larger tidal bays and estuaries and could be impacted. Potentially serious is the known propensity for Mississippi Silversides to feed on the larvae of other fishes and such predation might impact several other species like the federally endangered tidewater goby, *Eucyclogobius newberryi* (U. S. Fish and Wildlife Service 2005), other estuarine gobies, killifish, sculpin, and others (Luttrell et al 1999; Baerwald et al. 2012). Reduction or management of these populations may be necessary in face of their possible adverse impacts. In addition, Foss et al. (2007) considered coastal non-indigenous aquatic species entirely in terms of coastal dispersal. The inland movement of estuarine fresh water from San Francisco Bay into southern California is also transporting freshwater and estuarine aquatic organisms. Small fishes leak through this system and many other smaller organisms must be carried along also. More study is needed to assess the impact of these invasive species in southern California and elsewhere in the southwestern United States (Minckley and Marsh 2009).

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Larval Duration, Settlement, and Larval Growth Rates of the Endangered Tidewater Goby (*Eucyclogobius newberryi*) and the Arrow Goby (*Clevelandia ios*) (Pisces, Teleostei)

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Abstract.—The early life history of the federally endangered Tidewater Goby (*Eucyclogobius newberryi*) and its sister species the Arrow Goby (*Clevelandia ios*) has been poorly documented to date. Both are endemic to estuarine habitats throughout the California coast, however, habitat use differs between these two species. The Arrow Goby is commonly found in fully marine tidal bays and mudflats. The Tidewater Goby, however, prefers lagoons with some degree of seasonal isolation from the sea. Here, we used otoliths to examine the larval duration, size at settlement, and growth rates of newly settled gobies collected from 18 estuaries in California. The Tidewater Goby had a larval duration that was ~2 days shorter than the Arrow Goby (23.95 vs. 26.11 days, respectively), but a larger size at settlement based on back-calculated size (12.38 vs. 10.00 mm SL) due to a faster larval growth rate (2.86 vs. 2.60 $\mu m/day^{-1}$). There are several reasons that could explain these differences in larval traits, such as differences in temperature or food resources between the two estuary types, or the faster, annual life cycle of the Tidewater Goby relative to the Arrow Goby.

Many fish species inhabit estuarine habitats during their early life history. These habitats are quite variable, with some remaining open to the ocean year round and others typically closing seasonally. Species that inhabit seasonally closing estuaries may exhibit different larval traits than those that inhabit permanently open estuaries, and these traits may contribute to genetic isolation by limiting dispersal (Bilton et al. 2002, Watts and Johnson 2004). For example, Dawson et al. (2002) found genetic evidence of limited dispersal in the Tidewater Goby (*Eucyclogobius newberryi*), which inhabits seasonally closed estuaries, whereas its sister species the Arrow Goby (*Clevelandia ios*), which inhabits open systems, lacked regional genetic divergence. This difference is likely due to greater marine larval dispersal and gene flow between populations of arrow gobies. Larval duration has long been thought to influence dispersal, and differences in larval duration could confound this interpretation.

Closed estuaries experience greater seasonal variation in environmental conditions than is seen in estuaries perennially open to marine influence, and such variation is known to significantly influence larval development (McCormick and Molony 1995, Green and Fisher 2004). Along the California coast, many estuaries are partially or completely isolated from tidal influence either seasonally or episodically (Jacobs et al. 2011). Opening or "breaching" is usually a function of streamflow (Rich and Keller 2013), which is driven by seasonal precipitation. Isolation, or closure, occurs when a sand bar or raised beach berm impounds systems during periods of lowered "summer" streamflow, creating variable salinity. Such dynamic lagoonal systems are a product of

the Mediterranean climate that characterizes California. Similar lagoonal processes are known to occur in other regions of the globe with similar climate (Jacobs et al. 2011).

The federally endangered Tidewater Goby is a California endemic that occurs in estuaries that experience seasonal or episodic closure (Swift et al. 1989). The Tidewater Goby is a small benthic fish that seldom exceeds 55 mm standard length (SL) (Miller and Lea 1972). Lagoons with seasonally closing stream mouths on the outer coast are the typical Tidewater Goby habitat, although they also occupy or historically occupied, naturally closing, tide-gated, or marginal pond habitats around Humboldt, Tomales, and San Francisco Bays (Swift et al. 1989, Moyle 2002, U.S. Fish and Wildlife Service 2005). This species exhibits local genetic divergence at a finer geographic scale than any other Pacific coast vertebrate (Barlow 2002, Dawson et al. 2002, Earl et al. 2010). Its preference for small and isolated estuaries is one of the main reasons why it is predisposed to local extirpation (Lafferty et al. 1999a,b).

Dispersal of the Tidewater Goby is associated with high streamflow events (Lafferty et al. 1999a,b), which cause breaching of the estuary mouth, permitting dispersal (Earl et al. 2010). Breaching events occur most frequently during winter months when reproduction is limited and larvae are generally absent. As confirmed by genetic divergence, marine larval dispersal appears to be extremely limited, if it occurs at all (Barlow 2002, Dawson et al. 2002, Earl et al. 2010). This conclusion is supported by the work of Hellmair and Kinziger (2014), which showed that small tidewater gobies (<25 mm total length) experience higher mortality rates than larger individuals (>25 mm) when salinity was raised from 6‰ to 26‰. Presumably this intolerance to seawater in young tidewater gobies is related to the isolated nature of their lagoonal habitats during the summer peak reproductive months (Swenson 1999). Thus, dispersal appears limited to adult movement over sandy substrate following breaching events (Earl et al. 2010).

The Arrow Goby is the sister species to the Tidewater Goby (Dawson et al. 2002), and it ranges from Bahia Magdalena, Baja California Sur (C. Swift, pers. comm.) to British Colombia (Miller and Lea 1972). Similar to the Tidewater Goby, the Arrow Goby is a small benthic fish that rarely exceeds 60 mm SL (Miller and Lea 1972, Hart 1974). It prefers more open, fully tidal estuaries and mudflats, which are typically cooler and higher in salinity. This preference for open estuaries is thought to facilitate marine larval dispersal.

Here, we compare the early life history of the Arrow Goby and the Tidewater Goby collected from eighteen California estuaries. Larval traits were determined from daily bands and settlement marks in lapillar otoliths of recently settled gobies. Larval duration, size at settlement, and pre-settlement growth rates were compared between the two species.

Materials and Methods

Study Sites

Gobies were collected from eighteen estuaries in California (Fig. 1). Sites were chosen based on the presence of healthy and abundant populations of the Arrow Goby or Tidewater Goby, in addition to their mouth dynamics (closed vs. open estuary mouth). The Tidewater Goby was collected at ten seasonally closing estuaries: Ten Mile River (39°32′43.86″N, 123°45′25.04″W); Salmon Creek (38°21′10.87″N, 123°03′57.19″W); Rodeo Lagoon (37°49′54.41″N, 122°31′43.31″W); San Gregorio (37°19′14.29″N, 122°24′03.38″W); Moore Creek (36°57′4.50″N, 122°03′29.85″W); San Luis Obispo Creek (35°11′13.35″N, 120°43′33.47″W); Santa Ynez River (34°41′30.57″N, 120°35′00.70″W);

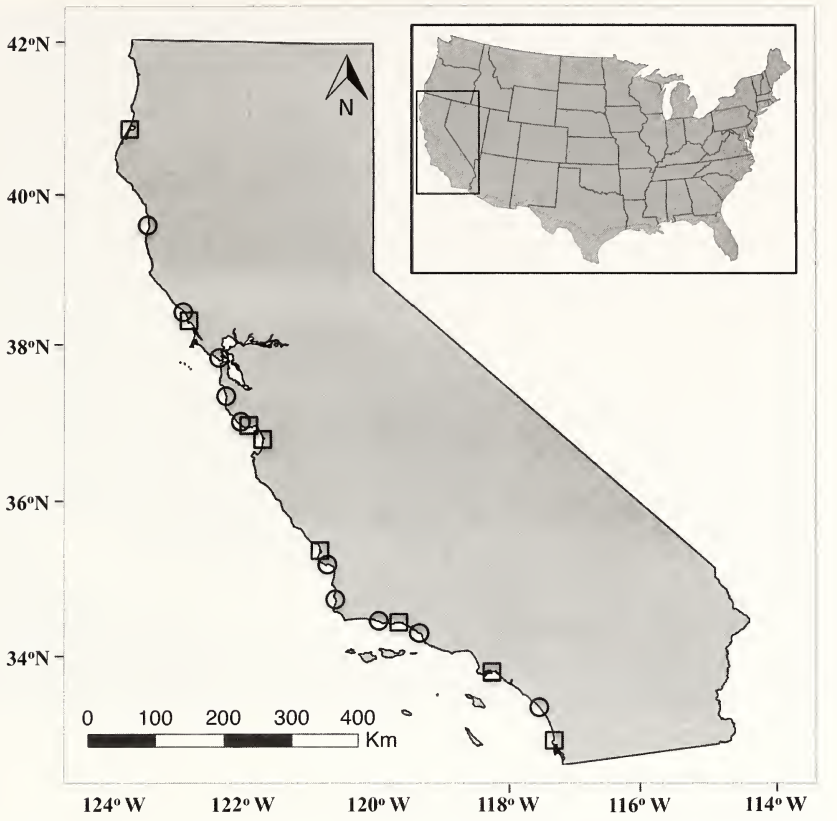

Fig. 1. Map of the 18 study sites located along the California coastline. The Arrow Goby (squares) was collected at 8 sites, and the Tidewater Goby (circles) was collected at 10 sites.

Arroyo Burro Lagoon (34°24′11.77″N, 119°44′35.12″W); Santa Clara River (34°14′07.19″N, 119°15′27.46″W); and Las Flores Marsh (33°17′25.79″N, 117°27′53.91″W). The Arrow Goby was collected at eight estuaries that are typically fully tidal: Arcata Bay (40°51′30.57″N, 124°06′00.08″W); Bodega Bay (38°18′59.42″N, 123°02′43.12″W); San Lorenzo River (36°57′56.41″N, 122°00′45.46″W); Elkhorn Slough (36°48′40.14″N, 121°44′38.77″W); Morro Bay (36°57′56.41″N, 122°00′45.46″W); Carpinteria Salt Marsh (34°23′52.97″N, 119°32′16.72″W); Colorado Lagoon (33°45′10.52″N, 118°07′47.37″W); and Los Peñasquitos (32°55′57.84″N, 117°15′29.11″W). Due to the differences in habitat preference of the Arrow Goby and Tidewater Goby, none of the eighteen study sites had both species present at the time of collection.

Collection Methods

Larval, transitional, and recently settled gobies (Fig. 2) were collected between August and October of 2011. Both species were collected using a 3.7 x 1.2 m beach seine with a 1.6-mm mesh, and in some cases, a one-man push net with 1.6-mm mesh (Strawn 1954). The Arrow Goby was collected at low tide in all eight study sites. The ten study sites where the Tidewater Goby was collected were all completely closed to marine tidal influence at the time of collection. Once collected, the fishes were euthanized and preserved in 95% ethanol.

Fig. 2. Photos showing the rapid development of the Tidewater Goby, exhibiting the transition from (A) a 20-day-old postflexion larva (9.3 mm SL), to (B) a 25-day-old transitional juvenile captured prior to settlement (10.8 mm), and (C) a 34-day-old settled juvenile (13.7 mm).

Otolith Analysis

Otoliths were used to measure larval traits of the study species. Otoliths have been used for these purposes in a wide variety of fishes, including many species in the family Gobiidae (Sponaugle and Cowen 1994, Hernaman et al. 2000, Radtke et al. 2001, Yamasaki and Maeda 2007, Wilson et al. 2009, Samhouri et al. 2009). Both the sagittal and lapillar otoliths were extracted from all individuals using standard techniques (Brothers 1987, Hellmair 2010) and placed in immersion oil for >30 days to clear (Samhouri et al. 2009). For both species, lapilli were used because they were clearer and easier to interpret than sagittae, and they did not require sectioning or polishing. Lapilli were read whole from images on a computer monitor that were captured by a digital camera mounted on a compound microscope at 200× magnification, with a polarizing filter placed between the light source and the first stage. Increment measurements were made along the longest axis, from the core to the outermost complete ring using Image-Pro Plus image analysis software.

Larval duration, size at settlement, and growth rates were estimated from the otoliths. Previous work has validated daily otolith increment deposition in the Tidewater Goby (Hellmair 2010), and increments were assumed to be daily in the Arrow Goby. Settlement was recorded in the otolith structure as a distinct transition in increment widths (Fig. 3), as noted in other gobies by Sponaugle and Cowen (1994). Larval duration was determined from a count of the rings from the hatch mark (first band from otolith core) to the settlement mark. Average pre-settlement growth rates were estimated as average

Fig. 3. Lapillar otolith of a juvenile Tidewater Goby (A), and a larval Tidewater Goby (B) with visible daily bands viewed at 200 x magnification. The black arrow indicates the settlement band. The white line indicates pre-settlement bands, and the black line represents post-settlement bands.

increment width between the hatch mark and the settlement mark (McCormick and Molony 1995). All otoliths were read twice by one person (B.T. Spies), and all unclear and abnormally shaped otoliths were discarded. If the two readings were more then 10% different, then that otolith was not included in any analysis. If the two readings were less than 10% different but not the same, then the second reading was used for the analysis.

Data Analysis

To validate that the presumed settlement mark actually corresponded to settlement, the number of presumed post-settlement bands was regressed against body length for both species. The x-intercept of the linear regression equation estimates size at settlement, which was compared to the size of fish known to have recently settled based on their morphology. Further regression analyses examined the relationship between body length and age (days) to determine whether otolith measurements provide accurate proxies of somatic traits (Booth and Parkinson 2011). Back calculation was used to estimate body size at settlement for each fish using the equation calculated by ordinary least square linear regression of body size (mm SL) on otolith radius, of the form $L = mx + b$; where L represents the body length, m represents the slope, x represents the otolith radius at settlement, and b represents the y-intercept. A nested ANOVA with the factors Species (fixed effect) and Site nested within species (random effect) was used to test whether larval traits differed between species and collection sites.

Results

Otolith-based estimates of larval traits appeared to be appropriate for both the Tidewater Goby and Arrow Goby due to the fact that body length was tightly related to age as estimated from otoliths (Arrow Goby: $r^2=0.75$, $n=317$; Tidewater Goby: $r^2=0.71$, $n=406$; Fig. 4). The number of post-settlement otolith bands and body length were also tightly related (Arrow Goby: $r^2=0.79$; Tidewater Goby: $r^2=0.73$) and the fitted lines predicted realistic sizes at settlement (Fig. 5). This result indicates that the distinguishable transition zone in the otolith is the settlement band (Fig. 3A), and that all bands between the core and the settlement mark indicate the larval duration (Sponaugle and Cowen

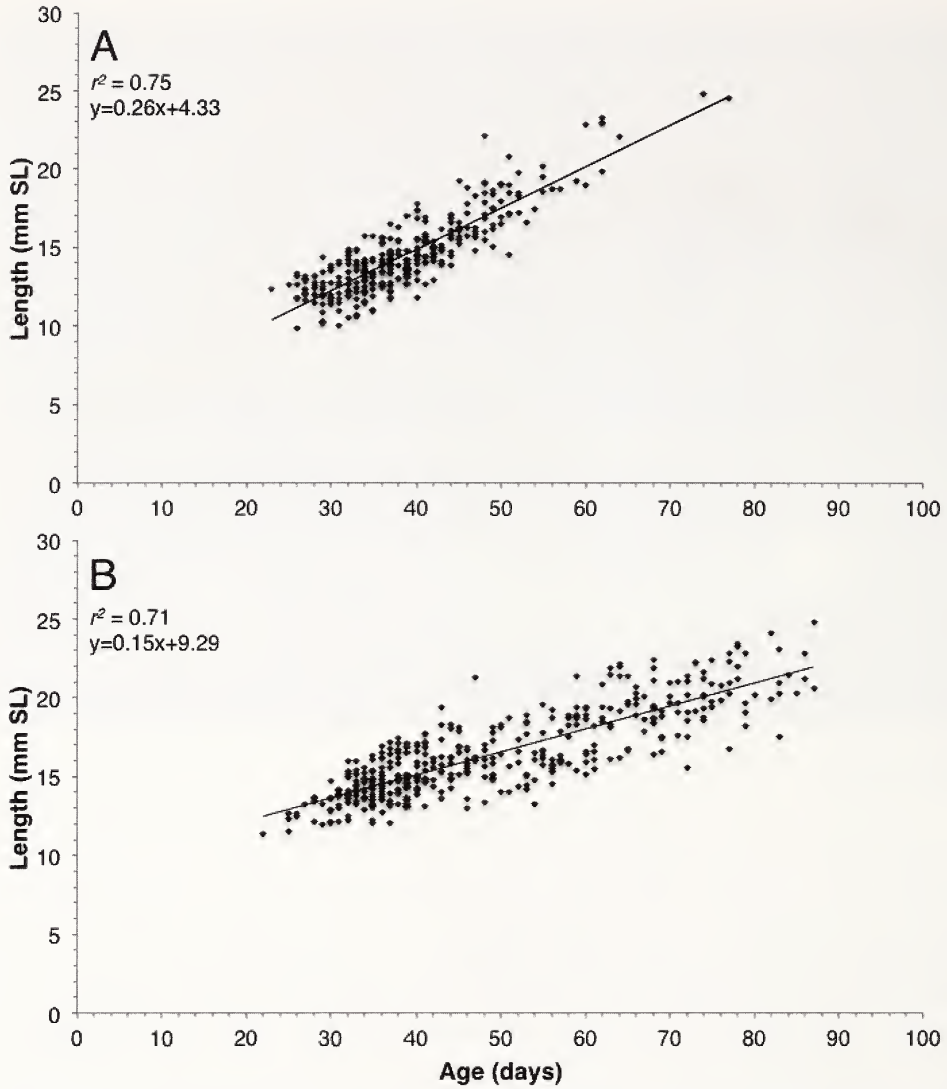

Fig. 4. Relationship between body length and age for the Arrow Goby (A) and Tidewater Goby (B).

1994). Otolith radius was a good proxy for body length, as indicated by a strong linear relationship between body length and otolith radius (Arrow Goby: r^2=0.80; Tidewater Goby: r^2=0.78; Fig. 6). Based on back-calculation, mean ± SD size at settlement was 11.45 ± 0.23 mm SL for the Tidewater Goby and 9.32 ± 0.63 mm for the Arrow Goby, slightly smaller than the estimates of size at settlement based on the x-intercept of the regressions of post-settlement age on size (Fig. 5, Table 1).

The Arrow Goby had a significantly longer larval duration ($F_{1,705}$=227.3, p<0.0001), larger otolith radius at settlement ($F_{1,705}$=28.4, p<0.0001), and slower larval growth rates ($F_{1,705}$=399.8, p<0.0001) than the Tidewater Goby (Table 1). Size at settlement (back calculated) of the Tidewater Goby was significantly larger than that of the Arrow Goby ($F_{1,705}$=5360.1, p<0.0001). All larval traits varied significantly among sites for both species (larval duration: $F_{16,705}$=42.5, p<0.0001; otolith radius at settlement: $F_{16,705}$=43.9,

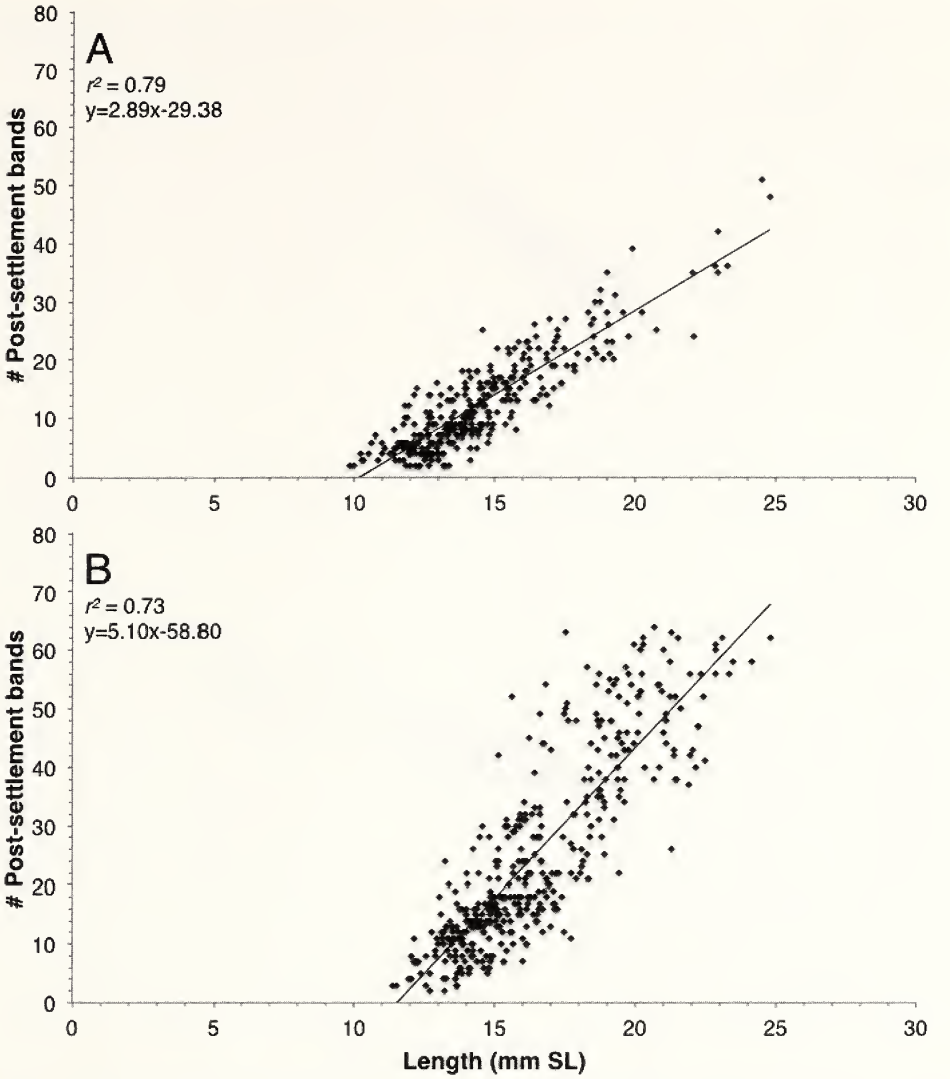

Fig. 5. Relationship between post-settlement age and body length for the Arrow Goby (A) and Tidewater Goby (B).

$p<0.0001$; pre-settlement growth rate: $F_{16,705}=33.53$, $p<0.0001$; back calculated body size at settlement: $F_{16,705}=25.9$, $p<0.0001$).

Discussion

Analysis of lapillar otoliths revealed that larval duration, size at settlement, and pre-settlement growth rates of the two sister species, the Arrow Goby and Tidewater Goby, were statistically different, though not dramatically different. The similarity between the two species in larval duration is somewhat surprising given known differences in their habitat usage and methods of dispersal. Despite inhabiting two different kinds of estuaries, "open" versus "closed", and dispersing as larvae (Arrow Goby) versus adults (Tidewater Goby), the duration of the larval phase was only 8% shorter in the Tidewater Goby. Due to faster larval growth rates, the Tidewater Goby settled at larger size than

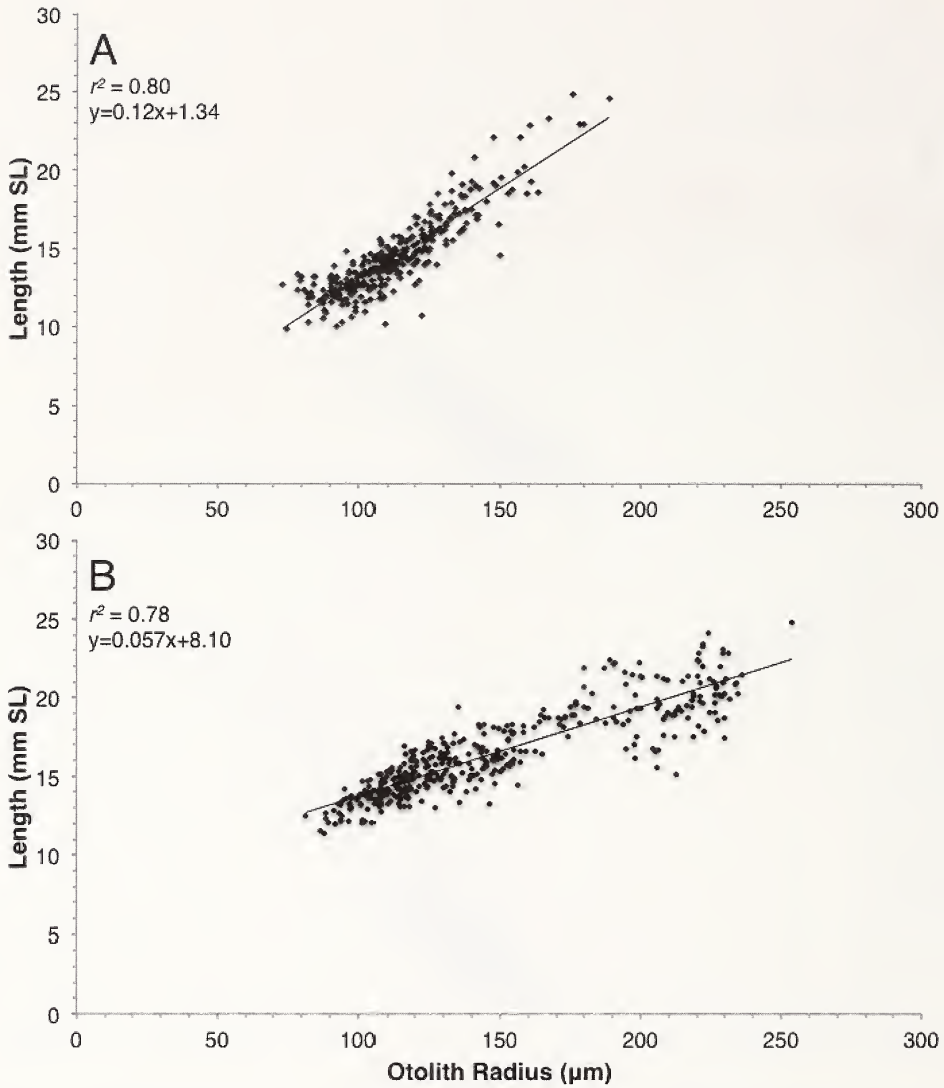

Fig. 6. Relationship between otolith radius and body length for the Arrow Goby (A) and Tidewater Goby (B).

Table 1. Estimated larval durations, settlement sizes (standard length), and growth rates of the Arrow Goby (*Clevelandia ios*) and Tidewater Goby (*Eucyclogobius newberryi*) pooled over all study sites (n = 8 and 10 study sites for the two species, respectively).

	Larval duration		Settlement		Growth rate	
Species	Range (days)	Mean ± SD (days)	Otolith radius (μm)	Length (mm)	Mean ± SD (μm/day^{-1})	N
E. newberryi	18 - 31	23.95 ± 2.71	75.62 ± 6.40	12.38 ± 0.36	2.86 ± 0.23	406
C. ios	20 - 33	26.11 ± 2.40	77.61 ± 6.37	10.00 ± 0.71	2.60 ± 0.22	317

did the Arrow Goby. It is likely that the Tidewater Goby has evolved the ability to settle and reach maturity faster than the Arrow Goby due to its shorter, annual life cycle.

Larval durations of other related goby species (e.g. *Gillichthys mirabilis*, *Ilypnus gilberti*, *Lepidogobius lepidus*, *Quietula y-cauda*), commonly referred to as the "bay gobies" (Teleostei: Gobionellidae) (Thacker 2009, Ellingson et al. 2014) have not yet been determined. In fact, detailed knowledge of early life history characteristics does not exist for many native fishes that occupy estuaries and wetlands in California. Larval traits have been studied more regularly in tropical gobies (Teleostei: Gobiidae), which on average, tend to exhibit more prolonged larval stages than those of the species in this study. Yamasaki and Maeda (2007) documented a 78-146 day larval duration in *Stiphodon percnopterygionus*, a stream-associated goby found in Okinawa Island, southern Japan. *Lentipes concolor*, an endemic Hawaiian amphidromous goby was found to have a larval duration between 63-106 days (Radtke et al. 2001). The goldspot goby (*Gnatholepis thompsoni*), commonly found on coral reefs in the Caribbean, was found to have a larval duration between 45-80 days (Samhouri et al. 2009), with the potential of reaching 112 days (Sponaugle and Cowen 1994). Another common goby in the Caribbean (*Coryphopterus glaucofraenum*), however, had a much shorter larval duration of 27 days (Sponaugle and Cowen 1994), similar to that found in this study for the Arrow Goby.

Previous estimates of larval characteristics of these two study species have varied widely, presumably due to methodological limitations. Estimates of larval duration for the Tidewater Goby have ranged from as little as several days (Capelli 1997) to a few weeks (Dawson et al. 2002). Past research on the Arrow Goby has provided a broad range of estimates of larval duration using both field collected and laboratory-reared specimens. However, none of these estimates were obtained from otolith analysis. Brothers (1975) estimated larval duration at approximately 30 days from the timing of annual reproduction and recruitment. Dawson et al. (2002) estimated a 2–4 week larval duration by extrapolating the time to reach 7 mm (10 days; Hart 1973) to the time to reach the average size at settlement of 13.1 ± 1.3 mm (range 10.0–16.6 mm) observed by Kent and Marliave (1997) for newly settled arrow gobies from British Colombia. Our back-calculated estimate of size at settlement (10.00 ± 0.6 mm) falls on the lower end of Kent and Marliave's (1997) range of size at settlement, but overlaps with measurements of nearshore postlarvae collected by Brothers (1975). Morphological descriptions of transitional juveniles (12.5 mm SL) from British Colombia are consistent with the morphology of juveniles in southern California estuaries that settled at a smaller size, perhaps indicating regional differences in size at settlement. It is possible, however, that some of these apparent differences in size at settlement are related to how fish were preserved in various studies, which can cause them to shrink (Hay 1982).

The larval traits investigated in this study varied among populations, possibly due to differences among estuaries in environmental conditions, such as temperature, water quality, or food resources. This could be one explanation for the different estimates of settlement size from this study, done in southern California, and that of Kent and Marliave (1997) conducted in British Colombia. Brothers (1975) found that the Arrow Goby lives for approximately one year in southern California, similar to the annual lifespan of the Tidewater Goby throughout its range, but has an extended lifespan in the more northern portions of its range (2-3 years). Swenson (1999) found that the average size of the Tidewater Goby was significantly larger in marsh habitats than in lagoons or creeks. She speculated that this was due to the more stable physical conditions of the marsh, which fosters improved growth, perhaps due to a more consistent or abundant

supply of prey. It is also worth noting that, given genetic isolation of populations (e.g. Earl et al. 2010), adaptation to local conditions is also possible in the Tidewater Goby. Our findings provide baseline estimates of some of the early life history traits of the Tidewater Goby and the Arrow Goby, but these attributes are likely to vary with environmental parameters.

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Male Mating Posture and Courtship Coloration of the Temperate Marine Tubesnout, *Aulorhynchus flavidus* (Gill)

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Species that engage in sexual reproduction often exhibit dynamic physical features and behavioral actions that serve to signal conspecifics. Body posture, vocalizations or the incorporation of bright coloration are typically used to establish dominance (Wiley 1973, Warner 1975, Clarke and Faulkes 1997, Peterson and Jacobs 2002) alert conspecifics of nearby threats or foraging opportunities (Godin and Morgan 1985, Beauchamp and Heeb 2001, Le Roux et al. 2009, Townsend et al. 2011) and for breeding purposes (Wiley 1973, Hagen et al. 1980, Christy 1983, Gibson 1989, DeMartini and Sikkel 2006). In many species females select a male based on their behavioral display of some desirable trait or their ability to express dominance or competitive superiority over other potential mates (DeMartini and Sikkel 2006). Such criteria are often not mutually exclusive in that particular features or actions may act to deter competitor males while simultaneously attracting females (Hagen et al. 1980, Cairns 1982). Understanding such physical characteristics or behavioral signals improves our knowledge of reproductive systems within and among taxonomic groups.

Reproductive strategies have been well documented in the marine realm, including monogamous pairs (Whiteman and Côte 2004), large broadcast breeding aggregations (Coleman et al. 1996, Colin 1996, Carolsfeld et al. 1997), sneak copulation (Pilastro and Bisazza 1999, Hurtado-Gonzales and Uy 2010) and nesting species (Limbaugh 1964, Wiley 1973). Limbaugh (1962) previously described the nesting habitat for the temperate marine tubesnout, *Aulorhynchus flavidus* (Gill), but male mating behavior has not been characterized. A proposed description of male mating behavior is reported here from observations of *A. flavidus* on display at the Aquarium of the Pacific (AOP) in Long Beach, California during early May, 2013.

Male *A. flavidus* pelvic fins are red in color (Fig. 1A) and are thought to remain that way year round (Love 2011). The heads of males are also dark blue to black with a prominent iridescent blue patch on their snout (Fig. 1B). Iridescent blue spots/coloration have also been observed along the full body length of males (Love 2011) while females are a drab brownish color throughout (Fig. 2). Although typically found at depths of 20 m, and as deep as 37 m (Love 2011), the preferred nesting habitat of *A. flavidus* is the upper blades of the macrophyte *Macrocystis pyrifera*. While bright coloration is common to tropical waters, it is disfavored in temperate marine habitats due to low light penetration at depth. The conspicuous coloration of males may be apparent only when actively breeding in the upper water column where red light is still present. It appears the pelvic fins are often folded up against the body (Fig. 1B) and covered partially by the pectoral fins when they are not actively displaying them. The anterior underside of male threespine stickleback (*Gasterosteus aculeatus*), another gasteriform species, are also red (Hagen et al. 1980) and both species breed in shallower water than they are typically found (~20–30 m depth). Similarities in external morphology despite differences in breeding habits

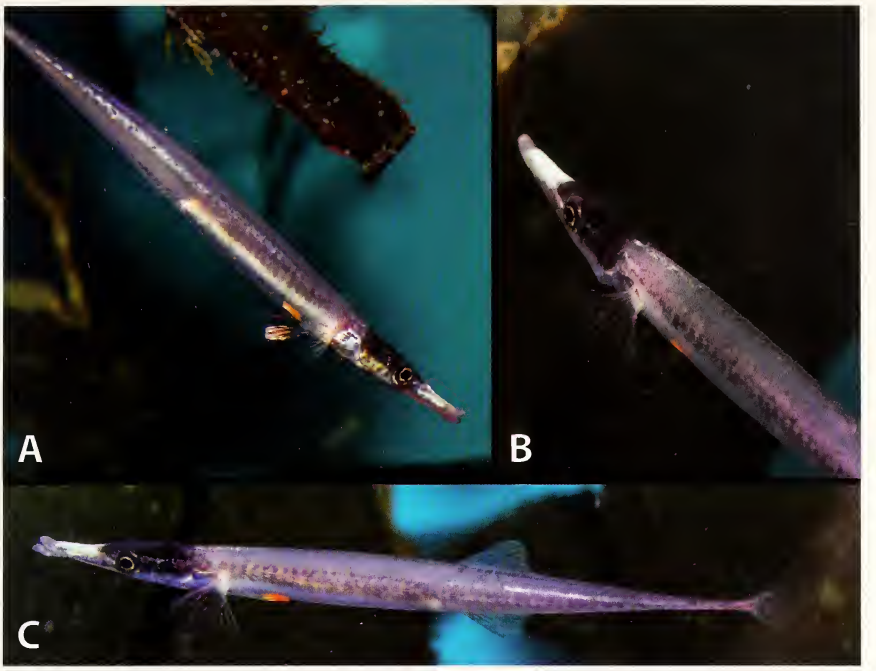

Fig. 1. A) During courtship male *A. flavidus* position themselves in a declined (head-down) position facing a prospective female. They will flare their fins and undulate the pelvic fins back and forth in an alternating sequence against body. B) Male heads are dark blue to black with a prominent iridescent blue patch on the snout. C) When not actively courting males slightly retract the dorsal and anal fins and the pelvic fins are tucked up close against the body.

perhaps suggest red coloration developed in a shared ancestor and has persisted over evolutionary time despite counter-selective pressures in temperate waters.

Male *A. flavidus* at AOP were observed flaring their fins in a declined (head-down) position (Fig. 1A) facing a nearby female, an action interpreted as a courtship display.

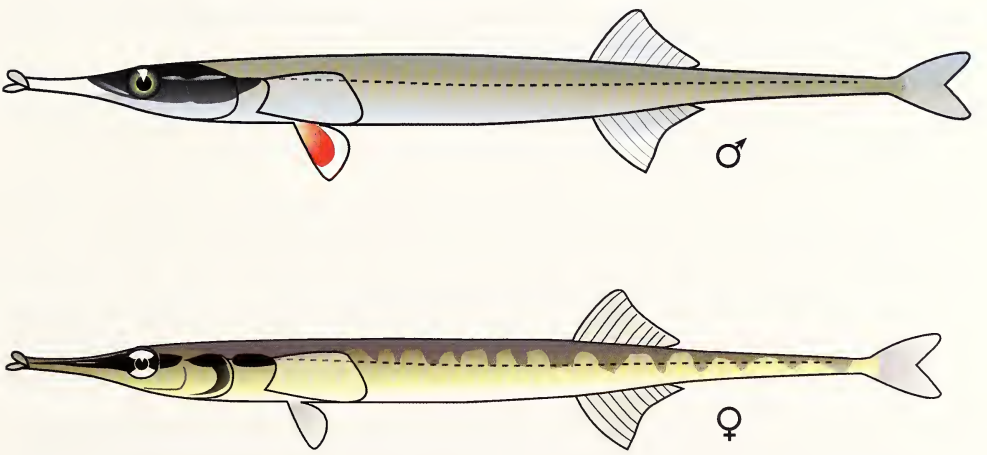

Fig. 2. Artist rendering of male (top) and female (bottom) *A. flavidus* body coloration. Notable differences between males and females are coloration along the length of the body, pelvic fins and the head. (Image by Larry G. Allen)

While maintaining this posture, they may undulate their fins lightly with accompanied full body undulations, a behavioral display common among other fishes (Limbaugh 1964, Wiley 1973, Steele and Anderson 2006). A similar posture was observed when conspecific males were present, but were typically followed by a chase to displace the competitor male, actions not taken toward females. Due to the similarity of these interactions, it is difficult to definitively determine whether this is a generic social interaction or whether a true courtship display. A lack of suitable nesting habitat (giant kelp fronds), due the nature of the display aquaria at AOP, might have precluded oviposition by females, although it is questionable whether female spawning response necessitates an established nest (Limbaugh 1962). While the results of this study may not provide a definitive description of male mating behavior, it does offer a cursory characterization of a previously undocumented aspect of the behavior of this species. Further behavioral studies focusing on conspecific interactions would elucidate subtle differences and may provide greater insight to the reproductive behavior of *A. flavidus*.

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Pilot California Spiny Lobster Postlarvae Sampling Program: Collector Selection

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Lobster (infraorder Astacidea) is perhaps the most intensively studied shellfish around the world due to its economic importance (Phillips 2006). Fishery management tools almost universally include catch reporting, but fishery-dependent data such as this often fails to adequately inform managers about the true state of the population (Erisman et al. 2011). Increasingly, fishery-independent surveys are being relied upon to provide the robust information fishery managers require, such as the California Cooperative Oceanic Fisheries Investigation (CalCOFI). The CalCOFI program attempts to understand and predict variations in the Pacific Sardine (*Sardinops sagax*) fishery, among others, in California through quarterly sampling of fish larvae and other biological and hydrographic data. This focus on larval stages stems from Hjort's seminal work in 1914, which hypothesized the recruitment and transition of larval forms into postlarval and juvenile life stages is a critical period in population dynamics (Houde 2008). In modern times, fishery management agencies expend significant effort towards cataloging and understanding recruitment levels and patterns which provide the foundation for most fishery management tools (e.g. stock assessments).

Recruitment monitoring is at the core of many of global lobster fishery management programs (Cruz et al. 1995; Acosta et al. 1997; Cruz and Adriano 2001; Phillips et al. 2005; Phillips and Melville-Smith 2005; Phillips et al. 2006; Arteaga-Ríos et al. 2007; Phillips et al. 2010). Recruitment monitoring of numerous lobster taxa globally have been well correlated with future catch-rate predictions, typically with a 4 to 5 year time lag (e.g. Gardner et al. 2002; Caputi and Brown 2011; Linnane et al. 2014). Long-term recruitment monitoring programs, such as that in Australia (Linnane et al. 2010), are vital in assessing future stock levels and setting the total allowable commercial catches.

Like many lobster species, the California Spiny Lobster (*Panulirus interruptus*) is an economically important fishery species, supporting one of California's most valuable fisheries with annual ex-vessel values exceeding $9 million (Porzio et al. 2012). However, unlike many of the world's lobster fisheries, no California Spiny Lobster recruitment monitoring program exists. Recent attempts to address this data gap have been made using plankton collection (Koslow et al. 2012) and power plant entrapment records (Miller 2014). Plankton collections were unable to reliably predict recent landings while entrapment records were more successful, but both articles noted the likely effect of unknown recreational harvest levels impacting the analyses and final conclusions. While informative, neither existing program fulfills the need for targeted information on California Spiny Lobster recruitment in southern California. Furthermore, as southern California power plants shift away from once-through-cooling, lobster entrapment data may soon be unavailable, in which case no regular abundance estimates of California Spiny Lobster postlarvae will be available.

Noting the clear need for lobster recruitment monitoring in California, a pilot program was initiated in Orange County, California with the hopes of establishing a model that

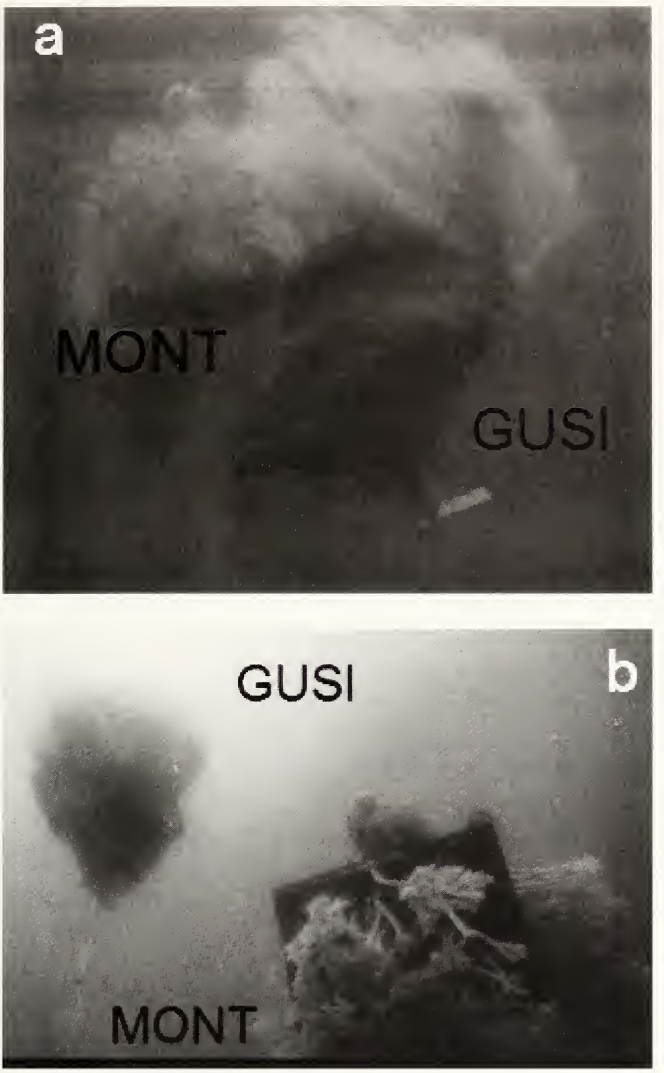

Fig. 1. Both GuSI and MONT type California Spiny Lobster postlarvae traps deployed at Abalone Point, California on 10 July 2013. a) GuSI in the forefront, b) MONT in the forefront.

could be expanded or replicated elsewhere in the state at minimal cost. Building upon the existing information on lobster recruitment monitoring elsewhere in the world, a pair of promising monitoring traps were identified for testing in southern California. Trap effectiveness varies greatly among different lobster species (Phillips and Booth 2008) thus it is important to compare the different trap types as done previously by Serfling and Ford (1974) and Phillips et al. (2001, 2005). Traps were chosen based on 1) likely cost, 2) likely ease of construction and use, and 3) reported effectiveness. Each trap design was modified slightly to maximize cost-effectiveness and ease of use. The first type (GuSI; Figure 1) was a modification of a design previously used in, among other places, Baja California, Mexico to successfully monitor postlarval California Spiny Lobster abundances (Arteaga-Ríos et al. 2007). The second type (MONT; Fig. 1) was a modification of a design used in Australia (Montgomery 2000).

Fig. 2. Postlarval California Spiny Lobster collected in a MONT traps offshore of Abalone Point Laguna Beach, California on 31 July 2013.

All materials used were purchased from at a local hardware store except marker buoys which were purchased at a local marine supply store. Total cost for each trap was less than $100. This fulfilled parts of two criteria, low cost and easy acquisition of materials for construction. The GuSI traps used were made by threading sisal rope through drilled holes in a plastic five-gallon bucket then covering the bucket in a burlap sack. Positive buoyancy resulted from lining the inside of the bucket with spray foam insulation. MONT traps were made by threading sisal rope through plastic peg board panels and connecting three panels together using plastic cable ties to form a triangle. A buoy was placed in the middle for buoyancy. In both cases, water motion frayed the sisal rope after deployment (Fig. 1). Refining the construction techniques as each trap was built resulted in a final estimated 1.0-1.5 hours to construct a trap of either design assuming the plastic pegboard panels were pre-cut to size.

One MONT and two GuSI traps were deployed on 10 July 2013 offshore of Abalone Point (33° 33.326N 117° 49.259W) on the coast of Laguna Beach, California at a depth of seven meters on sandy bottom habitat, with a rocky reef nearby and adjacent to a marine protected area. A second MONT trap and a third GUSI trap were deployed on 31 July

Fig. 3. Size series of postlarval Kelp Bass (*Paralabrax clathratus*) captured by a MONT trap set offshore of Corona del Mar in August 2013.

2013 and remained deployed through the last month of monitoring. Another trap string comprised of three MONT and one GuSI was deployed on 10 July 2013 just offshore of Corona del Mar, California in the lee of the Newport Bay jetty (33° 35.447N 117° 52.372W), but the three MONT traps were lost during a storm shortly after deployment. Two were recovered on the beach and the third was never found. Each of the recovered MONT traps was severely damaged, and two new MONT traps were deployed on the Corona del Mar string on 26 August to replace the lost traps.

On both the Abalone Point and Corona del Mar strings, the trap styles were alternated on each string so one design did not occur consecutively. Each trap was positively buoyant and remained at approximately one meter above the bottom with a mooring line attached to a communal anchor line. The communal anchor line was stretched between a

Table 1. Positive collections of California spiny lobster (Lobster), Kelp Bass, and all fish species combined (Total Fish) by service date, trap type, and location.

Date	# of Lobster	# Kelp bass	Total fish	Trap type	Location
7/31/2013	14	0	1	MONT	Abalone Point
8/26/2013	3	1	2	MONT	Abalone Point
8/26/2013	1	0	0	GuSI	Abalone Point
8/26/2013	2	0	0	GuSI	Abalone Point
8/26/2013	1	9	9	MONT	Corona del Mar
8/26/2013	2	5	6	MONT	Corona del Mar
9/26/2013	0	0	1	MONT	Abalone Point
9/26/2013	1	0	0	GuSI	Abalone Point
9/26/2013	0	0	1	GuSI	Abalone Point
Total	24	15	20		

Danforth anchor at the seaward end and a concrete block at the landward end, and a second concrete block was positioned at the midpoint for additional anchorage. The habitat was selected to minimize potential interference from natural habitat that may be preferred by the postlarvae (Montgomery 2000). No surfgrass (*Phyllospadix* spp.), believed to be the preferred California Spiny Lobster postlarval habitat (Barsky 2001) was in the immediate vicinity of the traps.

Servicing (inclusive of retrieval, sample collection, cleaning, and redeployment) occurred at nearly monthly intervals on 31 July and 26 August 2013. The final servicing, but not redeployment, occurred on 26 September 2013. No servicing occurred after the recreational fishery opened on 28 September 2013. Recovery was done by divers who cut the plastic cable ties connecting each trap to its mooring line. The traps were brought to the surface and taken aboard the boat where each trap was vigorously shaken 30 times while rotating the trap in a large trash can to remove individuals deeply embedded in the traps. Contents of the trash can were washed through a large, fine mesh (approximately 1 mm square mesh) aquarium net. The resulting sample was fixed in 4% seawater-buffered formalin in the field and transferred to 70% isopropanol after 72 hours in the fixative. Postlarval California Spiny Lobster (Fig. 2) and fish (Fig. 3) were sorted from the samples in the laboratory where they were enumerated, by species and by trap.

A total of nine MONT and 11 GuSI trap servicings were completed, which was analogous to a sample size of 20 traps for the purpose of this analysis. Eleven traps caught zero postlarval California Spiny Lobster. Nine positive catches were distributed amongst five MONT and four GuSI traps (Table 1). Standardizing the catch to the total sample size yielded 2.2 postlarval California Spiny Lobster/MONT trap and 0.4/GuSI trap. Twenty-one individuals were caught at Abalone Point while three were taken at Corona del Mar. Most of the MONT collection at Abalone Point occurred during the first deployment period when 14 individuals were taken. No postlarval individuals collected by the GuSI traps. Three postlarval individuals were caught by the GuSI traps and six in the MONT traps during the 26 August servicing. One individual was taken (GuSI) during the 26 September servicing at Abalone Point. The GuSI trap deployed at Corona del Mar never caught a postlarval individual.

The MONT traps also caught more recruiting fish (19 or 2.1/trap) than the GuSI traps (one or 0.1/trap). Corona del Mar MONT traps caught 15 of the 19 fish, including 14 Kelp Bass (*Paralabrax clathratus*). Furthermore, fouling communities developed on both designs at both locations, but the traps on the Corona del Mar string were also covered

by filamentous algae. Fouling rates were not expressly examined during the course of this study and warrant further investigation in the future.

Both designs showed stress and damage after the three-month deployment. Most of the burlap was removed from the GuSI traps but they were otherwise intact. The plastic panels used in the MONT traps were extensively cracked in those that survived the whole deployment. Some broke as noted previously. None of the traps (GuSI or MONT) were deemed fit for redeployment for a second season. The strength of the MONT trap could be easily improved by using stronger perforated plastic panels, although this would likely raise the cost.

Ultimately, the success or failure of the trap design at catching postlarval California Spiny Lobster was the most important criteria in this evaluation. While the sample size was small and impacted by various factors, the MONT trap showed the most promise. Recommendations to this study plan would include earlier deployment of MONT traps constructed out of stronger (thicker) perforated plastic panels on the Abalone Point string. These refinements would build upon the lessons learned during the pilot program and help refine the methodology so it could later be deployed on a greater scale to better monitor California Spiny Lobster recruitment.

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Avian Predators Target Nocturnal Runs of the Beach-Spawning Marine Fish, California Grunion, *Leuresthes tenuis* (Atherinopsidae)

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Abstract.—Tidal cycles are important cues for many marine and near-shore animals. Birds that typically feed at the water's edge during daytime low tides are rarely present on beaches at night. However, we found that several species of diurnal birds reliably attended and preyed upon the nocturnal spawning runs of a marine fish, *Leuresthes tenuis,* the California Grunion (Teleostei: Atheriopsidae) on the shores of Malibu Lagoon State Beach (MLSB), Los Angeles County, California, USA. Avian hunters of California Grunion included Black-crowned Night Heron *Nycticorax nycticorax,* Great Blue Heron *Ardea herodias*, Snowy Egret *Egretta thula,* and Western Gull *Larus occidentalis.* Spawning runs of California Grunion are synchronized by tides within a narrow window of time, two hours following the semilunar high tides of full and new moons. These silverside fish aggregate *en masse* predictably, and further increase their vulnerability by fully emerging from the water while spawning. This allows the birds to capture California Grunion terrestrially. On nights when spawning runs of California Grunion could potentially occur, birds were present on MLSB, often before the fish began to run onto shore. Number of birds was high for the nights of likely runs whether after full or new moons, whether or not the fish appeared, but not on other nights. We suggest that birds rely on tidal cues to anticipate spawning runs of California Grunion, not the amount of moonlight or the actual presence of fish on shore. Shorebirds were more likely to forage at night at sites close to their upland roosting and nesting areas than at sites with less upland habitat. Observers on nearby Will Rogers State Beach and Topanga State Beach saw comparable spawning runs of California Grunion but reported significantly fewer avian predators. At MLSB, when tide conditions were right, avian predators appeared on the beach with even greater predictability than did their potential prey.

During the remarkable spawning runs of California Grunion *Leuresthes tenuis* (Teleostei: Atherinopsidae), thousands of these silverside fish emerge from the ocean and actively move about on beaches to lay their eggs in the damp sand (Spratt, 1986). These huge aggregations are synchronized by the highest semilunar tides that occur after new and full moons. Although the nights of potential runs are somewhat predictable for human recreational anglers, the runs are highly variable in size and extent, and do not occur on all possible nights or all potential beaches within a single night (Walker, 1952). The actual time of appearance of the fish on shore is usually later than the peak of the tide, and observers report that on many nights with favorable tides, no fish appear at all (Martin et al., 2006). During the spawning season, in the spring and summer months,

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these extreme tides only occur late at night. It has been suggested that the reason for this unusual spawning behavior is that it may provide cover of darkness and less exposure to predators for the adults (Thompson, 1919; Walker, 1952; Spratt, 1986). However, spawning California Grunion attract both marine and terrestrial predators (Gregory, 2001; Sandrozinski, 2013). Large numbers of fishes in a spawning aggregation may attract aquatic predators (Sancho et al., 2000), but during open ocean spawning rushes, with few exceptions, actual take and kills of adult fish are rare (Moyer, 1987).

Shortly after the highest tide, a few nights after the full or new moon, a few California Grunion begin a run by briefly stranding themselves on shore. Dropping out of a receding wave, these marine fish jump and flip about on the sand searching for a mate. If successful, a female digs a hole in the soft, fluid sand with her tail (Martin, 1999; Martin et al., 2004). Upright with only her head still visible at the surface, she emits a clutch of up to 3000 eggs while one or several males surround her, adding milt before both adults return to the ocean on a subsequent wave. Beach spawning with these cryptic nests provides the eggs with good conditions for the developing embryos (Martin et al., 2009, 2011; Martin and Carter, 2013).

California Grunion nest on the sandy beaches of southern California, one of the most heavily populated coastlines of the globe. California beaches host millions of people on summer days, yet at night they are relatively quiet. Some beaches are surrounded by urban development and parking lots, while others are sited in more natural surroundings backed by lagoons and wildlife refuges. Anthropogenic impacts to the spawning grounds abound (Martin et al., 2006, 2013; Matsumoto and Martin, 2008; Martin, 2014). Although the habitat range of this species extends into northern Baja California and the central California coast, over 90% of the species occurs in heavily populated southern California, and the only known spawning habitat for this species is sandy beaches.

Shorebirds and herons are frequently observed on sandy beaches during the daytime, particularly near roosting areas such as lagoons, state parks, and bird sanctuaries. Most birds are visual predators, so foraging depends on available light and is usually diurnal, with some exceptions. Many herons eat fishes and are important intertidal predators, particularly during daytime low tides (Feunteun and Marion, 1994; Hoyer and Canfield, 1994). However, some shorebirds that forage at low tides may be active at night, even during very dark nights (Robert et al., 1989; McNeil et al., 1993; Dwyer et al., 2013).

With tide charts, humans can expect spawning runs of California Grunion within two hours after the highest tides following each full or new moon during the spawning season, March through August (Walker, 1949). Grunion spawn on the four nights after both new moon and full moons, and overcast skies that obscure the moon do not deter the runs (Walker, 1952). However, any or all nights may pass without a spawning run at any given beach. The strength of runs of California Grunion is variable from night to night, between beaches on a given night, and within and across seasons (Walker, 1949; personal observations). During smaller runs, California Grunion may be seen in the waves and some occasionally strand for brief periods without spawning. Actual runs, with numerous fish emerged out of water onto shore, occur on fewer than 50% of the nights when tides are favorable (unpublished data from Grunion Greeters). Outside of this period, no runs occur because the oviposition site is not accessible (Martin and Swiderski, 2001; Martin et al., 2004).

During nights of potential spawning runs of California Grunion, several species of herons and other birds have been observed at the high tides, apparently watching the waves in the dark and sometimes wading into the surf. The regular appearance of avian

predators, even before California Grunion start appearing on shore, suggests that birds may be able to anticipate runs in advance of seeing fish emerge. Once the run starts, these birds begin to catch fish. Nocturnal foraging may be affected by the light from the moon. For example, nocturnal foraging by shorebirds increases on nights with a visible moon (Dodd and Colwell, 1998). Nocturnal behavior and foraging change with the moon phase for many nocturnal birds, including Common Cranes *Grus grus* (Alonso et al., 1985), Common Poorwills *Phalaenoptilus nuttallii* (Mills, 1986; Brigham and Barclay, 1992; Woods and Brigham, 2008), and Australian Owlet-nightjars *Aegotheles cristatus* (Brigham et al., 1999).

Tidal cycles affect avian predators' access to marine prey resources. Many wading birds and shorebirds feed at low tides. Relatively few feed at high tides because marine organisms generally are covered by water. Because the lunar day is about 24 h 45 min long, the lowest and highest tides occur later on subsequent days. Diurnal animals that forage tidally may need to be able to feed at night occasionally. For example, at low tides, most species of shorebirds in a tidal lagoon foraged with comparable frequency during the day or at night (Robert et al., 1989), and Grey Herons *Ardea cinerea* arrived to feed at low tides early in the morning before sunrise (Sawara et al., 1990). Great Blue Herons *A. herodias* and Black-crowned Night Herons *Nycticorax nycticorax* fed during low tides after sunset in a salt marsh (Black and Collopy, 1982). During migrations, Semipalmated Sandpipers *Calidris pusilla* foraged on intertidal amphipods during nighttime low tides (McCurdy et al., 1997).

We tested the following hypotheses. First, we hypothesized that the birds would be present on the beach at night only when tides were favorable for spawning runs of California Grunion, but not on other nights. Following up, a second hypothesis was that these birds use tidal cues to determine appropriate nights, rather than either waiting for the arrival of fish on shore, or observing the available moonlight. Because the number of birds present at Malibu Lagoon State Beach can be large, we hypothesized that the number of avian predators during spawning runs of California Grunion may be correlated with adjacent upland habitat for wildlife. Thus Hypothesis 3 was that the number of birds present for spawning runs of California Grunion would be smaller at nearby beaches with similar California Grunion runs but less upland bird habitat.

Materials and Methods

Field observations were made at three locations within a 20 km linear segment of the shore in Los Angeles County, California. All three wide, sandy recreational beaches abut Pacific Coast Highway, a major thoroughfare lined with streetlights, and all support significant spawning runs of California Grunion. The first site is Malibu Lagoon "Surfrider" State Beach (34°02′07″ N, 118°40′42″ W). Adjacent to a restored coastal lagoon of Malibu Creek, MLSB is a roosting, feeding, and nesting area for up to 256 species of birds (Cooper, personal communication). The second, Topanga State Beach (34°02′15″ N, 118°34′58″ W), is a bluff-backed beach around a small, 1 acre seasonal lagoon at the outlet of Topanga Creek. TSB includes a narrow upland area with some trees and riparian habitat that extends shoreward for several miles through a canyon. The third, Will Rogers State Beach at Sunset Boulevard (34°02′16″ N, 118°33′24″ W) is an urban beach with no creek or upland natural habitat. Sandy WRSB is backed by rip rap, parking lots, a restaurant, a mini-mall, houses, and extensive urban development in the adjacent area shoreward of Pacific Coast Highway. The lights from the highway do not

illuminate the shoreline where runs occur, but each beach has small areas of the shoreline lit artificially by structures such as restaurants or a pier.

For Hypotheses 1 and 2, birds and California Grunion were observed by the authors for 27 nights from May to July, 1996 at MLSB. Observations were made for two hours between 2100 and 0100 starting at the time of the highest nocturnal tide, for seven sequential nights every two weeks. Observations started before any fish appeared on shore, and continued for up to two hours, ending either after the California Grunion departed, or all the birds left. Avian species on the beach were identified, counted, and observed for predatory behavior with a night vision monocular (ITT night mariner 160 Generation III), supplemented by occasional use of binoculars and a flashlight. Walking shoreward of the high tide, the observers were able to walk along the length of the shoreline with minimal disturbance to the birds at the water line.

For Hypotheses 2 and 3, the authors and volunteer Grunion Greeters observed three local beaches between the years 2004 and 2010. Award-winning citizen scientists, the Grunion Greeters have been observing runs of California Grunion since 2002 (Martin et al., 2006, 2007). These volunteers received training to observe and input data through a web-based portal at www.Grunion.org for specific nights and locations during spring and summer. Observations were made for two hours, starting at the high tide, between 2100 and 0100, following each full and new moon in April, May, and early June. Data gathered from 2004 to 2010 included a rating of the approximate number of fish on shore at the peak of the run using the Walker Scale, the duration of the run, the extent of shore involved, and the activity of the fish. Along with data on the California Grunion, observers noted weather conditions, cloud cover, wave action, presence of people including anglers, and the presence of birds and other predators. Observations were made in April, May, and June on the 10 nights per year when runs of California Grunion were most likely to occur, for a total of 86 run series observations. Malibu Lagoon State Beach was observed on ten additional summer nights when spawning runs were neither predicted nor seen in 2010. The strength and duration of spawning runs of California Grunion on shore were evaluated according to the Walker Scale (Martin, 2014; www.Grunion.org). Scores ranged from W-0, no fish or only a few fish on shore, to W-5, thousands of fish covering an extensive area of shoreline at peak levels for over an hour. Data were compared using the highest value of one semilunar tide series on each beach.

Results

On nights with tides conducive to a spawning run of California Grunion, large numbers of birds were present on shore at Malibu Lagoon State Beach (MLSB), but they were absent on other nights (Fig. 1), supporting Hypothesis 1. No California Grunion appeared on the shore on any night that was outside the forecast window (N = 21). A few California Grunion sometimes appeared on the night of a new or full moon, and larger runs occurred on subsequent nights. No California Grunion appeared before the night of a full or new moon; zero or just a few birds were present on this first night of each observation series at MLSB, as on other nights when no runs were expected.

On subsequent nights after the new and full moons, dozens of birds in a mixed flock appeared on the shores of MLSB. This happened for several nights during the tides that were favorable for California Grunion runs. After the fourth night following a full or new moon (the fifth night of each observation series), numbers of birds significantly declined, and birds remained scarce at night until the next semilunar high tide. The most common birds seen at the tides appropriate for spawning runs were three herons (Ardeidae) and

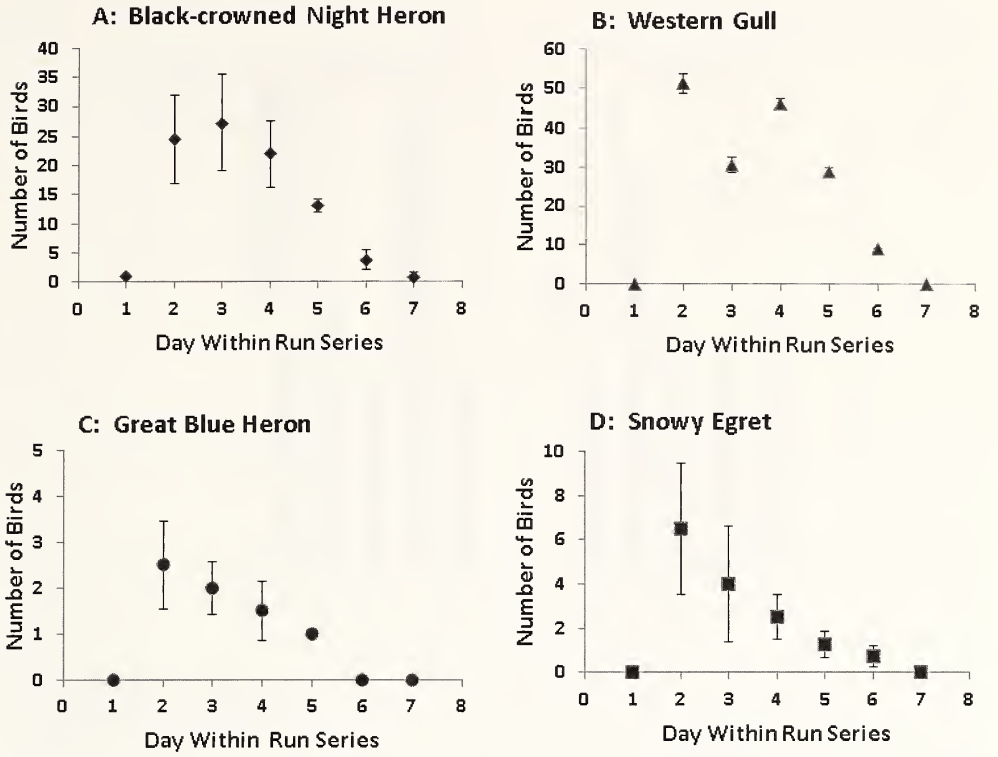

Fig. 1. The most common birds seen during spawning runs of California Grunion at Malibu Lagoon State Beach were (A) Black-crowned Night Heron *Nycticorax nycticorax,* (B) Western Gulls *Larus occidentalis,* (C) Great Blue Herons *Ardea herodias,* and (D) Snowy Egrets *Egretta thula.* Observation Night 2 is the night of the full or new moon phase, typically the highest semilunar tide. Numbers of birds (mean ± S.D.) on nights 2–5 were significantly greater than at other times or on other nights before or after the predicted runs. Note the different scales on the y-axis for each graph.

gulls (Laridae). The species seen most reliably and in greatest numbers were Black-crowned Night Heron (Fig. 1A), and Western Gull *Larus occidentalis* (Fig. 1B). Great Blue Heron (Fig. 1C) and Snowy Egret *Egretta thula* (Fig. 1D), were also commonly seen during the initial year of this study. Heermann's Gulls *L. heermanni* and California Gulls *L. californicus* were occasionally seen. All gull species were counted together because the individual species were difficult to distinguish reliably in low light at night.

At MLSB, the strength of the spawning run of California Grunion on shore, as indicated by the Walker score, had little effect on the presence or absence of the birds (Figure 2), supporting Hypothesis 2. If the tides were right, even on nights when no fish emerged from the waves to spawn on the beach, birds were still present on shore at night, often for several hours. In addition, the amount of moonlight did not affect the number of birds observed on these nights. Over the course of the study, on the nights of a potential run series, the number of birds was not different whether there was a new or a full moon (t-test, $df = 16$, $t = -0.355$, $p = 0.73$).

The runs of California Grunion were comparably large on the three study beaches. Runs of different strengths sometimes occurred on multiple nights of a series on each beach. Walker Scores for runs on both MLSB ($N = 35$) and WRSB ($N = 27$) did not differ (Wilcoxon Signed Rank test, $W = 5$, $z = 0.12$, $p = 0.90$). Both beaches had the

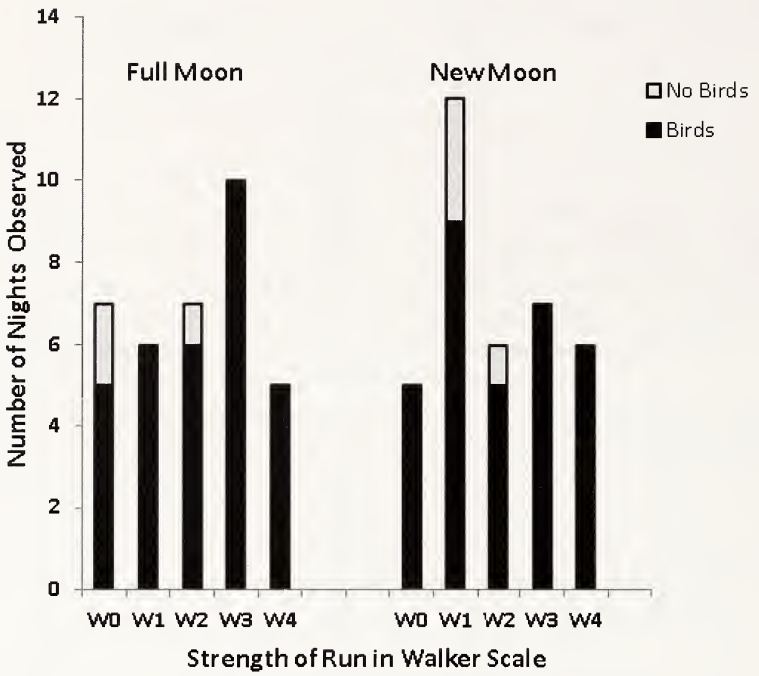

Fig. 2. The magnitude of spawning runs of California Grunion *Leuresthes tenuis*, as measured by the Walker Scale, does not affect the presence or absence of predatory birds at Malibu Lagoon State Beach. Nor does the amount of moonlight. Birds were present at MLSB on at least 90% of the nights when tides were conducive to spawning runs, whether after a full or a new moon.

same median and mode run size, with a Walker score of W-3. The median and mode Walker Score at TSB was W-4 ($N = 26$), significantly higher than at MLSB over the course of the observations (Wilcoxon Signed Rank test, $W = -165$, $z = -2.5$, $p = 0.01$). More than half the time, the size of the spawning runs of California Grunion at MLSB were smaller than the runs at one or both of the other two nearby beaches.

Although the runs of California Grunion are highly variable, semilunar tides appropriate for runs were positively and significantly correlated with the actual appearance of fish on shore on all three beaches (Fig. 3). On the other hand, the hunting birds appeared much more reliably on nights with appropriate tides at MLSB than at either TSB or WRSB (Table 1). At MLSB, the correlation between presence of birds and appropriate tides with potential runs was higher (*Rho* = 0.91, $p < 0.03$) than the correlation between bird presence and California Grunion presence on shore (*Rho* = 0.48, $p = 0.24$). However, on TSB birds were more likely to appear on nights when the fish actually appeared on shore (*Rho* = 0.85, $p < 0.04$) than on any night with appropriate tides but no run (*Rho* = 0.70, $p = 0.09$).

The number of birds present was significantly different at the three study sites during nights of potential spawning runs (Fig. 4), supporting Hypothesis 3. At MLSB, on average 74.5 +/− 16.1 birds attended nights of potential runs, and birds were present at least 90% of the nights that had tides appropriate for spawning runs. On other nights with less favorable tides, very few birds were seen on the shores of MLSB (t-test, $t = 5.12$, $df = 34$, $p < 0.0001$). At TSB, fewer birds were present than at MLSB during California Grunion runs (Mann Whitney U test, $U = 1.5$, $z = 3.91$, $p < 0.0001$). At TSB only 6.55

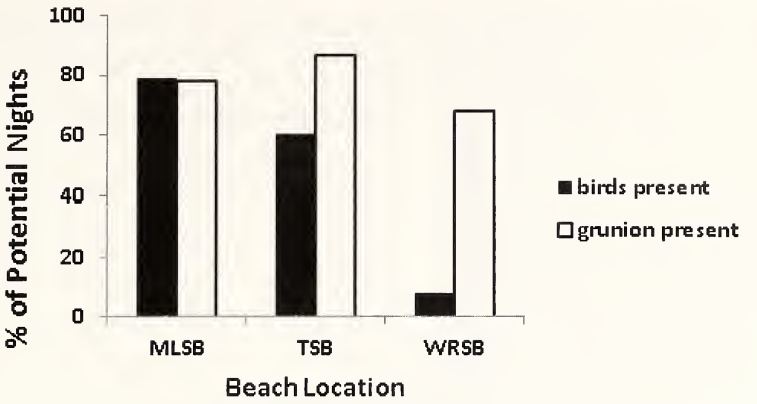

Fig. 3. On nights when tides were conducive to spawning runs, the majority of observers on all three beaches reported the presence of California Grunion. Birds were far more likely to be present on Malibu Lagoon State Beach (MLSB) than on Topanga State Beach (TSB) or Will Rogers State Beach (WRSB).

+/− 1.9 birds, usually Black-crowned Night Herons, attended runs (Fig. 4). At WRSB, birds were almost never seen during California Grunion runs, and those that did appear were always alone. On TSB, birds were occasionally seen, only on nights when the California Grunion emerged onto shore (*Rho* = 0.85, $p < 0.04$), and not when there were appropriate tides but no fish present (*Rho* = 0.70, $p = 0.09$). In a W0 run, when no fish actually spawned on the beach, some fish congregated in the water near shore and were sometimes caught by birds, although on many nights with appropriate tides, no California Grunion appeared at all. Members of all bird species present during the runs were observed eating California Grunion directly off the sand. When one California Grunion emerged from a wave onto the sand during a run, any bird that was nearby ran to it and attempted to grab it. In some cases the fish was caught just as it emerged; in other cases the fish was actively spawning; rarely a fish was stranded by a large wave pushing it high on shore. California Grunion are able to jump and move about on land to some extent, and this allowed a few to escape predation. No predation occurred in water deeper than a few centimeters in the wave wash, as the fish were able to swim quickly to safety. No bird was observed preying on anything but California Grunion during these runs.

Black-crowned Night Heron was the first species to arrive on any night, and the most persistent in remaining. This species usually arrived about half an hour before the highest

Table 1. Spearman Rank Correlations at three state beaches in Los Angeles County for nights when tides are appropriate for California Grunion runs, as compared with actual spawning runs of California Grunion, and as compared with presence or absence of predatory birds on shore. **Asterisks and bold type** indicate significant correlations ($P < 0.05$).

Correlations	Malibu Lagoon SB	Topanga SB	Will Rogers SB
Appropriate tides vs. presence of California Grunion	*Rho* = 0.64, P = 0.12	*Rho* = 0.70, P = 0.09	*Rho* = 0.76, P = 0.06
Appropriate tides vs. presence of birds on shore	***Rho* = 0.91, P = 0.03***	*Rho* = 0.70, P = 0.09	*Rho* = 0.19, P = 0.64
Presence of birds on shore vs presence of California Grunion	*Rho* = 0.48, P = 0.24	***Rho* = 0.85, P = .04***	*Rho* = 0.05, P = 0.91

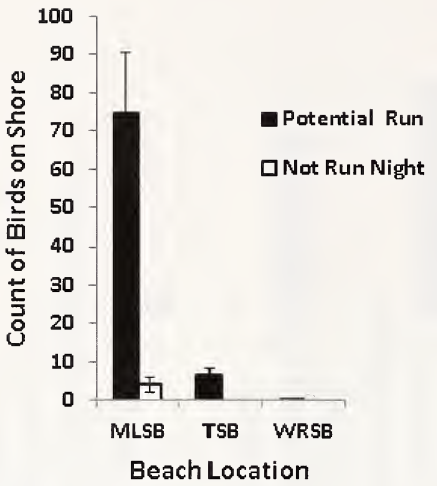

Fig. 4. Significantly more birds were present at Malibu Lagoon State Beach (MLSB) during nights of potential California Grunion runs, than on nights when runs are unlikely to occur. For California Grunion runs of similar sizes at nearby Topanga State Beach (TSB) and Will Rogers State Beach (WRSB), significantly fewer birds were observed. Different letters indicate significant differences.

tide and formed a single line of individuals spaced a meter or more apart, facing the waves along shore. Each stood quietly on the dry sand watching the waves until fish began to appear momentarily in receding waves. When a fish was sighted in a wave returning to the ocean, the Black-crowned Night Herons ran down the sand toward the water and usually caught the fish before it washed away into deeper water. Some faced away from the ocean with the back to the wave, letting the water wash up from behind under them. If a fish dropped out onto the sand as the wave receded, it was caught. If disturbed or if unsuccessful in one location, Black-crowned Night Herons flew through the darkness over water to another location on the beach. They sometimes called while flying over the surf at night, especially when conspecifics were actively feeding during a run. Closer to the water, Great Blue Herons and Snowy Egrets stood in the swash zone of incoming waves. Great Blue Herons, with longer legs, waded in deeper. Both species watched the water, and when a fish was spotted, caught it by spearing with the bill. After a successful catch, herons often moved a few steps up the shore out of reach of the waves, to manipulate the fish in the beak for swallowing. In the initial year of observations, gulls and Snowy Egrets were regularly present on shore at MLSB at night during spawning runs of California Grunion. Since 2004, fewer gulls and no Snowy Egrets appeared at night on MLSB, yet Black-crowned Night Herons and Great Blue Herons have been present consistently during spawning runs across the years. In the daytime, large numbers of gulls and Snowy Egrets are easily observed on MLSB and adjacent Malibu Lagoon.

Discussion

Avian predators are present on Malibu Lagoon State Beach (MLSB) during the nights of potential spawning runs of California Grunion, but not on other nights (Fig. 1), supporting our first hypothesis. Spawning runs of California Grunion provide a very temporary but bounteous and moderately predictable resource on sandy shores during nocturnal high tides. For birds that may rarely hunt at night, even a small run can provide ample food for a successful predator. Black-crowned Night Herons and Great

Blue Herons were reliably seen on nights following semilunar high tides (Fig. 1A and C). They arrived on the beach earlier than fish did, and birds were on the beach at MLSB on nearly all nights when the tides were appropriate, more frequently than the California Grunion were. However, these birds were not on the beach on other nights, when no run would be expected.

No matter how many or few fish actually appeared on shore, regardless of available moonlight, birds were present, waiting on shore before the fish emerged from the waves at MLSB. The bird species that appeared most consistently was Black-crowned Night Heron (Fig. 1). Black-crowned Night Herons have large eyes, special pigments, and a wide field of vision that enable them to forage for fish and amphibians during day and night (Katzir and Martin, 1998). They prey on tern and other bird colonies at night (Hunter and Morris, 1976; Brunton, 1997, 1999). Great Blue Herons are also known to forage at night (Black and Collopy, 1982). Black-crowned Night Herons and Great Blue Herons remained fairly consistent visitors at MLSB over the years of this study. These two species also attend California Grunion runs at other California beaches (Grunion Greeters, personal communication).

Snowy Egrets were frequently present in the first year of the study at MLSB, although in smaller numbers than the other species (Fig. 1D). Snowy Egrets no longer attend California Grunion runs at MLSB, with no reports since 2004, although a few individuals have been seen at other California beaches during runs (Grunion Greeters, personal communication). Many individuals in this species forage nearby in shallow wetlands such as Malibu Lagoon during the daytime, and also at the beach during low tides in daylight (Cooper, personal communication). Snowy Egrets generally feed in shallow water by stirring up fish with their feet; this species does not forage at high tide as a rule (Master et al., 2005). However, a California Grunion run is not a typical prey resource, so some individual Snowy Egrets have sometimes been able to take advantage of this opportunity.

Another avian predator on California Grunion runs was documented sixty years ago. Up to 30 Barn Owls *Tytlo alba* at one time were seen feeding on beach spawning runs of California Grunion in northern San Diego County, California (Gallup, 1949). This nocturnal predator is a common bird in open areas, and still occurs in coastal areas of California near beaches where California Grunion run, for example at Camp Pendleton in northern San Diego County, and in Malibu. However there have been no reports of Barn Owls at any runs of California Grunion in any location throughout the species range, over thousands of observations in the past ten years (Grunion Greeters, personal communication).

Birds appear to be able to recognize tidal cues on the nights when this resource may arrive, rather than light cues from the moon (Fig. 2) or the actual presence of fish on shore (Fig. 3). For visual predators including most birds, amount of available light is critical (Jetz et al., 2003). Light cues differ between the full and new moon phases. However, available moonlight had little effect on the presence or absence of birds during tides for spawning runs at MLSB. Birds were equally likely to be present after either new or full moon runs and on overcast nights, early or late in the four-night run series, at any strength of run (Fig. 2). This suggests these birds are more influenced by tidal height than by amount of moonlight or presence of fish out of water, supporting our second hypothesis. On the other hand, the nocturnal activity of Elf Owls *Micrathene whitneyi* and Western Screech Owls *Megascops kennicottii* does not depend on moon phase (Hardy and Morrison, 2000). White-chinned Petrels *Procellaria aequinoctialis* forage widely in the Southern Ocean during day and night while incubating eggs, with no influence of

moon phase (Weimerskirch et al., 1998). Shorebirds usually forage in daytime, but short days in winter may not be sufficient for gathering food so some nighttime foraging occurs, even when there is no moonlight (Pienkowski et al., 1984).

Longline fishermen report that birds are much more likely to be caught on nights with bright moonlight than when there is no moonlight (Brothers *et al.*, 2000; Moreno and Rubilar, 1996). Shy Albatross *Thalassarche cauta* also feed more during full moons, flying faster and farther on those nights than on dark nights (Hedd et al., 2001). At colonies of Black-vented Shearwater (*Puffinus opisthomelas*), gull predation occurs during moonlit but not dark nights (Keitt et al., 2004). Gull predation is also heavier during the full moon phase for Cassin's Auklets *Ptychoramphus aleuticus* (Nelson, 1989).

Artificial lights may impact foraging ability of wildlife at night (Rich and Longcore, 2006), either by increased effectiveness (Dwyer et al., 2013), or by increased risk of predation to animals that are active at night. Terrestrial insectivorous birds are attracted to powerful artificial lights for foraging (Lebbin et al., 2007). Wading birds increase foraging time and effectiveness with artificial lighting (Santos et al., 2010), and Black-crowned Night Herons are known to use intense shoreline illumination to forage at night in a salt marsh (Erwin et al., 1990). In the present study at MLSB, artificial lighting from street lights and a pier provide some illumination onto some areas of the beach where the avian predators were observed, and may contribute to the lack of effect of moon phase on their behavior. However this light is quite dim at the water's edge where the runs occurred. Occasionally observers used flashlights to see California Grunion on shore, and the birds quickly began to use the beams of light to assist their own prey capture.

Shorebirds rarely forage along the shoreline at high tide (Burger and Olla, 1984). However, spawning aggregations of the beach spawning Atlantic Silverside fish *Menidia menidia* occur during diurnal high tides, attracting avian species that prey on them in shallow water over seagrass beds (Middaugh, 1981). A congener of California Grunion, the Gulf Grunion *L. sardina,* spawns on sandy beaches in the Gulf of California, where some of the high tides appropriate for spawning occur in the daytime (Thomson and Muench, 1976). Avian predation is very intense on these daytime runs. Because of low wave energy at the top of this enclosed bay, Gulf Grunion spawn at the water's edge rather than out of water like California Grunion. Birds such as Brown Pelican *Pelicanus occidentalis*, cormorant *Phalocrocorax sp*, and several species of gulls, *L. occidentalis*, *L. delawarensis, L. californicus, L. heermani*, and *L. atricilla*, dive to feed on the fish in shallow water (Thomson and Muench, 1976), rather than catching them emerged on shore. The species of avian predators and their behavior during this aerial attack on Gulf Grunion differ from the species and their terrestrial hunting seen during nocturnal predation on California Grunion out of water.

Conclusions

Number of birds present during California Grunion runs was site-specific, much higher on MLSB than at two nearby beaches with equal or stronger runs. The comparison beaches, WRSB and TSB, are both adjacent to Pacific Coast Highway and both have restaurants and other structures with some outdoor lighting. However, these locations held far fewer avian predators. During nights when California Grunion runs were forecast, large numbers of birds were consistently present at MLSB, but only a few were seen occasionally at Topanga State Beach (TSB), and almost no birds attended California Grunion runs at Will Rogers State Beach (WRSB) (Fig. 3). At TSB, the avian species most consistently seen during the runs of California Grunion was Black-crowned Night

Heron, followed by Great Blue Heron, although in much smaller numbers than at MLSB (Fig. 4). As described earlier, the upland habitat around MLSB is far more extensive than at TSB or WRSB, creating a shorter distance for birds to fly from roosts to the beach at night.

In summary, birds, particularly Black-crowned Night Herons and Great Blue Herons, fed on nocturnal spawning runs of California Grunion and were reliably seen at tide-synchronized times of potential spawning runs, whether or not the fish actually appeared. When tide conditions were right, these avian predators appeared on the beach with even greater predictability than did their potential prey, the spawning fish.

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Fishes of Marine Protected Areas Near La Jolla, California

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Abstract.—The marine waters surrounding La Jolla, California have a diverse array of habitats and include several marine protected areas (MPAs). We compiled a list of the fish species occurring in the vicinity based on records of specimens archived in the Marine Vertebrate Collection (MVC) of the Scripps Institution of Oceanography (SIO). Collection of fishes from La Jolla in the MVC started in 1905, but greatly accelerated in 1944 when Carl L. Hubbs moved to SIO. By 1964, 90% of the 265 species recorded from the area had been collected and archived in the MVC. The fishes of La Jolla are dominated by species whose center of distribution is north of Point Conception (111 species), or between there and Punta Eugenia (96), with fewer species with southern distributions (57), and one exotic species. Reflecting the diversity of habitats in the area, soft-substrate species number 135, pelagic species 63, canyon-dwelling species 123 (including 35 rockfish species of the genus *Sebastes*), and hard-bottom species 140. We quantified the abundance of the latter group between 2002 and 2005 by counting visible fishes in transects along the rocky coastline of La Jolla, both within and adjacent to one of the region's MPAs. In 500 transects, we counted over 90,000 fishes representing 51 species. The fish communities inside and outside of the MPA were similar and, typical of southern California kelp forests, numerically dominated by Blacksmith, *Chromis punctipinnis* (Pomacentridae), and Señorita, *Oxyjulis californica* (Labridae). Natural history collections such as the MVC are important resources for conservation biology for determining the faunal composition of MPAs and surrounding habitats, and documenting both the disappearance and invasion of species.

The coastal environment in and around La Jolla, San Diego County, California is notable for its complex and diverse array of habitats within a relatively small area. These include kelp forests, rocky reefs, rocky intertidal, sandy beaches, sand and mud subtidal areas, eelgrass and surf-grass stands, pier pilings, and submarine canyons, as well as the pelagic environment. Because of the proximity of the La Jolla and Scripps submarine canyons, depths range to over 500 meters within less than 7 km of the coastline. These diverse habitats support a rich marine community, which has served as the focus of a

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variety of scientific investigations (e.g., Limbaugh 1955; Quast 1968; Craig et al. 2004; Brueggeman 2008).

The nearshore environment of La Jolla is especially important within the context of marine conservation because it houses a network of marine protected areas (MPAs) of varying size and age and with varying levels of use restrictions (Fig. 1). Historically, the first of these was the San Diego Marine Life Refuge established in 1957, which included the Scripps Coastal Reserve, a part of the University of California Natural Reserve system (McArdle 1997). Directly to the south is the San Diego-La Jolla Ecological Reserve (SDLJER), a small no-take reserve on the northern end of the La Jolla rocky coastline that was established in 1971. The San Diego-La Jolla Ecological Reserve Areas of Special Biological Significance was established in 1974 and largely overlapped the SDLJER (McArdle 1997). Recently the SDLJER was included in the Matlahuayl State Marine Reserve (CDFG 2013). In addition, the area on the southern part of the La Jolla peninsula was recently designated as the South La Jolla State Marine Reserve, and an area directly west of that was designated as the South La Jolla State Marine Conservation Area (CDFG 2013). These MPAs have a variety of use restrictions, but all recognize and seek to protect the biodiversity of this ecologically important region.

This study documents the fish fauna in and around this series of marine protected areas. The primary source of information on fishes occurring in the La Jolla area was the Scripps Institution of Oceanography's Marine Vertebrate Collection (MVC). The important roles of natural history collections such as the MVC to conservation biology have been widely documented (Allman 1994; Pyke and Ehrlich 2010; Drew 2011). These include compiling biotic inventories, documenting the loss or degradation of habitats and associated biota, documenting changes in the distribution and occurrence of native species, and documenting species invasions. In addition to compiling an inventory of fish species collected in the area and archived in the MVC, we report on diver surveys of the abundance and diversity of fishes in kelp forests, one of the most prominent habitats in the area, in and around the SDLJER (now the Matlahuayl State Marine Reserve) from 2002 to 2005.

Brief History of Fish Collecting in the La Jolla Area

The marine fishes of California have been studied for many decades and are well-known (Miller and Lea 1972, 1976; Hubbs et al. 1979; Love et al. 2005; Allen et al. 2006) with at least 519 species known from state waters (Horn et al. 2006). In addition to early collections of fishes from the San Diego area reported by Jordan and Gilbert (1880, 1881), the study of fishes in the San Diego region of southern California was begun in earnest with the *Albatross* surveys (Moring 1999) as reported by C.H. Gilbert (1890, 1896, 1915), as well as inventories by Eigenmann and Eigenmann (1890) and Eigenmann (1892).

The establishment of the Scripps Institution of Oceanography (SIO) in the San Diego region in 1903 and its subsequent move to La Jolla in 1905 marked a significant increase in the study of the region's biota (Hastings and Rosenblatt 2003). The on-site aquarium displayed many of the common shallow-water fish species of the area. In 1918, Percy S. Barnhart (Fig. 2A) was appointed as Collector and Curator of the Aquarium, and in 1926, Barnhart was elevated to the position of Curator of the Biological Collections, a position he held until 1948. Barnhart studied the local fishes leading to a publication on the fishes of southern California (Barnhart 1936), and he assembled a small collection of preserved specimens from the region that ultimately formed the basis of the SIO Marine Vertebrate Collection (MVC).

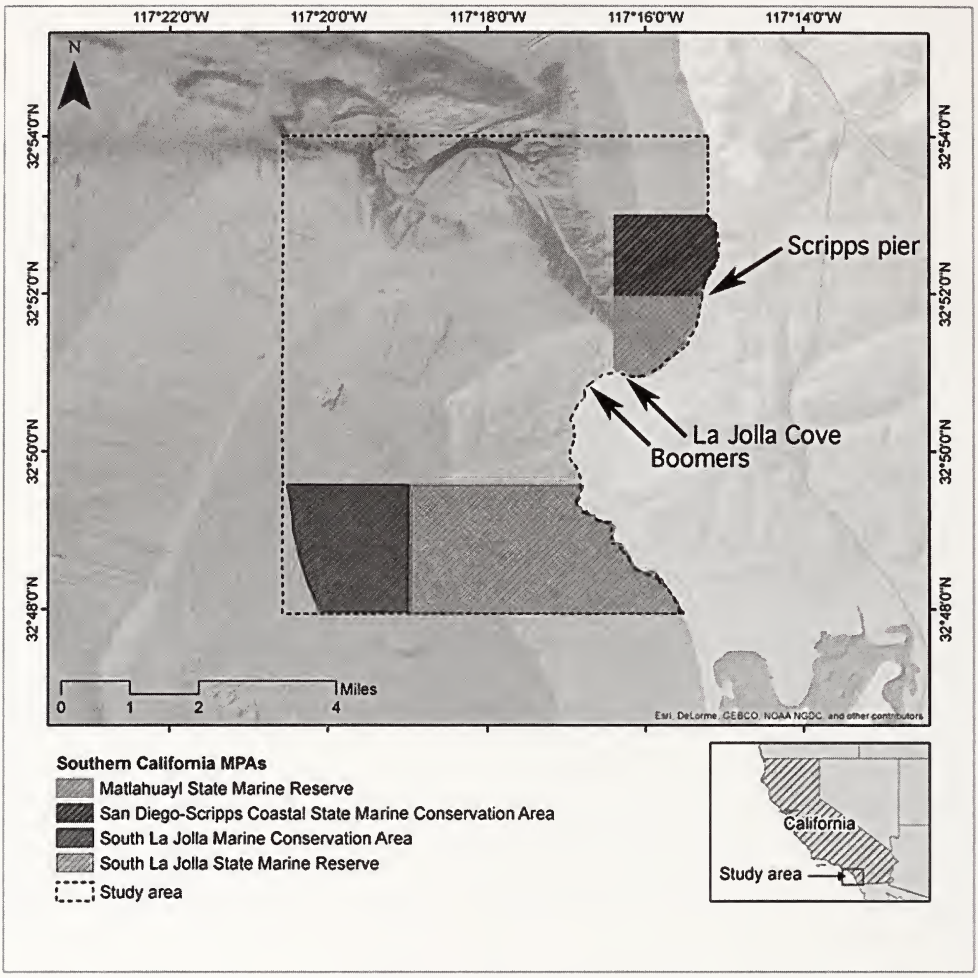

Fig. 1. Map of study area with MPAs designated. Kelp forest fishes were surveyed at La Jolla Cove and Boomers.

Knowledge of the ichthyofauna of the region greatly increased after 1944 when Carl L. Hubbs (Fig. 2B) moved to SIO and began actively archiving collections of fishes in the MVC. In negotiations regarding his forthcoming move from the University of Michigan to SIO, Hubbs wrote to then SIO Director Harald Sverdrup:

> "I would no doubt want to put considerable emphasis on systematic and variational studies of west coast marine fishes, particularly those in which speciation would be correlated with oceanographical (sic) conditions...I would no doubt be interested in exploratory work, for instance with the fauna of the deep basins off the southern California coast. I will probably be interested too in detailed analyses of the distribution of fishes along the entire west coast, again as correlated with the oceanographic conditions." (Shor et al. 1987, pp. 226-227).

Before his arrival in October 1944, Hubbs convinced Sverdrup to invest in facilities to store his anticipated collection of fishes, leading to the ultimate establishment of the

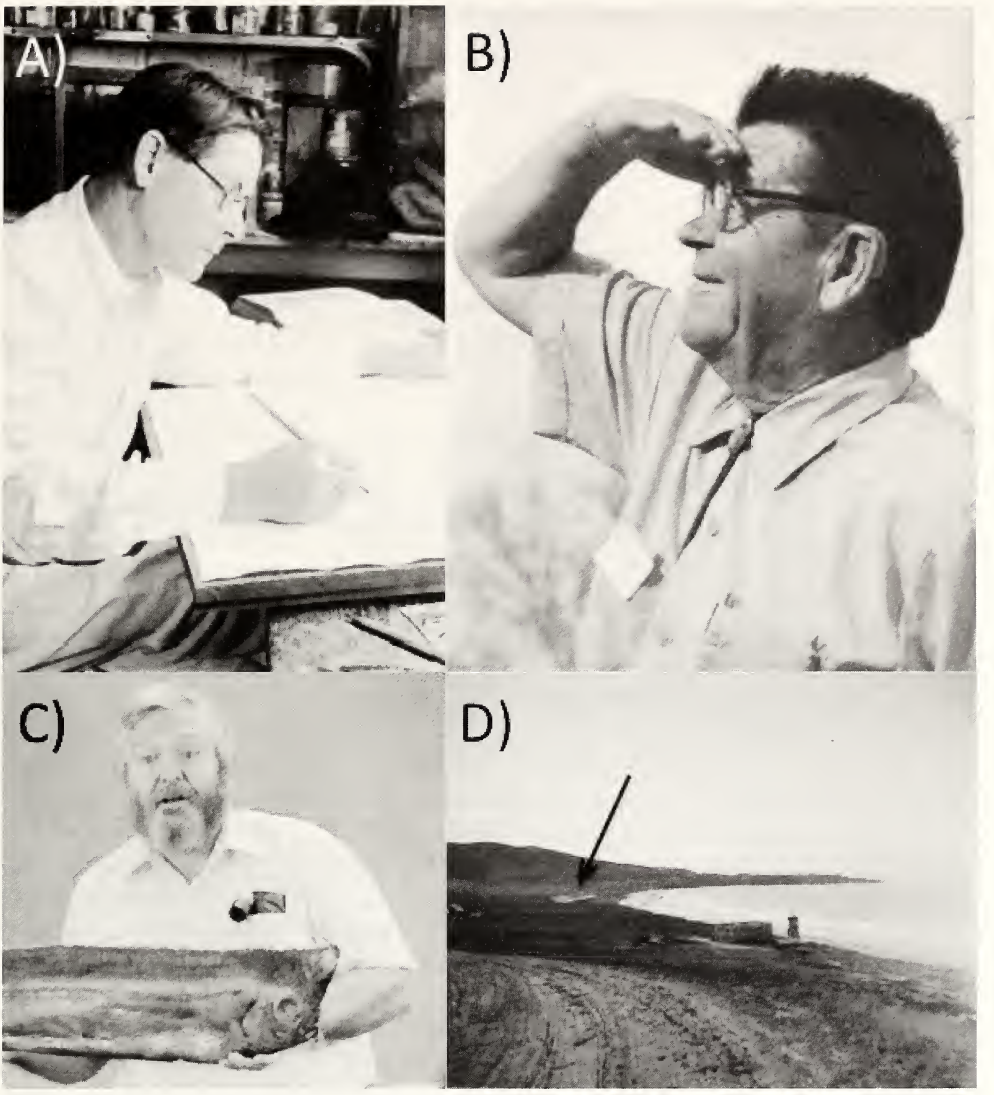

Fig. 2. Photos of A) Percy S. Barnhart, 1935; B) Carl L. Hubbs, 1973; C) Richard H. Rosenblatt, 1979; D) a view of La Jolla Shores and La Jolla peninsula looking southward from the SIO campus, circa 1910 (arrow indicates small embayment at La Jolla Shores). All images are from the Scripps Institution of Oceanography Archives, UC San Diego Library.

MVC (Shor et al. 1987). Hubbs wasted little time in collecting fishes from the surroundings of the SIO campus, amassing over 200 collections in his first year and over 500 by the end of the decade (Fig. 3).

Hubbs had another California project in mind when considering the move to La Jolla. In 1944 he wrote to W. I. Follett in Oakland, with whom he had been corresponding for a decade:

> "I look forward particularly to cooperating with you in making better known the California fish fauna. I no doubt will have new material published from time to time on the systematics and biology of the fishes but will definitely hope that you will

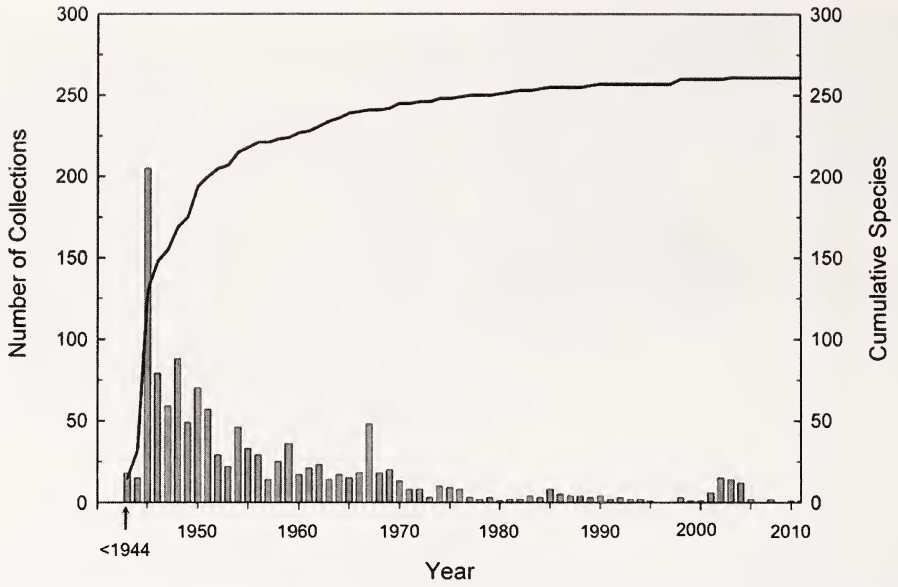

Fig. 3. Number of collections of fishes made within the study area and archived in the SIO Marine Vertebrate Collection by year (bars) and cumulative number of species recorded from those collections within the study area (line).

> maintain your plan to work toward a 'Fishes of California.' It will be a pleasure to make records and other information available for your project." (Shor et al. 1987, p. 227).

That project was published shortly after Hubb's death in 1979 (Hubbs et al. 1979).

In 1958, Professor and Curator Richard H. Rosenblatt (Fig. 2C) was hired to oversee the growing collection of fishes at SIO. He and other researchers and students at SIO actively collected fishes in and around the La Jolla region. By the end of 1969, over 1,000 collections and well over 3,000 lots of fishes from La Jolla had been archived in the MVC (Fig. 3). Local collecting of fishes declined after that time due to diverging research interests, and constraints of space in the MVC for storage of specimens. Since that time, the MVC has archived specimens of fishes from the La Jolla region primarily when new or unusual specimens become available, specimens from focused efforts associated with faunal inventories of the area (e.g., Craig et al., 2004; Craig and Pondella, 2006), and voucher specimens for the growing MVC tissue collection, established by H.J. Walker in 1993 (Hastings and Burton, 2008).

Materials and Methods

We compiled a list of fishes recorded from La Jolla, California based on specimens collected and archived in the MVC of the Scripps Institution of Oceanography, University of California San Diego (Table 1). We included all species collected less than 10 km from shore (east of 117°20.5′ W longitude) and from Torrey Pines State Beach southward to Tourmaline Beach (32°54′ N - 32°48′ N latitude). This area includes the entire rocky headland of La Jolla, as well as the primary conservation areas in the vicinity (Fig. 1). These include the San Diego-Scripps Coastal State Marine Conservation Area, the Matlahuayl State Marine Reserve, the South La Jolla State Marine Reserve and Marine Conservation Area (CDFG 2013).

While some collections date to the early 1900s and a few were made in recent years, most were made between 1944 and 1969 (Fig. 3). Archived specimens were collected using a wide variety of sampling methods and were taken from the beach or ocean surface to depths of over 500 meters. Species are listed in Table 1 arranged in taxonomic order. Common names of families and species follow those recognized by the American Fisheries Society (Page et al. 2013). Brief information on habitat or habitats occupied and special occurrences is provided for each species. Habitat type was divided into three categories as follows: *H* = *hard substrates*, including rocky reef, rocky intertidal, kelp forest, sides of pier pilings, boulders or any other type of hard substrate; *S* = *soft bottom*, including sand, mud, eelgrass and surfgrass; *P* = *pelagic,* including species that always swim well above the bottom, as well as those that periodically or regularly swim several meters above the bottom. Also indicated in Table 1 are the species collected in the La Jolla and Scripps Canyons from > 30 meters depth *(= Cn)*, and the species observed in transects conducted in and adjacent to the SDLJER (= *Tr*) between 2002 and 2005 (see below).

Frequency of occurrence is based on the number of lots (occurrences) of each species that have been archived in the MVC that were collected within the designated area, regardless of the abundance of the species. Common (*C*) species are those represented by eleven or more collections, uncommon (*U*) species were collected in the study area from three to ten times, and rare (*R*) species were collected only once or twice in the La Jolla study area. In a few cases, species that are known by us or reported by others to be more common in the study area than indicated by collection records are indicated with an asterisk (*). The biogeographic distribution of each species was designated based on the mid-point of the entire known range of the species. Range endpoints are from Horn et al. (2006), supplemented as needed based on published distribution records (e.g., Love et al. 2005). Southern species (*S*) are those whose range midpoint is south of Punta Eugenia on the outer coast of Baja California (27°50′ N), northern species (*N*) have range midpoints north of Point Conception (34°27′ N), and central species (*C*) have range midpoints between these well-established biogeographic barriers (Brusca and Wallerstein 1979; Horn et al. 2006).

Between 2002 and 2005, the abundance of fishes associated with kelp forests was visually surveyed at La Jolla Cove (within the SDLJER, now called the Matlahuayl State Marine Reserve) and an adjacent site (Boomers) a short distance beyond the reserve boundary (Fig. 1). Both sites have moderate relief rocky reefs (1-3 m high) scattered throughout the area and are dominated by red algal turf reefs and kelp forests (Parnell et al. 2005, 2006). Survey protocols were modeled after established techniques for assessing abundance and density of conspicuous fishes (McCormick and Choat 1987; Pondella et al. 2005). Randomly selected, quantitative belt transects were swum by two SCUBA divers for a period of 5 minutes over a distance of 50 m. All fishes (excluding pelagic species) observed within a two-meter window (i.e., one meter on either side of the diver and one meter above and below) along the transect were identified to species where possible, and the number of individuals was counted by each diver. If counts from the divers differed, the average was recorded. Each transect accounted for 100 m^2 of bottom area surveyed. Three replicate transects were conducted along rocky reef substrates at each of four depths (3 m, 6 m, 9 m, and 12 m) for a total of twelve transects at each site per survey period. Surveys were conducted every two months for a total of six periods per year between January 2002 and December 2005. At certain periods throughout the study, persistent foul weather prevented full surveys at each sample site, especially for the shallowest depth contours. However, at least six transects were conducted at every site during each sample period throughout the study except for July/August 2004 when continuous high surf precluded surveys at Boomers.

Table 1. List of fishes collected from La Jolla, California, and deposited in the SIO Marine Vertebrate Collection. Date = year of first MVC record from study area. Oc = frequency of occurrence in MVC collections from study area: C = common, 11 or more records; U = uncommon, 3 to 10 records; R = rare, 1 to 2 records; * indicates species known to be more common in the study area than collection records indicate (see text). Habitat (Hab) categories: H = hard bottom (reefs, etc); P = pelagic; S = soft bottom. "x" under Cn and Tr indicate, respectively, collection records for La Jolla or Scripps Canyons at > 30 meters depth, and occurrence in kelp forest transects in and around the Matlahuayl State Marine Reserve (formerly San Diego-La Jolla Ecological Reserve; see Table 3). SE = southern latitude endpoint of range (positive and negative values are north and south latitude, respectively); NE = northern latitude endpoint of range; mid = middle latitude of range. Distribution categories: So = southern, range midpoint south of Punta Eugenia; Ce = central, range midpoint between Punta Eugenia and Point Conception; No = northern, range midpoint north of Point Conception.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Myxiniformes										
Myxinidae – hagfishes										
Eptatretus mcconnaugheyi Wisner & McMillian, 1990	Shorthead Hagfish	1954	U	S	x	-	23	34	28.5	Ce
Eptatretus stoutii (Lockington, 1878)	Pacific Hagfish	1948	C	S	x	-	27	60	43.5	No
Chimaeriformes										
Chimaeridae – shortnose chimaeras										
Hydrolagus colliei (Lay & Bennett, 1839)	Spotted Ratfish	1945	C	S	x	-	28	60	44	No
Hexanchiformes										
Hexanchidae – cow sharks										
Hexanchus griseus (Bonnaterre, 1788)	Bluntnose Sixgill Shark	1974	R	P,H,S	x	x	31	53	42	No
Notorynchus cepedianus (Péron, 1807)	Broadnose Sevengill Shark	1948	U*	P,H,S	-	-	24	53	38.5	No
Squaliformes										
Squalidae – dogfish sharks										
Squalus suckleyi (Girard, 1855)	Pacific Spiny Dogfish	1945	C	P,S	x	-	26	60	43	No
Squatiniformes										
Squatinidae – angel sharks										
Squatina californica Ayres, 1859	Pacific Angel Shark	1945	C	H,S	x	-	24	60	42	No
Heterodontiformes										
Heterodontidae – bullhead sharks										
Heterodontus francisci (Girard, 1855)	Horn Shark	1945	C	H,S	x	x	24	36	30	Ce

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Lamniformes										
Alopiidae – thresher sharks										
Alopias vulpinus (Bonnaterre, 1788)	Thresher Shark	1945	C	P,H	-	-	27	50	38.5	No
Cetorhinidae – basking sharks										
Cetorhinus maximus (Gunnerus, 1765)	Basking Shark	1962	R	P	-	-	23	60	41.5	No
Lamnidae – mackerel sharks										
Carcharodon carcharias (Linnaeus, 1758)	White Shark	1945	U	P	-	-	-30	60	15	So
Isurus oxyrinchus Rafinesque, 1810	Shortfin Mako	1950	U*	P	x	-	-30	46	8	So
Carcharhiniformes										
Scyliorhinidae – cat sharks										
Cephaloscyllium ventriosum (Garman, 1880)	Swell Shark	1950	R*	H,S	-	-	-30	36	3	So
Triakidae – hound sharks										
Galeorhinus galeus (Linnaeus, 1758)	Tope	1945	C	P,H,S	-	x	26	55	40.5	No
Mustelus californicus Gill, 1864	Gray Smoothhound	1945	U	H,S	x	-	23	40	31.5	Ce
Mustelus henlei (Gill, 1863)	Brown Smoothhound	1945	U	S	x	-	23	40	31.5	Ce
Mustelus lunulatus Jordan & Gilbert, 1882	Sicklefin Smoothhound	1945	R	S	-	-	8	33	20.5	So
Triakis semifasciata Girard, 1885	Leopard Shark	1945	C	H,S	x	-	23	40	31.5	Ce
Carcharhinidae – requiem sharks										
Carcharhinus obscurus (Lesueur, 1818)	Dusky Shark	1963	R	P	-	-	18	33	25.5	Ce
Prionace glauca (Linnaeus, 1758)	Blue Shark	1945	C	P	x	-	-30	60	15	So
Rhizoprionodon longurio (Jordan & Gilbert, 1882)	Pacific Sharpnose Shark	1948	R	P	-	-	-10	33	11.5	So
Sphyrnidae – hammerhead sharks										
Sphyrna lewini (Griffith & Smith, 1834)	Scalloped Hammerhead	1981	R	P	-	-	8	34	21	So
Sphyrna zygaena (Linnaeus, 1758)	Smooth Hammerhead	1958	U	P	-	-	30	37	33.5	Ce
Torpediniformes										
Torpedinidae – torpedo electric rays										
Torpedo californica Ayres, 1855	Pacific Electric Ray	1949	R*	S	x	-	28	53	40.5	No

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Rajiformes										
Rhinobatidae – guitarfishes										
Platyrhinoidis triseriata (Jordan & Gilbert, 1880)	Thornback	1917	C	S	x	-	28	37	32.5	Ce
Rhinobatos productus Ayres, 1854	Shovelnose Guitarfish	1938	C	S	x	x	23	37	30	Ce
Zapteryx exasperata (Jordan & Gilbert, 1880)	Banded Guitarfish	1945	R*	S	-	x	9	33	21	So
Rajidae – skates										
Beringraja binoculata (Girard 1855)	Big Skate	1945	R	S	-	-	28	60	44	No
Raja inornata Jordan & Gilbert, 1881	California Skate	1945	C	S	x	-	8	48	28	Ce
Raja rhina Jordan & Gilbert, 1880	Longnose Skate	1946	U	S	x	-	28	60	44	No
Raja stellulata Jordan & Gilbert, 1880	Starry Skate	1950	U	S	x	-	32	60	46	No
Myliobatiformes										
Dasyatidae – whiptail stingrays										
Dasyatis dipterura (Jordan & Gilbert, 1880)	Diamond Stingray	1949	U	S	-	-	-5	50	22.5	So
Pteroplatytrygon violacea (Bonaparte, 1832)	Pelagic Stingray	1980	R	P	-	-	0	50	25	So
Urolophidae – round stingrays										
Urobatis halleri (Cooper, 1863)	Round Stingray	1945	C	H,S	-	x	8	40	24	So
Gymnuridae – butterfly rays										
Gymnura marmorata (Cooper, 1864)	California Butterfly Ray	1945	C	S	x	-	-10	34	12	So
Myliobatidae – eagle rays										
Myliobatis californica Gill, 1865	Bat Ray	1945	C	P,H,S	x	x	23	44	33.5	Ce
Anguilliformes										
Muraenidae – morays										
Gymnothorax mordax (Ayres, 1859)	California Moray	1945	C	H	-	-	25	34	29.5	Ce
Ophichthidae – snake eels										
Ophichthus triserialis (Kaup, 1856)	Pacific Snake Eel	1948	U	S	-	-	-10	40	15	So
Ophichthus zophochir Jordan & Gilbert, 1882	Yellow Snake Eel	1982	R*	S	-	-	-10	40	15	So
Congridae – conger eels										
Gnathophis cinctus (Garman, 1899)	Hardtail Conger	1952	R	S	-	-	23	34	28.5	Ce

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Nettastomatidae – duckbill eels										
Facciolella equatorialis (Gilbert, 1890)	Dogface Witch Eel	1948	R	P	-	-	7	34	21	So
Clupeiformes										
Engraulidae – anchovies										
Anchoa compressa (Girard, 1858)	Deepbody Anchovy	1963	R	P,S	-	-	31	35	33	Ce
Anchoa delicatissima (Girard, 1854)	Slough Anchovy	1950	U	P,S	-	-	24	33	28.5	Ce
Cetengraulis mysticetus (Günther, 1867)	Anchoveta	1945	R	P,S	-	-	-8	34	13	So
Engraulis mordax Girard, 1854	Northern Anchovy	1945	C	P,H,S	-	-	23	53	38	No
Clupeidae – herrings										
Clupea pallasii Valenciennes, 1847	Pacific Herring	1945	R	P	-	-	30	77	53.5	No
Etrumeus teres (DeKay, 1842)	Round Herring	1985	U	P	-	-	-33	37	2	So
Harengula thrissina (Jordan & Gilbert, 1882)	Flatiron Herring	1951	R	P	-	-	-10	32	11	So
Sardinops sagax (Jenyns, 1842)	Pacific Sardine	1945	C	P,H,S	-	-	23	55	39	No
Argentiniformes										
Argentinidae – argentines										
Argentina sialis Gilbert, 1890	Pacific Argentine	1977	R	P,S	-	-	23	44	33.5	Ce
Salmoniformes										
Salmonidae – trouts and salmons										
Oncorhynchus gorbuscha (Walbaum, 1792)	Pink Salmon	1945	R	P	-	-	32	60	46	No
Stomiiformes										
Sternoptychidae – Marine Hatchetfishes										
Argyropelecus sladeni Regan, 1908	Lowcrest Hatchetfish	1952	U	P	-	-	-33	58	12	So
Aulopiformes										
Synodontidae – lizardfishes										
Synodus lucioceps (Ayres, 1855)	California Lizardfish	1954	C	S	-	-	28	38	33	Ce
Alepisauridae – lancetfishes										
Alepisaurus ferox Lowe, 1833	Longnose Lancetfish	1965	U	P	-	-	-33	58	12	So

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Paralepididae – barracudinas										
Magnisudis atlantica (Kroyer, 1868)	Duckbill Barracudina	1955	U	P	-	-	-33	58	12	So
Lampridiformes										
Trachipteridae – ribbonfishes										
Trachipterus altivelis Kner, 1859	King-of-the-salmon	1970	U	P	-	-	-33	58	12	So
Ophidiiformes										
Ophidiidae – cusk-eels										
Chilara taylori (Girard, 1858)	Spotted Cusk-eel	1946	C	S	x	-	27	45	36	No
Ophidion scrippsae (Hubbs, 1916)	Basketweave Cusk-eel	1945	C	S	x	-	28	34	31	Ce
Bythitidae – viviparous brotulas										
Brosmophycis marginata (Ayres, 1854)	Red Brotula	1964	U	S	x	-	31	57	44	No
Gadiformes										
Merlucciidae – merlucciid hakes										
Merluccius productus (Ayres, 1855)	Pacific Hake	1939	C	P,S	x	-	24	60	42	No
Batrachoidiformes										
Batrachoididae – toadfishes										
Porichthys myriaster Hubbs & Schultz, 1939	Specklefin Midshipman	1945	C	H,S	-	-	24	34	29	Ce
Porichthys notatus Girard, 1854	Plainfin Midshipman	1946	C	H,S	x	-	22	57	39.5	No
Atheriniformes										
Atherinopsidae – New World silversides										
Atherinops affinis (Ayres, 1860)	Topsmelt	1944	C	P,H	-	x	23	50	36.5	No
Atherinopsis californiensis Girard, 1854	Jacksmelt	1945	C	P,H	-	x	28	44	36	No
Leuresthes tenuis (Ayres, 1860)	California Grunion	1945	C	P,H,S	-	-	24	37	30.5	Ce
Beloniformes										
Belonidae – needlefishes										
Strongylura exilis (Girard, 1854)	California Needlefish	1945	C	P	-	-	-10	37	13.5	So
Scomberesocidae – sauries										
Cololabis saira (Brevoort, 1856)	Pacific Saury	1945	C	P	-	-	20	60	40	No

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Exocoetidae – flyingfishes										
Cheilopogon heterurus (Rafinesque, 1810)	Blotchwing Flyingfish	1946	U	P	-	-	0	32	16	So
Cheilopogon pinnatibarbatus (Bennett, 1831)	Smallhead Flyingfish	1945	U	P	-	-	22	46	34	Ce
Cyprinodontiformes										
Fundulidae – topminnows										
Fundulus parvipinnis Girard, 1854	California Killifish	1951	R	S	-	-	24	35	29.5	Ce
Gasterosteiformes										
Aulorhynchidae – tubesnouts										
Aulorhynchus flavidus Gill, 1861	Tubesnout	1951	C	P,H,S	x	x	27	57	42	No
Syngnathiformes										
Syngnathidae – pipefishes										
Cosmocampus arctus (Jenkins & Evermann, 1889)	Snubnose Pipefish	1944	U	H,S	x	-	23	38	30.5	Ce
Syngnathus auliscus (Swain, 1882)	Barred Pipefish	1945	R	S	-	-	-8	34	13	So
Syngnathus californiensis Storer, 1845	Kelp Pipefish	1945	C	H,S	-	-	24	37	30.5	Ce
Syngnathus euchrous Fritzche, 1980	Chocolate Pipefish	1946	C	S	-	-	28	34	31	Ce
Syngnathus exilis (Osburn & Nichols, 1916)	Barcheek Pipefish	1945	C	S	-	-	24	38	31	Ce
Syngnathus leptorhynchus Girard, 1854	Bay Pipefish	1945	U	S	-	-	28	57	42.5	No
Macroramphosidae - snipefishes										
Macroramphosus gracilis (Lowe, 1839)	Slender Snipefish	1950	R	P,S	-	-	0	33	16.5	So
Scorpaeniformes										
Scorpaenidae – scorpionfishes										
Scorpaena guttata Girard, 1854	California Scorpionfish	1944	C	H,S	x	x	24	37	30.5	Ce
Sebastes alutus (Gilbert, 1890)	Pacific Ocean Perch	1947	U	H	x	-	32	60	46	No
Sebastes atrovirens (Jordan & Gilbert, 1880)	Kelp Rockfish	1945	C	H	x	x	27	37	32	Ce
Sebastes auriculatus Girard, 1854	Brown Rockfish	1945	C	H,S	x	x	26	57	41.5	No
Sebastes carnatus (Jordan & Gilbert, 1880)	Gopher Rockfish	1945	C	H	x	-	27	42	34.5	Ce
Sebastes caurinus Richardson, 1844	Copper Rockfish	1945	C	H	x	-	28	60	44	No
Sebastes chlorostictus (Jordan & Gilbert, 1880)	Greenspotted Rockfish	1945	C	S	x	-	28	47	37.5	No
Sebastes chrysomelas (Jordan & Gilbert, 1881)	Black-and-yellow Rockfish	1945	C	H	x	-	27	40	33.5	Ce

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Sebastes constellatus (Jordan & Gilbert, 1880)	Starry Rockfish	1945	C	H	x	-	24	40	32	Ce
Sebastes dallii (Eigenmann & Beeson, 1894)	Calico Rockfish	1946	C	H	x	-	27	37	32	Ce
Sebastes diploproa (Gilbert, 1890)	Splitnose Rockfish	1948	U*	S	x	-	28	61	44.5	No
Sebastes elongatus Ayres, 1859	Greenstriped Rockfish	1945	C	H,S	x	-	28	60	44	No
Sebastes ensifer Chen, 1971	Swordspine Rockfish	1949	U*	H,S	x	-	28	37	32.5	Ce
Sebastes entomelas (Jordan & Gilbert, 1880)	Widow Rockfish	1954	U	H	x	-	32	57	44.5	No
Sebastes eos (Eigenmann & Eigenmann, 1890)	Pink Rockfish	1945	U	H	x	-	28	37	32.5	Ce
Sebastes flavidus (Ayres, 1862)	Yellowtail Rockfish	1949	R	P,H	x	-	32	59	45.5	No
Sebastes goodei (Eigenmann & Eigenmann, 1890)	Chilipepper	1945	U	P,H	x	-	24	51	37.5	No
Sebastes hopkinsi (Cramer, 1895)	Squarespot Rockfish	1946	C	P,H	x	-	29	37	33	Ce
Sebastes lentiginosus Chen, 1971	Freckled Rockfish	1948	U	H	x	-	32	33	32.5	Ce
Sebastes levis (Eigenmann & Eigenmann, 1889)	Cowcod	1964	U	H	x	-	28	42	35	No
Sebastes melanostomus (Eigenmann & Eigenmann, 1890)	Blackgill Rockfish	1947	R	H	x	-	28	47	37.5	No
Sebastes miniatus (Jordan & Gilbert, 1880)	Vermilion Rockfish	1945	C	H	x	-	28	50	39	No
Sebastes mystinus (Jordan & Gilbert, 1881)	Blue Rockfish	1947	C	H	x	-	31	60	45.5	No
Sebastes ovalis (Ayres, 1862)	Speckled Rockfish	1946	U	H	x	-	31	42	36.5	No
Sebastes paucispinis Ayres, 1854	Bocaccio	1945	C	H	x	x	29	57	43	No
Sebastes rastrelliger (Jordan & Gilbert, 1880)	Grass Rockfish	1945	U	H	x	-	28	44	36	No
Sebastes rosaceus Girard, 1854	Rosy Rockfish	1948	C	H	x	-	27	48	37.5	No
Sebastes rosenblatti Chen, 1971	Greenblotched Rockfish	1948	C	H,S	x	-	28	37	32.5	Ce
Sebastes ruberrimus (Cramer, 1895)	Yelloweye Rockfish	1949	R	H	x	-	32	60	46	No
Sebastes rubrivinctus (Jordan & Gilbert, 1880)	Flag Rockfish	1945	C	H	x	-	32	60	46	No
Sebastes saxicola (Gilbert, 1890)	Stripetail Rockfish	1950	U*	S	x	-	27	57	42	No
Sebastes semicinctus (Gilbert, 1897)	Halfbanded Rockfish	1946	C	H,S	x	-	27	37	32	Ce
Sebastes serranoides (Eigenmann & Eigenmann, 1890)	Olive Rockfish	1947	C	H	x	x	28	41	34.5	Ce
Sebastes serriceps (Jordan & Gilbert, 1880)	Treefish	1945	C	H	x	x	28	37	32.5	Ce
Sebastes simulator Chen, 1971	Pinkrose Rockfish	1951	R	H,S	x	-	31	37	34	Ce
Sebastes umbrosus (Jordan & Gilbert, 1882)	Honeycomb Rockfish	1945	C	H	x	-	26	37	31.5	Ce
Sebastolobus alascanus Bean, 1890	Shortspine Thornyhead	1948	U	S	x	-	28	60	44	No
Triglidae – searobins										
Prionotus stephanophrys Lockington, 1881	Lumptail Searobin	1958	R	S	-	-	-10	46	18	No

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Epinephelidae – groupers										
Epinephelus analogus Gill, 1863	Spotted Cabrilla	1956	R	H	-	-	-10	34	12	So
Mycteroperca jordani (Jenkins & Evermann, 1889)	Gulf Grouper	1945	U	H	-	-	23	32	27.5	So
Mycteroperca xenarcha Jordan, 1888	Broomtail Grouper	1945	U	H	-	x	-5	37	16	So
Serranidae – sea basses										
Paralabrax clathratus (Girard, 1854)	Kelp Bass	1945	C	H	x	x	24	46	35	No
Paralabrax maculatofasciatus (Steindachner, 1868)	Spotted Sand Bass	1970	R*	S	-	x	23	36	29.5	Ce
Paralabrax nebulifer (Girard, 1854)	Barred Sand Bass	1945	C	H,S	x	x	24	37	30.5	Ce
Pronotogrammus multifasciatus Gill, 1863	Threadfin Bass	1984	U	H,S	x	-	-10	34	12	So
Perciformes										
Polyprionidae – wreckfishes										
Stereolepis gigas Ayres, 1859	Giant Sea Bass	1945	U*	H	-	x	30	40	35	No
Priacanthidae – bigeyes										
Pristigenys serrula (Gilbert, 1891)	Popeye Catalufa	1966	R	H	-	-	-10	34	12	So
Apogonidae – cardinalfishes										
Apogon pacificus (Herre, 1935)	Pink Cardinalfish	1998	R	H	-	-	0	32	16	So
Malacanthidae – tilefishes										
Caulolatilus princeps (Jenyns, 1840)	Ocean Whitefish	1945	C	H	x	-	-10	50	20	So
Lutjanidae – snappers										
Lutjanus peru (Nichols & Murphy, 1922)	Pacific Red Snapper	1989	R	H	-	-	-10	33	12	So
Haemulidae – grunts										
Anisotremus davidsonii (Steindachner, 1876)	Sargo	1945	C	H,S	-	x	24	37	30.5	Ce
Haemulon californiensis (Steindachner, 1876)	Salema	1945	C	H,S	-	x	-10	36	13	So
Sciaenidae – drums and croakers										
Atractoscion nobilis (Ayres, 1860)	White Seabass	1945	C	H,S	-	x	24	58	41	No
Cheilotrema saturnum (Girard, 1858)	Black Croaker	1945	C	H,S	-	x	24	34	29	Ce
Genyonemus lineatus (Ayres, 1855)	White Croaker	1945	U*	S	-	-	24	50	37	No
Menticirrhus undulatus (Girard, 1854)	California Corbina	1945	C	S	-	-	23	34	28.5	Ce
Roncador stearnsii (Steindachner, 1876)	Spotfin Croaker	1945	C	S	-	-	23	34	28.5	Ce

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Seriphus politus Ayres, 1860	Queenfish	1945	C	H,S	-	x	25	40	32.5	Ce
Umbrina roncador Jordan & Gilbert, 1882	Yellowfin Croaker	1945	C	S	-	-	23	34	28.5	Ce
Chaetodontidae – butterflyfishes										
Prognathodes falcifer (Hubbs & Rechnitzer, 1958)	Scythe Butterflyfish	1970	R	H	-	-	0	33	16.5	So
Kyphosidae – sea chubs										
Girella nigricans (Ayres, 1860)	Opaleye	1944	C	H	-	x	22	37	29.5	Ce
Hermosilla azurea Jenkins & Evermann, 1889	Zebraperch	1939	C	H	-	x	23	36	29.5	Ce
Medialuna californiensis (Steindachner, 1876)	Halfmoon	1944	C	H	-	x	23	41	32	Ce
Sphyraenidae – barracudas										
Sphyraena argentea Girard, 1854	Pacific Barracuda	1913	C	P,H	-	x	22	57	39.5	No
Sphyraena ensis Jordan & Gilbert, 1882	Mexican Barracuda	1998	R	P,H	-	-	0	33	16.5	So
Carangiformes										
Echeneidae – remoras										
Remora remora (Linnaeus, 1758)	Remora	1947	U	P	-	-	-30	37	3.5	So
Coryphaenidae – dolphinfishes										
Coryphaena hippurus Linnaeus, 1758	Dolphinfish	1952	R	P	-	-	-30	47	8.5	So
Carangidae – jacks										
Decapterus muroadsi (Temminck & Schlegel, 1844)	Amberstripe Scad	1960	R	P	-	-	0	36	18	So
Seriola lalandi Valenciennes, 1833	Yellowtail Jack	1946	U*	P,H	-	-	3	47	25	So
Trachurus symmetricus (Ayres, 1855)	Jack Mackerel	1945	C	P,H,S	x	-	24	57	40.5	No
Labriformes										
Labridae – wrasses										
Halichoeres semicinctus (Ayres, 1859)	Rock Wrasse	1905	C	H	-	x	23	34	28.5	Ce
Oxyjulis californica (Günther, 1861)	Señorita	1944	C	H,S	x	x	28	38	33	Ce
Semicossyphus pulcher (Ayres, 1854)	California Sheephead	1945	C	H	x	x	22	37	29.5	Ce
"Chromides"										
Embiotocidae – surfperches										
Amphistichus argenteus Agassiz, 1854	Barred Surfperch	1945	C	S	-	x	28	38	33	Ce
Amphistichus koelzi (Hubbs, 1933)	Calico Surfperch	1927	R	S	-	-	26	48	37	No

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Brachyistius frenatus Gill, 1862	Kelp Perch	1945	C	H,S	x	x	27	50	38.5	No
Cymatogaster aggregata Gibbons, 1854	Shiner Perch	1946	C	H,S	-	x	30	56	43	No
Embiotoca jacksoni Agassiz, 1853	Black Perch	1944	C	H,S	x	x	26	39	32.5	Ce
Embiotoca lateralis Agassiz, 1854	Striped Seaperch	1950	U	H,S	-	-	31	56	43.5	No
Hyperprosopon argenteum Gibbons, 1854	Walleye Surfperch	1945	C	H,S	-	x	28	50	39	No
Hypsurus caryi (Agassiz, 1853)	Rainbow Seaperch	1945	C	H,S	-	x	31	40	35.5	No
Micrometrus minimus (Gibbons, 1854)	Dwarf Perch	1944	C	H,S	-	x	28	38	33	Ce
Phanerodon atripes (Jordan & Gilbert, 1880)	Sharpnose Seaperch	1950	U	H,S	x	-	28	38	33	Ce
Phanerodon furcatus Girard, 1854	White Seaperch	1945	U	H,S	x	x	31	50	40.5	No
Rhacochilus toxotes Agassiz, 1854	Rubberlip Seaperch	1945	C	H	x	x	27	39	33	Ce
Rhacochilus vacca (Girard, 1855)	Pile Perch	1944	C	H	x	x	29	56	42.5	No
Zalembius roseus (Jordan & Gilbert, 1880)	Pink Seaperch	1950	U*	S	x	-	27	38	32.5	Ce
Pomacentridae – damselfishes										
Chromis punctipinnis (Cooper, 1863)	Blacksmith	1945	C	H	x	x	27	36	31.5	Ce
Hypsypops rubicundus (Girard, 1854)	Garibaldi	1945	C	H	-	x	24	36	30	Ce
Cottiformes										
Anoplopomatidae – sablefishes										
Anoplopoma fimbria (Pallas, 1814)	Sablefish	1947	U	S	x	-	28	60	44	No
Hexagrammidae – greenlings										
Hexagrammos decagrammus (Pallas, 1810)	Kelp Greenling	1956	R	H	x	-	32	55	43.5	No
Ophiodon elongatus Girard, 1854	Lingcod	1945	U	H,S	x	-	29	57	43	No
Oxylebius pictus Gill, 1862	Painted Greenling	1945	C	H	x	x	29	50	39.5	No
Zaniolepis frenata Eigenmann & Eigenmann, 1889	Shortspine Combfish	1937	C	S	x	-	27	43	35	No
Zaniolepis latipinnis Girard, 1858	Longspine Combfish	1951	C	S	-	-	27	43	35	No
Cottidae – sculpins										
Artedius corallinus (Hubbs, 1926)	Coralline Sculpin	1945	U	H	-	-	30	48	39	No
Artedius lateralis (Girard, 1854)	Smoothhead Sculpin	1951	U	H	-	-	30	55	42.5	No
Artedius notospilotus Girard, 1856	Bonyhead Sculpin	1944	U	H	x	-	30	48	39	No
Chitonotus pugetensis (Steindachner, 1876)	Roughback Sculpin	1947	U*	S	x	-	25	54	39.5	No
Clinocottus analis (Girard, 1858)	Woolly Sculpin	1945	C	H	-	-	27	39	33	Ce
Icelinus cavifrons Gilbert, 1890	Pit-head Sculpin	1953	U*	S	x	-	24	36	30	Ce

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Icelinus filamentosus Gilbert, 1890	Threadfin Sculpin	1969	R	S	x	-	32	54	43	No
Icelinus limbaughi Rosenblatt & Smith, 2004	Canyon Sculpin	1954	U	H,S	x	-	32	34	33	Ce
Icelinus quadriseriatus (Lockington, 1880)	Yellowchin Sculpin	1950	R	S	-	-	22	38	30	Ce
Icelinus tenuis Gilbert, 1890	Spotfin Sculpin	1965	R	S	-	-	28	50	39	No
Leiocottus hirundo Girard, 1856	Lavender Sculpin	1945	R	H	-	-	31	34	32.5	Ce
Leptocottus armatus Girard, 1854	Pacific Staghorn Sculpin	1945	U	S	-	-	30	56	43	No
Oligocottus rubellio (Greeley, 1899)	Rosy Sculpin	1944	C	H	-	-	30	40	35	No
Oligocottus snyderi Greeley, 1898	Fluffy Sculpin	1944	U	H	-	-	30	57	38.5	No
Orthonopias triacis Starks & Mann, 1911	Snubnose Sculpin	1950	R	H	-	-	29	37	33	Ce
Ruscarius creaseri (Hubbs, 1926)	Roughcheek Sculpin	1945	C	H	-	-	27	36	30.5	Ce
Scorpaenichthys marmoratus (Ayres, 1854)	Cabezon	1945	C	H	x	x	26	56	41	No
Agonidae – poachers										
Agonopsis sterletus (Gilbert, 1898)	Spearnose Poacher	1954	U*	S	x	-	27	35	31	Ce
Odontopyxis trispinosa Lockington, 1880	Pygmy Poacher	1954	R	S	x	-	28	57	42.5	No
Xeneretmus latifrons (Gilbert, 1890)	Blacktip Poacher	1950	U	S	x	-	30	49	39.5	No
Xeneretmus triacanthus (Gilbert, 1890)	Bluespotted Poacher	1965	R	S	-	-	30	52	41	No
Liparidae – snailfishes										
Careproctus melanurus Gilbert, 1892	Blacktail Snailfish	1990	R	S	x	-	32	54	43	No
Liparis mucosus Ayres, 1855	Slimy Snailfish	1946	U	H	-	-	29	50	39.5	No
Bathymasteridae – ronquils										
Rathbunella alleni Gilbert, 1904	Stripefin Ronquil	1954	C	H	x	-	29	38	33.5	Ce
Rathbunella hypoplecta (Gilbert, 1890)	Bluebanded Ronquil	1960	U	H	x	-	31	50	40.5	No
Ronquilus jordani (Gilbert, 1889)	Northern Ronquil	1974	R	H	-	-	33	59	46	No
Zoarcidae – eelpouts										
Eucryphycus californicus (Starks & Mann, 1911)	Persimmon Eelpout	<1944	R	S	-	-	33	37	35	No
Lycodes pacificus Collett, 1879	Blackbelly Eelpout	1950	R	S	x	-	31	58	44.5	No
Lyconema barbatum Gilbert, 1896	Bearded Eelpout	1965	R	S	-	-	30	42	36	No
Stichaeidae – pricklebacks										
Esselenichthys carli (Follett & Anderson, 1990)	Threeline Prickleback	1950	U	H,S	x	-	30	36	33	Ce
Esselenichthys laurae (Follett & Anderson, 1990)	Twoline Prickleback	1954	R	H,S	-	-	32	38	35	No
Plectobranchus evides Gilbert, 1890	Bluebarred Prickleback	1950	U	S	x	-	32	55	43.5	No

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Pholidae – gunnels										
Apodichthys fucorum Jordan & Gilbert, 1880	Rockweed Gunnel	1945	U	H,S	-	-	30	53	41.5	No
Ulvicola sanctaerosae Gilbert & Starks, 1897	Kelp Gunnel	1945	U	H,S	-	-	31	36	33.5	Ce
Anarhichadidae – wolffishes										
Anarrhichthys ocellatus Ayres, 1855	Wolf-eel	1946	U	H	x	-	32	57	44.5	No
Blenniiformes										
Labrisomidae – labrisomid blennies										
Alloclinus holderi (Lauderbach, 1907)	Island Kelpfish	1950	U	H	-	x	27	34	30.5	Ce
Cryptotrema corallinum Gilbert, 1890	Deepwater Blenny	<1944	R	H	-	-	30	34	32	Ce
Paraclinus integripinnis (Smith, 1880)	Reef Finspot	1917	C	H	-	-	24	34	29	Ce
Clinidae – kelp blennies										
Gibbonsia elegans (Cooper, 1864)	Spotted Kelpfish	1945	C	H	-	x	24	35	29.5	Ce
Gibbonsia metzi Hubbs, 1927	Striped Kelpfish	1944	C	H	-	-	27	50	38.5	No
Gibbonsia montereyensis Hubbs, 1927	Crevice Kelpfish	1949	U	H	-	-	31	53	42	No
Heterostichus rostratus Girard, 1854	Giant Kelpfish	1944	C	H	-	x	22	53	37.5	No
Chaenopsidae – tube blennies										
Neoclinus blanchardi Girard, 1858	Sarcastic Fringehead	1945	C	H,S	x	-	28	37	32.5	Ce
Neoclinus stephensae Hubbs, 1953	Yellowfin Fringehead	1953	C	H,S	x	-	27	36	31.5	Ce
Neoclinus uninotatus Hubbs, 1953	Onespot Fringehead	1963	R	H,S	x	-	32	38	35	No
Blenniidae – combtooth blennies										
Hypsoblennius gilberti (Jordan, 1882)	Rockpool Blenny	1915	C	H	-	-	24	34	29	Ce
Hypsoblennius jenkinsi (Jordan & Evermann, 1896)	Mussel Blenny	1915	C	H	-	-	16	34	25	So
Gobiesociformes										
Gobiesocidae – clingfishes										
Gobiesox eugrammus Briggs, 1955	Lined Clingfish	1955	U	H	-	-	29	33	31	Ce
Gobiesox maeandricus (Girard, 1858)	Northern Clingfish	1976	R	H	-	-	29	55	42	No
Gobiesox rhessodon Smith, 1881	California Clingfish	1944	C	H	x	-	27	35	31	Ce
Rimicola eigenmanni (Gilbert, 1890)	Slender Clingfish	1932	C	H	-	-	26	33	29.5	Ce
Rimicola muscarum (Meek & Pierson, 1895)	Kelp Clingfish	1945	U	H	-	-	31	52	41.5	No

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Gobiiformes										
Gobiidae – gobies										
Acanthogobius flavimanus (Temminck & Schlegel, 1845)	Yellowfin goby	2003	R*	S	-	-	-	-	-	-
Ilypnus gilberti (Eigenmann & Eigenmann, 1889)	Cheekspot Goby	1967	R	S	-	-	23	38	30.5	Ce
Lepidogobius lepidus (Girard, 1858)	Bay Goby	1950	R	S	-	-	28	50	39	No
Lethops connectens Hubbs, 1926	Halfblind Goby	1944	U	H	-	-	31	35	33	Ce
Lythrypnus dalli (Gilbert, 1890)	Bluebanded Goby	1946	C	H	x	x	23	36	29.5	Ce
Lythrypnus zebra (Gilbert, 1890)	Zebra Goby	1950	U	H	x	-	18	36	27	So
Rhinogobiops nicholsii (Bean, 1882)	Blackeye Goby	1946	C	H,S	x	x	27	53	40	No
Typhlogobius californiensis Steindachner, 1879	Blind Goby	1944	U	H	-	-	25	35	30	Ce
Acanthuriformes										
Luvaridae – louvars										
Luvarus imperialis Rafinesque, 1810	Louvar	1956	R	P	-	-	-33	48	8.5	So
Scombriformes										
Trichiuridae – cutlassfishes										
Lepidopus fitchi Rosenblatt & Wilson, 1987	Pacific Scabbardfish	1948	U	P	x	-	23	40	31.5	Ce
Scombridae – mackerels										
Auxis thazard (Lacepède, 1800)	Frigate Mackerel	1972	R	P	-	-	-10	33	11.5	So
Sarda chiliensis (Cuvier, 1832)	Pacific Bonito	1945	U	P	-	-	-30	57	13.5	So
Scomber japonicus Houttuyn, 1782	Pacific Chub Mackerel	1917	C	P	x	-	-30	57	13.5	So
Scomberomorus sierra Jordan & Starks, 1895	Pacific Sierra	1962	R*	P	-	-	-5	33	19	So
Xiphiiformes										
Istiophoridae – billfishes										
Istiophorus platypterus (Shaw, 1792)	Sailfish	1960	R	P	-	-	-30	32	1	So
Stromateiformes										
Centrolophidae – medusafishes										
Icichthys lockingtoni Jordan & Gilbert, 1880	Medusafish	1955	U	P	-	-	27	57	42	No

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Stromateidae – butterfishes										
Peprilus simillimus (Ayres, 1860)	Pacific Pompano	1960	R	P,S	-	-	25	49	37	No
Pleuronectiformes										
Paralichthyidae – sand flounders										
Citharichthys sordidus (Girard, 1854)	Pacific Sanddab	1946	C	S	x	-	23	60	41.5	No
Citharichthys stigmaeus Jordan & Gilbert, 1882	Speckled Sanddab	1945	C	H,S	x	-	23	60	41.5	No
Citharichthys xanthostigma Gilbert, 1890	Longfin Sanddab	1945	C	S	x	-	10	36	23	So
Hippoglossina stomata Eigenmann & Eigenmann, 1890	Bigmouth Sole	1945	C	S	x	-	23	37	30	Ce
Paralichthys californicus (Ayres, 1859)	California Halibut	1945	C	H,S	x	-	25	50	37.5	No
Xystreurys liolepis Jordan & Gilbert, 1880	Fantail Sole	1945	C	S	x	-	23	36	29.5	Ce
Pleuronectidae – righteye flounders										
Eopsetta jordani (Lockington, 1879)	Petrale Sole	1945	C	S	x	-	28	60	44	No
Glyptocephalus zachirus Lockington, 1879	Rex Sole	1950	U	S	-	-	28	60	44	No
Lepidopsetta bilineata (Ayres, 1855)	Rock Sole	1948	R	H,S	x	-	32	60	46	No
Lyopsetta exilis (Jordan & Gilbert, 1880)	Slender Sole	1948	U	S	-	-	28	51	39.5	No
Microstomus pacificus (Lockington, 1879)	Dover Sole	1950	R	S	-	-	23	60	41.5	No
Parophrys vetulus (Girard, 1854)	English Sole	1946	C	S	x	-	23	60	41.5	No
Pleuronichthys coenosus Girard, 1854	C-O Sole	1962	R	H,S	x	-	31	57	44	No
Pleuronichthys decurrens Jordan & Gilbert, 1881	Curlfin Sole	1952	U	S	-	-	28	60	44	No
Pleuronichthys guttulatus Girard, 1856	Diamond Turbot	1945	U	S	x	-	25	40	32.5	Ce
Pleuronichthys ritteri Starks & Morris, 1907	Spotted Turbot	1946	U	S	x	-	25	35	30	Ce
Pleuronichthys verticalis Jordan & Gilbert, 1880	Hornyhead Turbot	1945	U*	S	x	-	25	37	31	Ce
Cynoglossidae – tonguefishes										
Symphurus atricaudus (Jordan & Gilbert, 1880)	California Tonguefish	1961	R*	S	x	-	22	41	31.5	Ce
Tetraodontiformes										
Balistidae – triggerfishes										
Balistes polylepis Steindachner, 1876	Finescale Triggerfish	1950	U	H,S	-	-	-30	41	5.5	So
Ostraciidae – boxfishes										
Lactoria diaphana (Bloch & Schneider, 1801)	Spiny Boxfish	1952	U	P	-	-	0	34	17	So

Table 1. Continued.

Scientific name	Common name	Date	Oc	Hab	Cn	Tr	SE	NE	mid	Dist
Tetraodontidae – puffers										
Sphoeroides lobatus (Steindachner, 1870)	Longnose Puffer	1998	R	S	-	-	-33	34	0	So
Diodontidae – porcupinefishes										
Diodon holocanthus Linnaeus, 1758	Balloonfish	1959	R	P,H,S	-	-	-30	32	1	So
Molidae – molas										
Mola mola (Linnaeus, 1758)	Ocean Sunfish	1945	U	P	-	-	0	55	27.5	So

Table 2. Numbers of species recorded in the La Jolla region (Table 1; excluding one exotic species, the Yellowfin Goby, *Acanthogobius flavimanus*) by distribution and frequency of occurrence categories for all species and those found in selected habitats.

	Northern	Central	Southern	Total
All species				
Common	44	58	11	113
Uncommon	38	25	20	83
Rare	29	13	26	68
Total	111	96	57	264
Hard-bottom species				
Common	33	40	5	78
Uncommon	21	13	6	40
Rare	10	4	8	22
Total	64	57	19	140
Soft-bottom species				
Common	25	27	4	56
Uncommon	21	16	4	41
Rare	20	9	9	38
Total	66	52	17	135
Pelagic species				
Common	12	3	3	18
Uncommon	3	4	13	20
Rare	6	2	17	25
Total	21	9	33	63
Canyon species				
Common	31	32	5	68
Uncommon	20	17	3	40
Rare	13	2	0	15
Total	64	51	8	123

Results

Two hundred sixty-five species of fishes from 95 families have been recorded within the study area based on verified records in the MVC (Table 1). By 1964, 20 years after Hubbs had arrived at SIO, 238 of these species (90%) had been recorded from the immediate vicinity of La Jolla, a reflection of the intensive collecting effort made by Hubbs and associates before that time (Fig. 3). Of the 265 species recorded, 113 are common, 83 are uncommon, and 68 species are rare based on records in the MVC (Table 2; excluding one "rare" exotic species). The faunal composition of the region is typical of southern California fish communities in that it is primarily a mixture of warm-temperate and cool-temperate fishes (Hobson 1994; Horn et al. 2006). Species with central ranges number 96, those with northern ranges total 111, and those with southern ranges total 57 (Table 2). Most "common" species have range midpoints in the central region (58 species) or northern region (44) with relatively few (11) with southern range midpoints. "Uncommon" species are also dominated by species with central (25), and northern (38) ranges. Few "rare" species have central distributions (13) and more have northern (29) or southern (26) distributions. A single exotic species (*Acanthogobius flavimanus*, Gobiidae) rarely has been recorded from La Jolla.

Hard-bottom Species

The rocky-reef and kelp-forest fishes of La Jolla are perhaps the best-known group due to their visibility and the fact that they have been studied repeatedly there and elsewhere in the state (e.g., Limbaugh 1955; North and Hubbs 1968; Quast 1968; Feder et al. 1974; Kobayashi 1979; Ebeling et al. 1980; Shane 1996; Paddock and Estes 2000; Pondella et al. 2000; Froeschke et al. 2006). In our survey, 140 species associated with hard substrates were recorded from the study area (Table 1). The majority of these have northern (64 species) or central (57) distributions, while relatively few (19) have southern distributions (Table 2).

We recorded 51 of these species (excluding schooling species) in the 252 transects at La Jolla Cove and 248 transects at Boomers (Table 3). Although we counted well over 90,000 fishes (52,520 fishes at La Jolla Cove and 41,330 at Boomers), this represents only 36% of the hard bottom species recorded from the vicinity. This difference is attributable to several factors. For example, small, cryptobenthic species are rarely observed by divers, some hard-bottom species are restricted to depths greater than those surveyed by divers, the surveys extended for only four years compared to several decades of collecting in the area, and rare species are unlikely to be recorded during such surveys. The top twelve species by abundance are listed in Table 4. At both sites, the numerically dominant species were the Blacksmith, *Chromis punctipinnis* (Pomacentridae), and the Señorita, *Oxyjulis californica* (Labridae) and ten of the top twelve species were identical (Table 4). The mean density of all species of fishes over the entire sampling period at La Jolla Cove (mean = 1.95/100 m^2, SE = 0.29) and at Boomers (mean = 1.51, SE = 0.21) did not differ significantly ($t = 1.21$, $P > 0.05$). Throughout the study period, the abundance of Blacksmith and Señorita varied greatly and drove many of the overall changes in density. These cycles were characterized by large recruitment pulses, followed by increases in adult densities.

Soft-bottom Species

The fishes recorded from La Jolla include 135 species known to occur on or over soft substrates (Table 1). Similar to the hard-bottom fishes, this group is dominated by species with northern (66 species) or central (52) distributions, with relatively few (17) with southern distributions (plus one exotic). Excluding the exotic, twelve of these species are listed as "resident bay" species by Allen et al. (2006). Several La Jolla records for these are from the "La Jolla Beach and Tennis Club," but these mostly date between 1950 and 1963, and these species have not (or rarely) been collected in the area since that time. For example, the Deepbody Anchovy, *Anchoa compressa,* is based on a single record (SIO 63-22 - large series) from 1963, the Slough anchovy, *Anchoa delicatissima,* is based on four records, one from 1950 (SIO 50-227, 1 specimen), two from 1951 (SIO 51- 37, 1 specimen; SIO 51-378, 10 specimens) and one from 2002 (SIO 02-26, 1 specimen), and the California Killifish, *Fundulus parvipinnis*, is based on a single specimen collected in 1951 (SIO 51-37). Historically there was a small embayment in the vicinity of the La Jolla Beach and Tennis Club that has since disappeared (Fig. 2D). Although common in other embayments in the San Diego region (Allen et al. 2002), this component of the ichthyofauna has been largely eliminated from the La Jolla area by this habitat alteration.

Pelagic Species

In addition to several coastal fish species that regularly swim in the water column (e.g., the silversides and some drums), the proximity of deep waters to the La Jolla coastline contributes to the local diversity of fishes as several oceanic species closely approach the

Table 3. Densities of fishes per 100 m^2 observed during belt transects in La Jolla Cove (A) and Boomers (B). Species are arranged alphabetically by genus and species name. Means, standard error (SE) and percent occurrence (O) represent six sampling periods for each year (except for Boomers 2003 with five).

A) La Jolla Cove

	2002			2003			2004			2005			2002-2005		
	Mean	SE	O	Mean	SE	O	Mean	SE	O	Mean	SE	O	Mean	SE	O
Alloclinus holderi	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Amphistichus argenteus	0	-	0	0	-	0	0	-	0	0.347	0.347	17	0.087	0.087	4
Anisotremus davidsonii	0.667	0.269	83	0.504	0.392	50	4.250	1.806	100	0.292	0.127	67	1.428	0.554	75
Atherinops affinis	0	-	0	0	-	0	0.639	0.545	33	0.022	0.022	17	0.165	0.139	12
Atherinopsis californiensis	3.750	3.427	33	0.708	0.708	17	0	-	0	0.139	0.139	17	1.149	0.876	17
Atractoscion nobilis	0.069	0.054	33	0	-	0	0	-	0	0	-	0	0.017	0.014	8
Aulorhynchus flavidus	1.083	2.573	17	0.028	0.028	17	0	-	0	0	-	0	0.278	0.263	8
Brachyistius frenatus	0.153	0.153	17	0.796	0.518	67	1.042	0.385	67	0.722	0.287	67	0.678	0.182	54
Cheilotrema saturnum	0.208	0.208	17	0	-	0	0.028	0.028	17	0.028	0.028	17	0.066	0.052	12
Chromis punctipinnis	76.361	14.075	100	47.370	11.480	100	96.861	32.763	100	108.86	30.677	100	82.362	12.289	100
Cymatogaster aggregata	0	-	0	0.083	0.083	17	0.333	0.333	17	0.097	0.062	33	0.128	0.085	17
Embiotoca jacksoni	1.986	0.312	100	1.384	0.300	100	1.778	0.283	100	2.038	0.348	100	1.794	0.155	100
Galeorhinus galeus	0.042	0.028	17	0	-	0	0.083	0.083	17	0.055	0.055	17	0.045	0.025	17
Gibbonsia elegans	0.014	0.014	17	0.014	0.014	17	0	-	0	0.014	0.014	17	0.010	0.006	12
Girella nigricans	7.389	2.254	100	8.292	2.895	100	12.764	3.521	100	5.419	1.187	100	8.466	1.340	100
Haemulon californiensis	0	-	0	0	-	0	3.333	3.333	17	0	-	0	0.833	0.833	4
Halichoeres semicinctus	7.722	2.097	100	3.606	0.547	100	5.653	1.494	100	6.611	1.088	100	5.898	0.735	100
Hermosilla azurea	0	-	0	0.292	0.275	33	0.736	0.736	17	0.167	0.108	33	0.299	0.193	21
Heterodontus francisci	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Heterostichus rostratus	0.125	0.085	33	0.116	0.041	67	0.750	0.618	83	0.122	0.077	67	0.278	0.157	62
Hexanchus griseus	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Hyperprosopon argenteum	1.347	1.314	33	0	-	0	0.972	0.624	33	0	-	0	0.580	0.361	17
Hypsurus caryi	0.264	0.113	83	0.222	0.159	50	0.125	0.096	33	0.247	0.076	100	0.215	0.268	67
Hypsypops rubicundus	13.583	2.263	100	10.903	2.153	100	13.361	1.755	100	16.500	1.953	100	13.587	1.037	100
Lythrypnus dalli	0	-	0	0	-	0	0.958	0.909	33	0	-	0	0.240	0.229	8
Medialuna californiensis	1.083	0.243	100	1.199	0.578	83	1.653	0.052	100	2.500	1.262	100	1.609	0.367	96
Micrometrus minimus	0.083	0.053	33	0.111	0.073	33	0.375	0.152	67	0.861	0.384	83	0.358	0.118	54
Mycteroperca xenarcha	0.014	0.014	17	0	-	0	0	-	0	0	-	0	0.003	0.003	4

Table 3. Continued.

A) La Jolla Cove

	2002			2003			2004			2005			2002-2005		
	Mean	SE	O	Mean	SE	O	Mean	SE	O	Mean	SE	O	Mean	SE	O
Myliobatis californica	0	-	0	1.037	1.037	17	0.028	0.028	17	0	-	0	0.266	0.259	8
Oxyjulis californica	29.597	9.147	100	42.005	23.735	100	97.056	20.271	100	52.678	7.767	100	55.334	9.429	100
Oxylebius pictus	0.028	0.017	33	0.014	0.014	17	0.153	0.097	33	0.050	0.023	50	0.061	0.026	33
Paralabrax clathratus	8.000	1.308	100	9.894	3.526	100	14.056	3.997	100	15.345	2.328	100	11.823	1.523	100
Paralabrax maculatofasciatus	0.014	0.014	17	0.083	0.083	17	0.028	0.028	17	0	-	0	0.031	0.022	8
Paralabrax nebulifer	0.528	0.178	83	2.056	0.443	100	1.625	0.911	67	2.433	1.308	100	1.660	0.415	87
Pluanerodon furcatus	0.236	0.220	33	0	-	0	0.250	0.250	17	0.125	0.093	50	0.153	0.083	25
Rhacochilus toxotes	0.069	0.040	50	0.074	0.055	33	0.153	0.097	33	0.189	0.128	50	0.121	0.042	42
Rhacochilus vacca	0.056	0.035	33	0.319	0.273	33	0.083	0.057	33	0.083	0.30	67	0.135	0.069	42
Rhinobatos productus	0.014	0.033	17	0	0	0	0	-	0	0	-	0	0.003	0.003	4
Rhinogobiops nicholsii	0	-	0	0.069	0.069	17	0.056	0.041	33	0	-	0	0.031	0.020	12
Scorpaena guttata	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Scorpaenichthys marmoratus	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Sebastes atrovirens	0.139	0.063	67	0.69	0.045	33	0.403	0.232	50	0.414	0.333	67	0.256	0.101	54
Sebastes auriculatus	0	-	0	0	-	0	0.014	0.014	17	0	-	0	0.003	0.003	4
Sebastes paucispinis	0	-	0	0.153	0.153	17	0	-	0	0	-	0	0.038	0.038	4
Sebastes rastrelliger	0	-	0	0	-	0	0.042	0.042	17	0	-	0	0.010	0.010	4
Sebastes serranoides	0.111	0.272	17	0	-	0	0	-	0	0.014	0.014	17	0.031	0.028	8
Sebastes serriceps	0.014	0.014	17	0	-	0	0	-	0	0	-	0	0.003	0.003	4
Semicossyphus pulcher	3.653	0.552	100	5.551	1.338	100	6.972	2.350	100	7.769	1.417	100	5.986	0.793	100
Seriphus politus	0	-	0	0	-	0	0	-	0	0.028	0.028	17	0.007	0.007	4
Sphyraena argentea	1.653	0.836	50	1.046	1.013	33	0	-	0	0.042	0.042	17	0.685	0.339	25
Stereolepis gigas	0	-	0	0.028	0.028	17	0.028	0.028	17	0.180	0.121	50	0.059	0.033	21
Urobatis halleri	0	-	0	0	-	0	0	-	0	0	-	0	0	0	0
Zapteryx exasperata	0.014	0.014	17	0	-	0	0.014	0.014	17	0	-	0	0.007	0.005	8

Table 3. Continued.

B) Boomers

	2002			2003			2004			2005			2002-2005		
	Mean	SE	O	Mean	SE	O	Mean	SE	O	Mean	SE	O	Mean	SE	O
Alloclinus holderi	0.014	0.014	17	0	-	0	0	-	0	0	-	0	0.004	0.004	4
Amphistichus argenteus	1.250	1.250	17	0	-	0	0	-	0	0	-	0	0.326	0.326	4
Anisotremus davidsonii	0.816	0.398	67	1.236	0.881	50	1.261	0.525	80	0.700	0.243	83	0.984	0.270	70
Atherinops affinis	0	-	0	0	-	0	0.050	0.050	20	0.011	0.011	17	0.014	0.011	9
Atherinopsis californiensis	0.139	0.139	17	1.389	1.389	17	0	-	0	0	-	0	0.398	0.362	9
Atractoscion nobilis	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Aulorhynchus flavidus	0.083	0.083	17	0	-	0	0.233	0.233	20	0	-	0	0.072	0.054	9
Brachyistius frenatus	0.014	0.014	17	0.268	0.237	33	8.789	7.425	80	5.525	4.589	100	3.426	2.006	56
Cheilotrema saturnum	0.014	0.014	17	0	-	0	0.017	0.017	20	0.014	0.014	17	0.011	0.006	13
Chromis punctipinnis	46.806	10.016	100	34.569	11.096	100	55.994	30.932	100	72.880	32.705	100	52.413	11.123	100
Cymatogaster aggregata	0	-	0	0	-	0	0.022	0.022	20	0	-	0	0.005	0.005	4
Embiotoca jacksoni	1.797	0.415	100	2.856	0.678	100	3.928	0.885	100	3.703	1.375	100	3.034	0.461	100
Galeorhinus galeus	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Gibbonsia elegans	0	-	0	0.018	0.018	17	0.067	0.149	20	0	-	0	0.019	0.015	9
Girella nigricans	6.359	2.796	100	3.287	1.248	100	7.106	1.826	100	3.547	2.363	100	4.986	1.070	100
Haemulon californiensis	0.042	0.028	33	0	-	0	0	-	0	0	-	0	0.011	0.008	9
Halichoeres semicinctus	4.155	0.699	100	3.694	1.078	100	4.684	1.289	100	11.466	4.080	100	6.057	1.275	100
Hermosilla azurea	0.472	0.472	17	0.250	0.218	33	0.033	0.020	40	0.083	0.057	33	0.217	0.133	30
Heterodontus francisci	0	-	0	0.014	0.014	17	0	-	0	0.014	0.014	17	0.007	0.005	9
Heterostichus rostratus	0.093	0.024	100	0.056	0.035	33	0.139	0.093	60	0.080	0.022	83	0.090	0.023	70
Hexanchus griseus	0	-	0	0	-	0	0.017	0.017	20	0	-	0	0.004	0.004	4
Hyperprosopon argenteum	0.361	0.361	17	0	-	0	0	-	0	0	-	0	0.094	0.094	4
Hypsurus caryi	0.236	0.153	33	0.315	0.193	50	0.128	0.054	60	0.408	0.237	67	0.278	0.087	52
Hypsypops rubicundus	14.835	2.683	100	16.685	8.118	100	27.117	6.050	100	18.172	5.526	100	18.858	2.919	100
Lythrypnus dalli	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Medialuna californiensis	2.266	1.248	100	1.042	0.476	100	1.456	0.679	80	1.903	0.835	83	1.676	0.419	91
Micrometrus minimus	0.177	0.046	83	0.139	0.109	33	0.978	0.441	80	0.347	0.159	67	0.385	0.121	65
Mycteroperca xenarcha	0.014	0.014	17	0.028	0.028	17	0	-	0	0	-	0	0.011	0.008	9
Myliobatis californica	0	-	0	0	-	0	0	-	0	0.011	0.011	17	0.003	0.003	4

Table 3. Continued.

B) Boomers

	2002			2003			2004			2005			2002-2005		
	Mean	SE	O	Mean	SE	O	Mean	SE	O	Mean	SE	O	Mean	SE	O
Oxyjulis californica	51.956	23.659	100	21.717	6.494	83	70.011	26.699	100	62.411	14.528	100	50.720	9.574	96
Oxylebius pictus	0.012	0.012	17	0.051	0.037	33	0.033	0.020	40	0	-	0	0.024	0.011	22
Paralabrax clathratus	7.367	2.127	100	5.861	1.725	100	8.055	2.165	100	11.558	3.924	100	8.215	1.323	100
Paralabrax maculatofasciatus	0	-	0	0.028	0.028	17	0	-	0	0.042	0.042	17	0.018	0.013	9
Paralabrax nebulifer	0.381	0.226	100	0.180	0.062	67	0.255	0.108	60	0.133	0.041	83	0.237	0.065	78
Phanerodon furcatus	0.292	0.275	33	0	-	0	0.089	0.089	20	0.292	0.275	33	0.171	0.100	22
Rhacochilus toxotes	0.228	0.064	100	0.055	0.055	17	0.339	0.318	40	0.139	0.028	83	0.184	0.069	61
Rhacochilus vacca	0.294	0.083	83	0.232	0.124	50	0.017	0.017	20	0.133	0.051	67	0.175	0.044	56
Rhinobatos productus	0	-	0	0.014	0.014	17	0.022	0.022	20	0	-	0	0.008	0.006	9
Rhinogobiops nicholsii	0.049	0.036	33	0.037	0.037	17	0	-	0	0	-	0	0.023	0.013	13
Scorpaena guttata	0	-	0	0	-	0	0	-	0	0.014	0.014	17	0.004	0.004	4
Scorpaenichthys marmoratus	0.012	0.012	17	0	-	0	0	-	0	0	-	0	0.004	0.004	4
Sebastes atrovirens	0.156	0.061	83	0.037	0.037	17	0.100	0.100	20	0.055	0.028	17	0.087	0.029	35
Sebastes auriculatus	0	-	0	0	-	0	0	-	0	0.014	0.014	17	0.004	0.004	4
Sebastes paucispinis	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Sebastes rastrelliger	0	-	0	0	-	0	0.017	0.017	20	0	-	0	0.004	0.004	4
Sebastes serranoides	0.778	0.626	33	0	-	0	0.050	0.050	20	0.014	0.014	17	0.217	0.168	17
Sebastes serriceps	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Semicossyphus pulcher	2.678	0.384	100	4.292	0.671	100	4.900	1.269	100	5.153	1.808	100	4.238	0.580	100
Seriphus politus	0	-	0	0	-	0	0	-	0	0	-	0	0	-	0
Sphyraena argentea	0	-	0	1.250	1.250	17	0.150	0.150	20	0.028	0.028	17	0.366	0.326	13
Stereolepis gigas	0.014	0.014	17	0.028	0.028	17	0	-	0	0	-	0	0.011	0.008	9
Urobatis halleri	0.028	0.017	33	0	-	0	0.200	0.200	20	0	-	0	0.051	0.043	13
Zapteryx exasperata	0.028	0.017	33	0.042	0.042	17	0.033	0.033	20	0	-	0	0.025	0.013	17

Table 4. Rank order list of the top twelve species of fishes at two sites in La Jolla between 2002 and 2005.

	La Jolla Cove	Boomers
Chromis punctipinnis (Blacksmith)	1	1
Oxyjulis californica (Señorita)	2	2
Hypsypops rubicundus (Garibaldi)	3	3
Paralabrax clathratus (Kelp Bass)	4	4
Girella nigricans (Opaleye)	5	6
Halichoeres semicinctus (Rock Wrasse)	6	5
Semicossyphus pulcher (California Sheephead)	7	7
Embiotoca jacksoni (Black Perch)	8	9
Paralabrax nebulifer (Barred Sand Bass)	9	-
Medialuna californiensis (Halfmoon)	10	10
Anisotremus davidsonii (Sargo)	11	11
Haemulon californiensis (Salema)	12	-
Brachyistius frenatus (Kelp Perch)	-	8
Amphistichus argenteus (Barred Surfperch)	-	12

shoreline in this area. This includes several large, mobile species of chondrichthyan fishes (Klimley et al. 2002), flyingfishes (Exocoetidae), tunas (Scombridae), the Louvar (*Luvarus imperialis*), and the Ocean Sunfish (*Mola mola*), as well as small mesopelagic species such as the Lowcrest Hatchetfish (*Argyropelecus sladeni*, Sternoptychidae) that become stranded on shore during storms. Interestingly, of the 63 species classified as pelagic, the "common" species are dominated by species with northern distributions (12 of 18 species), while the "uncommon" and "rare" species are dominated by species with southern distributions (30 of 45 species; Table 2).

Canyon Species

Among the most striking features of the La Jolla coastal zone is the proximity of the La Jolla and Scripps submarine canyons to the coastline (Brueggeman 2008). The heads of these canyons come within a few hundred meters of the shore, and the canyons descend to depths of over 500 meters within 7 km of the coastline. These canyons include steep rock walls, as well as sand and mud substrates that support a variety of fishes. Species recorded there number 123, with 68 common, 40 uncommon, and 15 rare species (Table 2). The canyon ichthyofauna is dominated by species with northern (64 species) or central (51) distributions, with relatively few (8) species with southern distributions (Table 2).

Notable among the canyon species are a surprisingly large number of rockfishes: 35 species of the genus *Sebastes* have been collected from the La Jolla canyons (Table 1). In addition, a few relatively rare or poorly known species have been taken from this habitat including the Canyon Sculpin, *Icelinus limbaughi* (Rosenblatt and Smith 2004) and the Deepwater Blenny, *Cryptotrema corallinum*. Some of these species, although rarely collected within the study area, may be more common in similar, high-relief habitats in other portions of southern California (Love and Schroeder 2007).

Discussion

The present study compiles records of 265 species collected within the immediate vicinity of the marine protected areas of La Jolla. Thus, these MPAs have the potential to

provide some measure of protection for half of the 519 marine fish species recorded from state waters (Horn et al. 2006). This inventory is based exclusively on fish specimens collected within the designated study area and archived in the MVC. Other fish species are known to occur in the region and likely occur or have occurred sporadically within the study area. These include a number of species known to be common in the San Diego area (Allen et al. 2002) such as the bonefish *Albula* sp. (Albulidae), the Striped Mullet, *Mugil cephalus* (Mugilidae), the Shortfin Corvina, *Cynoscion parvipinnis* (Sciaenidae), and several species of gobies (e.g., *Clevelandia ios*, *Gillichthys mirabilis, and Quietula y-cauda*). In addition, a number of southern species of fishes have periodically been collected in the San Diego area, often in association with El Niño events (e.g., Lea and Rosenblatt 2000). These include species such as the Cortez Angelfish, *Pomacanthus zonipectus* (Pomacanthidae), and the Three Banded Butterflyfish, *Chaetodon humeralis* (Chaetodontidae), which have been observed (but not collected) within the La Jolla study area (Lea et al. 1989; Pondella et al. 1998). As predicted more than a half century ago (Hubbs 1948), these records suggest that the number of southern species in the La Jolla area will likely increase as a result of climate change.

Natural history collections, especially those with a regional focus, are critical resources for documenting the biodiversity of particular areas. Sampling regimes of most natural history collections are not, however, designed with conservation biology in mind. Instead they traditionally have focused on the discovery and description of new species, creating biotic inventories for particular regions, and documenting species distributions. Few natural history collections are capable of documenting changes in the abundance of particular organisms because they typically lack repeated, quantitative samples from the same sites. They may, however, provide information on the occurrence and relative abundance of cryptic fishes that are often overlooked by diver surveys and other quantitative sampling methods. Also, because of the long time-scale represented in many natural history collections, they provide a more complete inventory of species occurring in an area than is typically available from ecological surveys alone.

In some cases, natural history collections provide insight into the importance of particular habitats to the overall diversity within a region. For example, this survey highlights the importance of the La Jolla submarine canyon as habitat for a number of rockfish species and other rare and poorly known deep-water fishes. In addition, natural history collections can document long-term changes in species composition. The historical collections in the MVC document the demise of one ecological component in La Jolla, bay species, via habitat destruction, and the appearance of an exotic species in the area. In contrast, quantitative ecological surveys such as visual surveys conducted by divers, are key to documenting the abundance and short-term changes in abundance of readily visible reef species and thus they are important in evaluating the performance of MPAs (Agardy 1997). These surveys supplement data from natural history collections on the temporal trends of species abundances, including those of importance to recreational and commercial fisheries.

The role of natural history collections in conservation biology would be facilitated by periodic resampling of key habitats and archiving of collected specimens on a regular basis. The extent to which this may be possible is dependent upon staffing of collections, available resources for collection and storage of specimens, and area restrictions on collecting activities. Resampling using historically successful methods may be problematic in many instances as collecting methods may be difficult to repeat. For example, many of the collections in the La Jolla and Scripps Canyons were made by Hubbs prior to

extensive coastal development in the area. He was able to use collecting methods that are now impractical, including dispersal of large amounts of rotenone or discharge of explosives at depth. These are unthinkable in the current environment of dense human populations and activities in the area, and regulations protecting the region's biota. Instead, newer technologies such as submersibles and ROVs may be applied (Starr et al. 2008; Lindholm et al. 2012; Stierhoff et al. 2013), but these often provide low resolution of species identities and rarely reveal small or cryptic species. While the MPAs within the La Jolla region and those in other areas appropriately limit collecting within their boundaries, managers should be encouraged to permit reasonable levels of collection of specimens as long as the specimens are archived in a suitable natural history collection where they will be available to future generations of researchers.

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Clarifying the Northern Extent of the Diamond Stingray (*Dasyatis dipterura*) in Southern California

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Accurate records of biogeographic distributions (latitude and elevation) are becoming increasingly important as species shift their distribution in response to global climate change (Walther et al. 2002). The Southern California Bight is a transition zone between the Oregonian and San Diegan biogeographic zones (Horn et al. 2006). Therefore, range extensions are commonly documented in the area (Pondella 1997; Lea and Rosenblatt 2000; Miller and Curtis 2008; Moore et al. 2011; among others). On 27 October 2011, a single Diamond Stingray (*Dasyatis dipterura*) was taken in Marina del Rey harbor (33° 58.973′N 118° 27.245′W) in Marina del Rey, California during an environmental survey using a 7.6-m otter trawl at a depth of 4.3 m. The individual weighed 1.65 kg and measured 247 mm disc width (Figure 1). Key characters used in the identification to differentiate it from other common species, such as Round Stingray (*Urobatis halleri*) and Bat Ray (*Myliobatis californica*), include the disc shape and the presence of a keel on the tail. The tail keel is unique to Diamond Stingray in comparison to both Round Stingray and Bat Ray. Being alive and in apparently good health, the animal was photographed and released.

Diamond Stingray nomenclature has a multifaceted history. Originally described in a May 1880 publication by Jordan and Gilbert (1880) and again by Jordan and Gilbert (1882) as *Dasybatis dipterurus*, the current nomenclatural combination first appeared in Jordan and Evermann (1896). Garman (1880) described *Tygon brevis* in his October 1880 review of collections at the Harvard University Museum of Comparative Zoology. Garman (1913) synonymized all prior names, including *T. brevis*, under *Dasybatus brevis,* but lacked any reference to Jordan and Gilbert (1880). Instead, Garman (1913) included Jordan and Gilbert (1881), which introduced the name *Dasybatus dipterurus*. Nishida and Nakaya (1990) followed Garman (1913) and treated *Dasyatis dipterurus* (Jordan & Gilbert, 1880) with *Dasybatus brevis*. Eschmeyer (1998) noted *dipterurus* predated *brevis* (May and October 1880, respectively) and therefore synonymized *brevis* under *dipterurus* and recognized *dipterura* as the correct species name. Accordingly, Nelson et al. (2004) removed reference to *brevis* from North American waters in recognition of Eschmeyer's clarification of the species' nomenclature. We utilize the presently accepted *Dasyatis dipterura* (Page et al. 2013).

The Diamond Stingray northern range limit is no less enigmatic than its nomenclature. Current literature (Love et al. 2005) lists the northern range endpoint as central California (Grove and Lavenberg 1997 as *Dasyatis brevis*), although the true northern extent is unsubstantiated by a voucher specimen collected north of 33.7°N latitude, or Long Beach, California [LACM 48829.001; Fishnet2 (www.fishnet2.net); SIO (http://collections.ucsd.edu); MCZbase (http://mczbase.mcz.harvard.edu)]. Prior work recorded a range to southern California and "possibly British Columbia" (Hart 1973). The Hart reference was founded on records of a *Dasyatis* sp. being caught in Kyuquot on

Fig. 1. Two pictures taken of a live Diamond Stingray (*Dasyatis dipterura*) collected on 27 October 2011 using a 7.6-m otter trawl in Marina del Rey harbor, Marina del Rey, California. Top image shows the disc and the lower image displays the tail with both a spine and a keel.

Vancouver Island, British Columbia (Williamson 1930). Therefore, the true identity of the species occuring in British Columbia is uncertain and standing as the northern extent of *D. dipterura* is unconfirmed (Ebert 2003; Smith personal communciation). Diamond Stingray was included in the 1993 list of fishes of British Columbia in deference to Hart, but noted a lack of voucher specimens. Its inclusion was for continuity only as a "hypothetical occurrence" (Gillespie 1993). The Resouces Inventory Committee (2002)

also excluded Diamond Stingray from their checklist of British Columbia fishes due to the lack of a voucher specimen for the earlier references.

Polling southern California ichthyologists and field sampling personnel resulted in one confirmed record taken in Santa Monica Bay area or from points north of the bay. Diamond Stingray was reportedly taken along the Malibu coast (nominally 34° 1.0′N 118° 47.0′W) during surveys of surfzone fishes (C. Lowe, personal communication), or approximately 30 km upcoast of Marina del Rey. No size information or photographs were available for the Malibu collection. All other reported records were from south of Palos Verdes Peninsula (nominally 33° 44.0′N 118° 20.0′W), mostly along the beaches of Long Beach and San Diego where catches were historically more common. We conclude that the verifiable northern range limit of Diamond Stingray is Santa Monica Bay, California based on the Malibu and Marina del Rey collections reported here. The lack of verifiable collections north of Santa Monica Bay precludes extending this range any farther poleward.

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CONTENTS

Expansion of the Non-native Mississippi Silverside, *Menidia audens* (Pisces, Atherinopsidae), into Fresh and Marine Waters of Coastal Southern California. Camm C. Swift, Steve Howard, Joel Mulder, Daniel J. Pondella II, and Thomas P. Keegan 153

Larval Duration, Settlement, and Larval Growth Rates of the Endangered Tidewater Goby (*Eucyclogobius newberryi*) and the Arrow Goby (*Clevelandia ios*) (Pisces, Teleostei). Brenton T. Spies, Berenice C. Tarango, and Mark A. Steele 165

Male Mating Posture and Courtship Coloration of the Temperate Marine Tubesnout, *Aulorhynchus flavidus* (Gill). Michael J. Schram and Larry G. Allen 176

Pilot California Spiny Lobster Postlarveae Sampling Program: Collector Selection. Eric F. Miller 180

Avian Predators Target Nocturnal Runs of the Beach-Spawning Marine Fish, California Grunion, *Leuresthes tenuis* (Atherinopsidae). Karen L. M. Martin and Jennifer Griem Raim 187

Fishes of Marine Protected Areas Near La Jolla, California. P. A. Hastings, M. T. Craig, B. E. Erisman, J. R. Hyde, and H. J. Walker 200

Clarifying the Northern Extent of the Diamond Stingray (*Dasyatis dipterura*) in Southern California. Eric F. Miller, Wayne H. Dossett, and Jennifer L. Rankin 232

Cover: Artist rendering of male (top) and female (bottom) Aulorhynchus flavidus body coloration (image by Larry G. Allen).