CONTRIBUTIONS IN SCIENCE

BIOLOGY AND DISTRIBUTION OF THE TIDEWATER GOBY, EUCYCLOGOBIUS NEWBERRYI (PISCES: Gobiidae) OF CALIFORNIA

CAMM C. SWIFT, JACK L. NELSON, CAROLYN MASLOW, AND THEODORE STEIN
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BIOLOGY AND DISTRIBUTION OF THE TIDEWATER GOBY, EUCYCLOGOBUS NEWBERRYI (PISES: GOBIIDAE) OF CALIFORNIA

CAMM C. SWIFT,¹ JACK L. NELSON,² CAROLYN MASLOW,³ AND THEODORE STEIN⁴

ABSTRACT. Eucyclogobius newberryi, the tidewater goby, is restricted to coastal, brackish-water habitats in California, originally from the mouth of the Smith River in Del Norte County, south to Agua Hedionda Lagoon, San Diego County. A southern Californian study population in Aliso Creek Lagoon, Orange County, has an annual life cycle entirely within the lagoon. Males dig vertical nesting burrows 10–20 cm deep in clean, coarse sand commencing in late April–early May at water temperatures of 18–22°C and salinities of 5–10‰. Adult males and females do not differ in length. During courtship, females have more striking breeding colors and display more aggressiveness than males. Females roam widely and court individual males that remain in or close to a nesting burrow. The male occupies an enlarged area of the burrow, where eggs hang from the ceiling and walls. Larvae hatch in 9–10 days at 5–7 mm and live in midwater about vegetation until 15–18 mm SL when they become benthic. Juvenile and adult fish feed visually from the substrate, primarily on ostracods, amphipods, snails, and chironomid larvae and pupae. Among California bay gobies, Eucyclogobius represents an extreme of small size, reduced squamation, short life span, low-salinity habitat, brief association with burrows, and only seasonally high aggression. The lack of a marine phase in the life history indicates that genetic exchange seldom occurs between separate lagoons. The present-day distribution may be a relict from an earlier period when brackish and/or estuarine conditions were more widespread and/or continuous. Low vagility, restricted habitat, and short life span make populations vulnerable to elimination by human activities and many populations have disappeared, particularly in southern California and in the San Francisco Bay area.

INTRODUCTION

The tidewater goby, Eucyclogobius newberryi (Girard, 1857) (Fig. 1), has been poorly known because of its small size and restriction to brackish water habitats of coastal California. The species is of interest because of its narrow adaptation to brackish water, a rare condition among fishes, particularly on the west coast of North America. The disappearance of populations has begun to raise concern about the future of the species (Deacon et al., 1979; Potter, 1982; Ono et al., 1983). In this paper we describe the natural history of one southern Californian population, review the relevant literature, present the results of a field- and museum-collection survey for its occurrence, describe its behavior in the field and laboratory, and discuss conservation strategies.

Previous work, including some of the early results of this study, is summarized by Moyle (1976) and Swift (1980). Tidewater gobies containing ovarian eggs in all months of the year were found in Aliso Creek Lagoon by Goldberg (1977). The distribution and seasonal occurrence of larvae of Eucyclogobius in Rodeo Lagoon (Fort Cronkite), Marin County, were studied by Wang (1982). Food habits and habitat requirements in San Antonio Creek, Santa Barbara County, based on quarterly samples were described by Irwin and Soltz (1984).

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5. Observations on behavior were curtailed at the Aliso Creek site due to Nelson’s then ongoing work. After his death his unpublished manuscript was made available. Since many of his findings confirm or extend Aliso Creek observations, they are here included, and Nelson is listed as a coauthor of this paper.
Figure 1. Female tidewater goby, from Aliso Creek Lagoon, LACM 42369-1, 33 mm SL, scale = 10 mm.

General natural history information appears in faunal works and other papers (Girard, 1857; Jordan, 1893; Jordan and Evermann, 1898; C.L. Hubbs, 1921, 1926; Dill and Shapovalov, 1939; Miller, 1939, 1943; Needham, 1940; C. Hubbs, 1947; Shapovalov and Taft, 1954; Hubbs and Miller, 1965; Elderidge and Bryan, 1972; Fierstine et al., 1973; MacDonald, 1977; Bell, 1978, 1979; Leidy, 1984; McGinnis, 1984).

The following errors in identification were discovered, based on examination of museum specimens (or the lack thereof) or on discrepancies in the original accounts. The account of *Eucyclogobius* by Carpelan (1961) was based on *Gliclichthys mirabilis*, and the records for Carquinez Straits (Messersmith, 1966) are also misidentifications. Gravid *Gliclichthys* from Mendocino County reported by Starks and Morris (1907) were based on *Eucyclogobius*, as was the record of *Gliclichthys* from Waddell Creek (Snyder, 1938). The *Gliclichthys* reported by Metz (1912) from Aliso Creek Lagoon in Orange County represent the population of tidewater gobies herein studied.

**METHODS AND MATERIALS**

**TIME OF FIELD STUDY**

Field observations were conducted at Aliso Creek from March 1973 to January 1977, but mostly from December 1973 to August 1975. The California coastline was surveyed for the species in 1970-1975, again in 1980-1982. Several biologists besides the authors provided information on localities during the study.

**COLLECTIONS**

Museum collections canvassed include California Academy of Sciences (CAS), Natural History Museum of Los Angeles County (LACM), Scripps Institution of Oceanography (SIO), University of Michigan Museum of Zoology (UMMZ), University of California, Los Angeles (UCLA), National Museum of Natural History (USNM), Moss Landing Marine Laboratory (ML), Humboldt State University, and Santa Barbara Museum of Natural History (SBMNH). Museum records, including specimens collected during our surveys, are listed in the Appendix.

Collections were made with small seines and dip nets; selected samples were preserved in 10% formalin and transferred after a week to 45% isopropynol or 70% ethanol.

**BEHAVIOR**

Behavior was observed both in the field and in aquaria. Field observations were with the unaided eye, standing or sitting 1.5-5 m from fish in clear water up to 0.5 m deep. Observations in 1972 and 1973 in Waddell Creek and Bean Hollow lagoons, San Mateo and Santa Cruz counties, respectively, were made by Nelson. He made all laboratory observations presented in this paper on fish in aquaria 19 × 40 × 23 cm and 28 × 74 × 30 cm with water of 10% salinity at room temperatures of 21-25°C.

Because of his death, many of Nelson's observations have not been confirmed. Details of some of his methods are lacking, and thus are distinguished in the results section.

**LIFE HISTORY**

Length frequencies were taken from live individuals, most of which were returned to the lagoon. Standard length (to the nearest millimeter) and weight (to the nearest milligram) were taken on 3 December 1973 from live fish collected the previous day. Fish weighed were blotted dry, weighed fresh, preserved, and later sexed; all had empty digestive tracts. Otoliths and scales were examined for age marks; otoliths were treated with Beechwood Cresote (Sawyer, 1967) for examination whole under 50× magnification.

**FOOD**

Diet was analyzed from the contents of the whole intestinal tract in three lots (37 specimens) of half-grown to
adult fish. Most data are from fish taken in initial seine hauls from undisturbed areas. For each stomach, the volume of each individual food organism was visually estimated using 25× magnification. Food items were pooled for all fish from one locality and date.

**REPRODUCTIVE BIOLOGY**

Fecundity was determined by complete counts of ovarian eggs, using fully gravid fish apparently full of yellow eggs that were mostly 0.5–1.0 mm in diameter. No size classes were apparent in these large eggs; smaller grayish, un-yolked eggs 0.1–0.4 mm in diameter were not counted. In a few fish that apparently had already spawned, these smaller eggs predominated; these fish were not included in computations.

Embryonic development was described from live material collected in the gastrula stage and maintained in petri dishes until hatching. Post-hatching larvae were illustrated from preserved specimens collected in the lagoon.

The relationships between standard length and weight and between standard length and number of eggs were described with log-transformed variables (natural logs) in least squares and geometric mean regressions (Sokal and Rohlf, 1981).

**SALINITY**

Salinity preference was determined by taking salinity data with collections, and salinity tolerance during three experiments conducted in a greenhouse from 10 February to 3 June 1975 at prevailing photoperiods in Los Angeles. Water temperatures ranged from 12.2 to 15.5°C. Test fish and controls were held in aerated 3.5-liter jars half-full of water. Fish were fed dry fish food every other day. Fish were observed twice a day for the first three or four days and daily thereafter, and dead fish were removed. Salt water was Instant Ocean sea salt diluted with deionized water, and all salinities (field and laboratory) were determined with an American Optical Company Refractometer accurate to 0.6‰. Fish were transferred directly from holding water into water at test salinities.

Experiment 1 on 10 February–7 March 1975 was with fish collected on 14 December 1974 and maintained in freshwater. Eight to 10 fish each were tested at 18.0, 35.4, 48.6, 60.0, 70.8, and 81.6‰; a control group remained in fresh water (1.8‰). Experiment 2, 20 March–11 April 1975, fish collected on 12 March in 13.2‰ were tested at 33.6, 44.4, 46.2, 49.2, and 55.2‰; a control group was held in fresh water (0‰). Experiment 3, 11 April–2 June 1975, utilized two groups of fish held at 13.2‰ since 12 March; a control group at 16.2‰ and test group at 40.2‰. Experiment 3 fish experienced a gradual increase in salinity due to evaporation.

**SAND PARTICLE SIZE**

A sample of sand from the vicinity of breeding burrows was analyzed for particle-size distribution with a settling tube.
cooler temperatures for short periods. In summer and fall the lagoon is usually cooler than the ocean and warmer than the stream by 3-4°C.

Similar seasonal cycles have been described for other lagoons in southern California (Carpelan, 1967), and for Lake Merced (Miller, 1958; Fahy, 1974), Waddell Creek Lagoon (Shapovalov and Taft, 1954), and Salinas River Lagoon (Hubbs, 1947; Smith, 1953) in central California, all of which historically held tidewater gobies.

RESULTS

AGE, GROWTH, RECRUITMENT, AND MORTALITY

No distinct annual markings could be found on otoliths or scales from 20 adult fish. Scales do not develop until fish are about two-thirds grown (25-30 mm SL). Then only those posterolaterally on the body grow large enough to overlap each other. Scales never develop anterodorsally or anterocentrally on the body.

Spawning commences in April or May at Aliso Creek and at Waddell and Bean Hollow lagoons. At this time only large adult fish were present at Aliso Creek. Several other museum collections taken in late spring before spawning begins also contain only large fish, despite the frequent abundance of small individuals into the winter (Fig. 3). Although length-frequency data (Fig. 3) appear to indicate that small individuals present in December 1973 grew into the younger of two size (age) classes in June, no small individuals were present during the observations on breeding behavior in April and May. Therefore the smaller class of fish sampled in June must be derived from the most recent spring spawning. The progression of this June peak through the summer indicates these early offspring predominate in the fall and winter population. Late summer and fall spawning was much less successful in 1974; fewer smaller individuals were present. Our data indicate that *Eucylogobius* has an annual life cycle in southern California; specimens in museum collections suggest a similar pattern farther north (Fig. 4).

Considerable post-spawning mortality is indicated by a reduction in numbers of large individuals from midsummer onward, particularly males, and the frequent occurrence of emaciated and dead adults. Aquarium males fed little or not at all while guarding eggs and often appeared emaciated. Eggs take 9-11 days to hatch and with multiple clutches, males may go longer with minimal feeding. Females predominate in the sample of 3 December 1973, and female: male ratios from 1.6:1 to 3.1:1 cannot be rejected at the 0.01 level by the log-likelihood-ratio test (Sokal and Rohlf, 1981). Lengths of adult fish collected on 12 March 1975 (Fig. 5) did not differ significantly between sexes (t = 1.498, df = 1.36, p = 0.2) nor did the sex ratio deviate significantly from 1:1. Apparently older female fish die over the winter leaving the younger-year class with a 1:1 sex ratio.
Figure 3.  Length-frequency of successive collections of *Eucyclogobius newberryi* at Aliso Creek Lagoon, 1973–1975.

Figure 4.  Length-frequency of four populations of tidewater goby, *Eucyclogobius newberryi*, summer 1975. Locality details in text. Localities arranged north to south. Rodeo Lagoon is in Capitola, Santa Cruz County, also known as Corcoran Lagoon.

LENGTH AND WEIGHT

The length-weight relationships on 3 December 1975 for the Aliso Creek population as a whole, indicate that females are only slightly, and not significantly, heavier than males and no fish exceeded 1 g in weight (Table 1). There is little variability and narrow confidence limits because gonads were much reduced and stomachs empty. Gravid females are probably significantly heavier than males early in the breeding season.

POPULATION SIZE

From late summer to early fall at Aliso Creek Lagoon, a few hundred gobies could be collected with a few sweeps of a small seine in most areas of the lagoon. Extrapolation to the whole lagoon indi-
muddy substrate. Seventeen fish taken on 27 October 1973 at Aliso Creek contained 70% chironomid pupae by volume, 25% small invertebrate eggs, and 5% fragmentary algae. Ten fish (29–37 mm SL) collected on 13 June 1974 at Aliso Creek contained 4% snails, 60% ostracods, 30% chironomid larvae and pupae, and 6% amphipods. Eight of 10 specimens (29–39 mm SL) taken on 22 May 1970 at Jalama Creek, Santa Barbara County, contained food: 27% ostracods, 18% mayfly nymphs, and 55% chironomid larvae; two specimens were empty. In the fall of 1973, ostracods, amphipods, snails, and dipteran larvae were found in stomachs of 20 fish collected on 15 March 1973 from Waddell Creek. Fifty-seven ostracods (among 12 fish), 64 snails (among nine fish), and 14 dipteran larvae (among four fish) were tallied. Fish from San Antonio and Shuman lagoons, Santa Barbara County (Irwin and Soltz, 1984), contained ostracods, amphipods, chironomid larvae, and a minor contribution by aquatic insects and mysids.

**HABITS**

Tidewater gobies occur on the substrate in loose aggregations of a few to several hundred individuals with no apparent size segregation. Fish move along the bottom in short spurts. Individuals occasionally hover in midwater along steep drop-offs or in dense aquatic vegetation. Except for adult males in the breeding season, fish do not burrow into the substrate in either nature or an aquarium. The escape mode is fleeing in long dashes (1–2 m) into deeper water or aquatic vegetation.

Tidewater gobies were typically abundant in shallow water (≤1 m deep), but deep water was seldom sampled. However, many smaller lagoons have little or no water deeper than 1 m.

**FOOD**

Half-grown to adult tidewater gobies were seen feeding on live animals on the surface of sandy or muddy substrate. Seventeen fish taken on 27 October 1973 at Aliso Creek contained 70% chironomid pupae by volume, 25% small invertebrate eggs, and 5% fragmentary algae. Ten fish (29–37 mm SL) collected on 13 June 1974 at Aliso Creek contained 4% snails, 60% ostracods, 30% chironomid larvae and pupae, and 6% amphipods. Eight of 10 specimens (29–39 mm SL) taken on 22 May 1970 at Jalama Creek, Santa Barbara County, contained food: 27% ostracods, 18% mayfly nymphs, and 55% chironomid larvae; two specimens were empty. In the fall of 1973, ostracods, amphipods, snails, and dipteran larvae were found in stomachs of 20 fish collected on 15 March 1973 from Waddell Creek. Fifty-seven ostracods (among 12 fish), 64 snails (among nine fish), and 14 dipteran larvae (among four fish) were tallied. Fish from San Antonio and Shuman lagoons, Santa Barbara County (Irwin and Soltz, 1984), contained ostracods, amphipods, chironomid larvae, and a minor contribution by aquatic insects and mysids.

**PREDATION**

Two documented occurrences of predation on tidewater gobies are known. A 32-cm-TL _Salmo_
gairdnerii caught in upper Gaviota Creek Lagoon in August 1960 contained 6–10 gobies, about 75–100 mm TL. (J. Radovich, pers. comm.); some or all of these may have been tidewater gobies. Sculpins (Cottus) have been observed to feed on *Eucyclogobius* in an aquarium (G. Barlow, pers. comm.).

**SALINITY RELATIONS**

All sizes of tidewater gobies usually occur at the upper end of lagoons at salinities ≤ 10%. Of 60 collections 39 were at 0–10%, 12 at 10–20%, 10 at 20–30%, and one at 42%, the last in Bennett Slough, a tributary of Elkhorn Slough, Monterey County. Records of ≤ 10% are given by Hubbs (1947) and Fierstine et al. (1973). Fish from 20–25 and 30% in Corcoran Lagoon, Santa Cruz County, are reported by Bell (1979). An adult specimen, CAS IX-24-1923 labeled Pebble Beach, Pescadero, California, may be from a marine habitat, from Pescadero Creek, or nearby Bean Hollow or Waddell Creek lagoons. Despite four years of extensive nearshore sampling for fish larvae off southern California (G. McGowen and M. Sowby, pers. comm.), the only marine records of larvae are two taken on 13 January 1980 in the vicinity of San Onofre Power Plant, San Diego County, immediately after heavy local runoff due to a large storm.

In the first salinity tolerance experiment (see Methods), all fish from 60.0, 70.8, and 81.6% expired in six hours; at 48.6% all fish expired in 24 hours. Those in fresh water (control), 18%, and 35.4% all survived for 25 days.

In the second experiment, 80% of fish at 50.7% expired in 24 hours, and the two remaining fish died in nine days. All the fish at 45.5% died in six days, and 80–100% of the fish at 35.0, 36.75, and 40.25% survived 22 days, as did controls at 13.2%. In the third experiment, two groups of fish experienced a gradual rise in salinity due to evaporation for 53 days. One group began at 16.2%, the other at 40.2%. At the end, salinity was 25.2% and 61.8%, respectively. Survival was 75% and 59%, respectively, with the die-off of fishes widely scattered over this time interval.

Experimental groups of fish in salinities above 41% experienced high mortality. In the third long experiment with slow change in salinity, over half the fish survived hypersaline conditions (up to 1.75 times that of seawater). Controls in fresh water survived up to 84 days from time of collection.

During winter rains and high flows of inlet streams, tidewater gobies can usually be collected a few tens of meters upstream in small creeks like Aliso Creek, and up to 1.5 to 2 km in larger streams like the Santa Clara, Ten Mile, and Smith rivers. In San Antonio Creek, Santa Barbara County, fish have been recorded up to 8 km inland (LACM records; Irwin and Soltz, 1984).

During summer algal blooms and when hydrogen sulfide (H₂S) builds up in the substrate, most fish are at the upper end where freshwater inflow exists or at the seaward end where occasional high-tide waves wash in from the ocean. Such summer restriction in habitat commonly occurs in disturbed and polluted lagoons. But in relatively undisturbed situations, fish remain scattered throughout, particularly over a sandy substrate.

**PARASITES**

The only parasite noted on *Eucyclogobius* was the digenetic trematode *Cryptocotyle lingua*, which occurred on the skin of many adults from Corcoran Lagoon.

**LIVE COLOR**

Nonbreeding life colors in juveniles and adults of both sexes are light semitranslucent gray, brown, or olive with black flecking and/or mottling. The dorsal, caudal, and anal fins are dusky, and the distal one-fifth or so of the spinous dorsal and a narrow distal edge of the soft dorsal and anal fins are cream, pale yellow, or pale orange. The body has few to many fine pearly white spots. Females often appear darker than males. At Aliso Creek, breeding males near burrows appear similar to nonbreeding individuals. In females the anterior half of the body and the spinous and soft dorsal fins, the anal fin, and the body between them often become strikingly black, except for a narrow distal edge of the fins which remains pale. The head, posterior, and tail body, remain similar in color to males. Much of this black pigment is lost in preservation.

Breeding females in central California are tan to reddish brown with a gold-brown to dark-brown area extending backward from the pectoral insertion to the vent. Melanophore patterns that change with behavior (dark-brown or black) overlying the yellowish abdomen may be responsible for observed variation in shades of gold to brown. Dorsal and anal fins are velvet black with white margins. The flanks of the females can become blue-black during bouts of aggressiveness. In central California, breeding males have a sooty-black head and body with small white spots on the dorsal and lateral surfaces. The dorsal and anal fins are sooty-black with a white margin. The dorsals also have small white spots. The caudal is translucent with five columns of white spots. In both males and females, the pelvic have a prominent elongate white spot and the pectorals are colorless.

**REPRODUCTIVE BIOLOGY**

A genital papilla is present in both sexes, about four times larger in females than males (Fig. 6). Most
fish over 25 mm SL can be sexed externally by this difference. Smaller papillae in nonbreeding individuals also exhibited a size differential between the sexes. Inactive gonads of both sexes are similar in size, but the testes were almost invariably half (and usually more) covered with black melanophores. Testes are 3–6 mm long, 1–2 mm wide, roughly triangular in cross section, and show little seasonal variation in size.

Ovarian eggs are spherical and up to 1.2 mm in diameter when mature. Counts of mature eggs range from 179 to 594 in fully gravid fish that lack smaller eggs. Egg number is related to length of the fish (Table 2, Fig. 7). Excluding the smallest fish, the lowest egg number was 272 for a fish 26.9 mm SL, probably about the minimum size for sexual maturity in females.

The vitelline membrane becomes elongate and pear-shaped after fertilization, essentially identical to that of the eggs of *Typhlogobius californiensis* (Eigenmann, 1892; Breder, 1943) and *Gillichthys mirabilis* (Weisel, 1947). The fertilized ova are pale iridescent yellow with a cluster of 15–20 small oil droplets against one side. The yolk is 1.5–1.7 mm in diameter, and the vitelline membrane is 2 mm wide and 5–6 mm long. The eggs are attached by the pointed ends to sand grains lining the burrow.

Hatching of eggs from nests in the wild from central California took nine days at 21–25°C. Eggs collected from Aliso Creek had the blastodisc developed, and it encircled about one-third of the yolk. About 30 such eggs held in the laboratory at 18–21°C hatched in 9–10 days. By the second day the body was elongate with otic cups and lens vessels visible. Flexing of the body was noted on the third day, and the heart beat began on the fifth day.

Larvae hatched in the laboratory are 5–6 mm long; 6–7-mm-SL and larger larvae are commonly collected free-living in lagoon vegetation (Fig. 8). Six-millimeter larvae had complete median fin folds, small, paddle-like pectorals, and no visible sign of pelvic fins. The air bladder is a simple longitudinal...
oval. A longitudinal series of stellate melanophores forms thin dorsal and ventral median black lines with many fine lateral processes (Fig. 8A). One to three melanophores occur at each jaw articulation. A small patch of cells lies at the base of the caudal fin fold. At 8–9 mm many fin rays are ossified, but the fin folds are still low and rounded (Fig. 8B); a few melanophores appear on the head and posteriorly on the body, a pelvic fin bud develops, a dark patch of melanophores is present immediately posterior to the anus and hindgut, and the air bladder is more elongate. At 11–12 mm SL the dorsal, anal, and caudal fins have a full complement of fin rays (Fig. 8C). Melanophores have migrated out onto the caudal rays, and many more are on the head and body. The distinctive mid-dorsal and mid-ventral lines give way to the mottled adult pattern. Complete development of the pelvic fins (and attainment of the juvenile stage) takes place at 16–18 mm SL. Fish orient largely to the substrate at this time.

At Aliso Creek, breeding commenced in late April 1974 in the upper end of the lagoon. Water temperature was 18–19°C and salinity was low, but not recorded. About 30 burrows were found on 28 April 1974, concentrated on a sand shoal 3 m long, 0.5 m wide, and in an 11-m linear series parallel to one steep, north-facing shoreline. The shoreline entered the water at about a 45° angle. The burrow entrances, as those on the sandbar, all were 24–30 cm deep. At Bean Hollow Lagoon, the burrows found were restricted to a 4-m² area of sandy mud. The entrances of the more or less vertical burrows at Aliso Creek were surrounded by a rounded area of cream or yellowish sand (42–160 mm diameter, n = 26, x = 72.3) that contrasted with the darker adjacent undisturbed sand. Distances between the edges of the clear sandy areas ranged from 50 to 550 mm (n = 22, x = 143.5). Hand excavation of seven burrows revealed either a male (three burrows) or a male and female (four burrows) 75–100 mm below the surface. A clump of about 50 eggs was found with one pair.

Male fish occupied several of the clear areas around the burrow entrances at Aliso Creek Lagoon. Two males at separate burrows entered head first. Slowly and laboriously undulating the body in a backward-swimming motion, they emerged tail first and dropped a mouthful of sand within 100 mm or so of the entrance. On 13 June the clear areas were not evident. One male excavated a burrow for about half an hour, completely disappearing 10–12 times for 10–20 seconds each. He was distracted by female fish five or six times, and once by a half-grown Gambusia. Subsequently the male moved 80–100 cm away, but returned in 10 minutes. In the next hour he removed mouthfuls of black sand five or six times.

At midday on 28 April, female fish (black coloration described above) often swam in midwater over the burrows. Several times females displayed to each other by maximally expanding the median fins while lined up in opposite directions side-to-

Table 2. Least squares and geometric mean regressions of standard length and number of mature ova using log-transformed data. X = standard length; Y = number of ova.

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>r</th>
<th>Least squares</th>
<th>Geometric mean</th>
<th>95% Confidence limit for slope</th>
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</thead>
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<tr>
<td>Aliso Creek</td>
<td>18</td>
<td>0.7886</td>
<td>ln X = 0.24382 ln Y + 1.9888</td>
<td>0.30916 ln Y + 1.58825</td>
<td>0.325977</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>ln Y = 2.5304 ln X - 2.7536</td>
<td>3.2346 ln X - 5.13732</td>
<td>0.3259432</td>
</tr>
<tr>
<td>Oak Knoll Creek</td>
<td>20</td>
<td>0.8873</td>
<td>ln X = 0.39437 ln Y + 1.07917</td>
<td>0.44447 ln Y + 0.79168</td>
<td>0.2284734</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>ln Y = 1.9962 ln X - 0.89316</td>
<td>2.24986 ln X - 1.78117</td>
<td>0.228399</td>
</tr>
<tr>
<td>Both combined</td>
<td>38</td>
<td>0.8517</td>
<td>ln X = 0.35803 ln Y + 1.3044</td>
<td>0.42040 ln Y + 0.502708</td>
<td>0.1771222</td>
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<tr>
<td></td>
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<td>ln Y = 2.0259 ln X - 0.96366</td>
<td>2.43768 ln X - 2.19578</td>
<td>0.1632797</td>
</tr>
</tbody>
</table>

Figure 7. Log-log plot of number of eggs versus standard length in female Eucyclogobius newberryi (n = 38). Open circles are Aliso Creek fish (LACM 35814-3, 21 January 1973, and 42369-1, 13 June 1974). Black dots are fish from Oak Knoll Creek, San Luis Obispo County (LACM 1007, 3 May 1958).
Larvae of tidewater goby, *Eucyclogobius newberryi* from Aliso Creek Lagoon, LACM 43748-1, collected on 22 May 1976. A. 6 mm SL; B. 9 mm SL; C. 11.5 mm SL. Scales = 1 mm.
side about 10–15 mm apart. Usually these encounters were near burrow entrances, and on two occasions the “winner” of such face-offs proceeded to enter the burrow with the male fish for several minutes. In a third episode, the second female fish followed the first into the burrow, but one female re-emerged after a few seconds and left the area.

Breeding males from central California observed in an aquarium pressed the sides of the head against the substrate, raised up the caudal end, and drove themselves head first into the burrow with vigorous swimming motions. They turned and undulated to the surface along the same path. The males deepened and widened the burrow, removing sand with the mouth until a small mound of fresh substrate surrounded the burrow entrance.

Central Californian males in an aquarium attempted to burrow into gravel and mud substrates about 4 cm. In coarse aquarium gravel the burrow collapsed, but the male continued to attempt burrow construction for four days. In substrate from Waddell Lagoon, a male dug a burrow next to the aquarium glass in two hours. Mucus was found on both gravel and mud-sand mixtures, indicating that body mucus cements and supports the burrows.

Central Californian males also rearranged the interior of their burrows and changed the entrance location. The entrance was closed by spitting a sand-mucus plug into the opening and reopening the burrow some distance away. In the laboratory, male fish closed the entrance to their burrows only from the inside. If the male was feeding or in the burrow with a female, the entrance remained open.

Closure made nests difficult to locate in the field; the substrate accumulated near the burrow entrance soon became inconspicuous. Ripe females appeared to have little trouble locating nest sites, conspicuous or not.

Female fish were often noted seeking out and courting males at the burrows. After a female begins courting, the male may blow a sand plug into the entrance. He may pop open the burrow entrance, exit, and line up parallel with the female. He may swim about the entrance with her, undulate his body, and exchange tail slaps. The male might then stop, rest with his head pressed to the substrate next to the burrow, and suddenly dart into the hole, soon followed by the female. Or he may dive inside and blow a sand plug or otherwise obstruct the burrow’s entrance to the female. Of 23 courtships lasting more than two minutes (Bean Hollow, 3 July 1973), only one led to a female successfully entering a male’s burrow. In the remaining 22 the male left his nest only five times. On 17 occasions the male either: (1) opened the entrance, poked his head out briefly, and then retreated and remained quiet; or (2) resealed the entrance. Laboratory behavior of male fish was essentially the same.

Egg laying was observed in a burrow next to the glass wall of an aquarium. The male remained close to the female as she suspended her eggs, one by one, from the roof and sides of the burrow. Occasionally the male rapidly undulated back and forth, rotating along his long axis while moving slowly within the nest, presumably releasing milt. Egg laying lasted one hour and 47 minutes. The female then left the burrow. The male did not fan or otherwise manipulate the eggs, but they appeared clean for five days. Then the male piled mud next to the glass, occluding further view. It is not known if the eggs were fertile or if they hatched, since no fry appeared in the aquarium. Eggs were found in varying states of development in individual burrows in the field in central California. Thus, males probably mate with more than one female.

Males were not very aggressive, and laboratory and field interactions between males were few. After constructing a burrow, they seldom ventured out during the day. When out, males occasionally reacted to one another by biting at the substrate, head-standing with the chin close to the ground, and curving the tail up over the body, undulating laterally. Rarely, males lined up parallel to one another and delivered blows using the caudal fin and posterior end of the body. In the field, males were observed to come close to each other without combat. In only one instance did one male enter another’s burrow without interference from the presumed owner. In the laboratory, males often attacked other males that attempted to enter their nests.

Laboratory observations indicated that females can influence a male building its nest. On two occasions, males digging at one site moved due to the activity of a female. Each time, the female approached the male, swam excitedly around him, moved nearby, and assumed a pre-digging stance (head pressed to the surface and tail raised off the substrate). On one occasion the female took mouthfuls of substrate and pushed her head into the substrate. On both occasions the male fish stopped digging at the original site, joined the female at the new location, and dug a successful burrow.

Ripe, sexually active females were aggressive. In the field and laboratory they attacked other ripe female fish. Females bit the substrate, aligned themselves parallel to one another, and exchanged tail slaps. When parallel or when approaching another individual, the aggressive female swam in a stiff posture with the dorsal, ventral, and caudal fins fully erect and usually resting on the tops of the extended pelvic fins. Female fish occasionally bit each other, and their aggression was more frequent and intense than that of the males. At Bean Hollow, only one instance of male-female aggression was observed, and none was observed at Waddell Lagoon. We witnessed 108 and 17 female-female aggressive interactions, respectively, at these sites during 60 minutes of observations at each location. However,
Figure 9. Distribution of the tidewater goby, *Eucyclogobius newberryi*. Solid circles represent populations viable in 1984, open circles represent museum records for localities where fish can no longer be found. In cases of close overlap, not all localities are plotted.
since males are seldom out of their burrows once the reproductive season begins, chance encounters between them are less frequent.

In the laboratory, female gobies established a social hierarchy. One female always displaced all other females in a given aquarium when they approached burrow sites. On a few occasions when nesting males chased other female fish, the dominant female placed herself between the male and the other female. The dominant female then nudged and swam about the male attempting to lead him back to his burrow. The number of egg clutches laid during the study indicated that many unwitnessed breedings occurred. Some of these may have involved subordinate females. All seven observed breedings (the female is allowed to enter the burrow) involved the high-ranking female.

In the field one female does not control access to all males. Rather, individual females assumed temporary dominance at single burrow sites. Successful females remained near a burrow for 30 minutes, occasionally longer. If unsuccessful after courting a male fish for some time, the female swam away or another female displaced the originally dominant fish. The single successful courtship witnessed in the field involved a female that was dominant at the time in the area.

Initially a ripe female entered a nesting area and swam slowly over the substrate. She settled to the bottom and placed her lower jaw on the substrate, or rested with her fins spread and hopped in a tight circle around an area of sand. Usually a hole appeared in the substrate, and a male extended its head out into the open. Occasionally the only evidence of the male’s presence was a rhythmic rise and fall of the substrate.

Once the male was visible, the female began swimming about the opening. She erected her dorsal and ventral fins maximally and hopped and dashed around the circumference of the aperture. Violent undulations of the body often occurred at this time, and the female often bumped the male’s head with her caudal fin or vent areas. She sometimes rested over the opening of the nest with her vent exposed to the male below or cupped the head of the male with the posterior end of her body. Many of these motor patterns were also observed in female-female aggression. However, the female never rushed at the male or bit or tail-slapped the male as much as she did another female. After a period of such activity, the male often allowed the female to enter its burrow. Not all courtships succeed, and some breedings occur without a courtship period.

Courtship activity usually led to some female-female aggression in both the laboratory and the field. If a female started to court a nesting male, other females were attracted. Melees of up to six females occurred. During 23 courtships observed at Bean Hollow on 3 July 1973, 18 were interrupted by one or more interloping female fish. All observed laboratory courtships were interfered with (n = 75), but the dominant female successfully defended the nest sites.

In the field, turnover of females could seldom be assessed without individual marks. However, on a few occasions where differences could be discriminated among the females, dominant females were displaced. In the laboratory, a few colorful females reverted to the olive-tan nonbreeding colors and were able to approach nesting males closely. Only an hour previously, they had been attacked by the dominant female. None of these reverted fish entered a burrow.

DISTRIBUTION

The distribution of the tidewater goby is from Tillas Slough (mouth of Smith River), Del Norte County, south to Agua Hedionda Lagoon, San Diego County, California (Fig. 9). These localities correspond almost exactly to coastal regions with littoral cells of sediment movement (Habel and Armstrong, 1977) that facilitate lagoon formation. It is apparently absent: (1) between Humboldt Bay and Ten Mile River, (2) between Point Arena and Salmon Creek, and (3) between Monterey Bay and Arroyo del Oso (about 3 km north of Piedras Blancas Light). The coastline is steep in these areas and lagoons are usually absent. Museum records exist for 87 localities as of mid-1984 and are listed in the Appendix. About 40 additional coastal streams and lagoons have been collected and appear suitable for the species, but no Eucyclogobius have ever been taken. Nine are so large that a small population of tidewater gobies could exist undetected, namely in the Klamath, Eel, Mattole, Noyo, Albion, Navarro, Garcia, Gualala, and Russian rivers.

ASSOCIATED FISHES

South of Point Conception, native species often collected with tidewater gobies are Leptocottus armatus, Fundulus parvipinnis, Atherinops affinis, Platichthys stellatus, Hypsopsetta guttulata, Gila orcutti, Gasterosteus aculeatus, and Salmo gairdnerii. North of Point Conception these species (except Fundulus and Gila) occurred, and Cottus asper is also common. In the Salinas River Lagoon, Hubbs (1947) also collected Catostomus miniatus (= C. occidentalis), Orthodon microlepidotus, Rhinichthys osculus, Ptychocheilus grandis, Cyprinus carpio, and Archoplites interruptus with Eucyclogobius. In a few larger lagoons both north and south, Cymatogaster aggregata and Symphysodon sp. occurred. Adult Leuresthes tenuis were occasionally taken in Aliso Creek Lagoon (at salinities of 6–7.2%) in the summer, probably carried in by waves during the fish’s nocturnal spawning. The introduced mosquito fish, Gambusia affinis, almost invariably occurred with Eucyclogobius in coastal
lagoons south of Point Conception but was usually absent from strictly coastal localities farther north.

**DISCUSSION**

On the Pacific coast of the United States the tidewater goby is almost unique among fishes in its restriction to low-salinity water. The brackish region of lagoons and/or estuaries in general contains few endemic organisms; through time few species have adapted exclusively to this habitat (Haedrich, 1983; Hedgpeth, 1983). The only other brackish-water species in California are *Hypomesus transpacificus* and *Pogonichthys microlepidotus* (Daniels and Moyle, 1983) known only from tidal fresh and brackish waters of the Sacramento–San Joaquin Delta. *Eucylogobius* is at the freshwater end of an ecological series (based on salinity) of phyletically related eastern Pacific temperate bay gobies (Ginsburg, 1945; Birdsong et al., 1988). Marine species are *Lepidogobius lepidus*, *Typhlogobius californiensis*, and *Lethops connectens*. Mostly estuarine are *Ilyimus gilberti*, *Quietula y-cauda*, and *Clevelandia ios*. Often occurring in low-salinity or fresh water are *Gillhichthys mirabilis* and *Eucylogobius newberryi*. However, *Gillhichthys* also often occurs in hypersaline conditions (Barlow, 1961a, 1961b, 1963), and is known from the widest range of salinities (Moyle, 1976). However, *Gillhichthys* can survive only about two weeks in fresh water (Barlow, 1961a), whereas *Eucylogobius* has survived at least 84 days.

The biology of *Eucylogobius* corresponds to one of two life history tactics proposed by Grossman (1979) for north temperate gobies, namely a combination of small size, short life span, and an annual life cycle, possibly with multiple reproductions per season. Young-of-the-year were collected by us from May to December at Aliso Creek, and by Wang (1982) in Rodeo Lagoon, Marin County. However, Goldberg (1977) found at least some females with mature eggs in all months (April 1974–April 1975) at Aliso Creek. He concluded that the capability for year-round spawning exists. Females in the 2 December 1974 collection (Fig. 3) have much reduced gonads (compared with April or May specimens), but some did contain a number of mature eggs. The potential for year-round spawning exists but probably is seldom, if ever, realized because of low temperatures and disruption of lagoons by winter rains.

The breeding behavior of the tidewater goby is noteworthy in the dominance and aggressiveness of female fish accompanied by their more striking, mostly black, breeding colors. This behavior is the opposite of the situation in most gobies (P.J. Miller, 1984), and for that matter most fishes (Potts, 1984; Potts and Wootton, 1984). However, black breeding colors are found in many male gobies (Miller, 1984). The aggressiveness of females is most pronounced in the confines of aquaria; it was more limited in the field. Much less interaction was noted between males, possibly because burrows were already established.

Considerable intraspecific aggression between individuals of burrow-inhabiting California gobies has been documented in laboratory-held *Lepidogobius lepidus* (Grossman, 1980), *Typhlogobius californiensis* (MacGinitie and MacGinitie, 1968), and *Gillhichthys mirabilis* (Weisel, 1947). Weisel (1947) also noted considerable blackening of body and fins, both in a dominant nesting male and other mature fish of both sexes. The color was transitory and elicited during aggressive bouts. *Eucylogobius* falls at the lower extreme in aggressiveness among these species and lacks territoriality during the nonbreeding season.

In *Eucylogobius*, only the male burrows and only in the breeding season, mostly and perhaps exclusively in coarse sand. Some Californian bay gobies (*Gillhichthys*, *Lepidogobius*, *Typhlogobius*, and *Clevelandia*) use the burrows of invertebrates (Ricketts et al., 1985). Hoffman (1981) showed that *Clevelandia* was not as strongly dependent on invertebrate burrows as was formerly believed. *Ilyimus gilberti* and *Quietula y-cauda* also build burrows in finer sand and/or mud in bays (Brothers, 1975). Such burrows may provide protection from the predation pressure on bay gobies documented by MacGinitie and MacGinitie (1968) and Horn (1980). The brackish habitat of *Eucylogobius* lacks commensal burrowing organisms, and aquatic predators appear far fewer. Lack of tidal fluctuation also obviates the need for a retreat at low tide.

Predation on *Eucylogobius* is virtually undocumented, but a variety of native bird and a few fish predators (*Leptocottus armatus*, *Cottus asper*, *Salmo gairdnerii*) occur in coastal lagoons. Smaller fishes like mosquitofish (at least in southern California) and stickleback could prey heavily on young gobies. Individual females with dark breeding colors often are obvious in spring and early summer, but the color (not present in preserved specimens) can be altered considerably in a few minutes. This ability obviously reduces the period of vulnerability to visual predators.

More native predatory fishes occur in the San Francisco and Monterey bay drainages. *Archoplites interruptus* (Centrarchidae) and *Hysterocharax traski* (Embiotocidae) were widespread in the delta and many tributaries of the bay. Subsequently, several exotic centrarchid species and the striped bass, *Morone saxatilis*, were introduced into San Francisco Bay tributaries. The three San Francisco Bay records of tidewater gobies are all seaward of the major tributaries of the bay where these predators occur. Hubbs (1947) reported collecting *Archoplites* (possibly introduced) and *Eucylogobius* together in the lower Salinas River in August 1946, and the last known collection of *Eucylogobius* from there was taken in 1951. Six coastal lagoons contain centrarchids but lack *Eucylogobius*: Lake Cleone, Mendocino County; Abbott's Lagoon, Marin County; Oso Flaco Lake, San Luis Obispo
County; Lake Merced, San Francisco County; and Buena Vista and Agua Hedionda lagoons, San Diego County. The latter three historically contained tidewater gobies. Many small *Lepomis cyanellus* were taken with *Eucyclogobius* on 21 January 1973 at Aliso Creek Lagoon. *Lepomis* were never taken again. Otherwise centrarchids and tidewater gobies have not been taken together and perhaps cannot coexist.

A black pigmented investment on the testes, as in mature *Eucyclogobius*, is rare in vertebrates. Specimens of related bay gobies (LACM) show it well developed in *Ilypnus gilberti*, variably developed in *Clevelandia ios*, and absent in *Gillichthys mirabilis*, *Quietula y-cauda*, *Q. guaymasiae*, *Lepidogobius lepidus*, *Typhlogobius californiensis*, and *Lethops connectens*. Otherwise it is unrecorded in gobies (Miller, 1984) and in most other fishes as well (Nagahama, 1983). Wootton (1976) notes its occurrence in *Gasterosteus aculeatus*. It rarely occurs in lizards and mammals, and two alternative (but unproven) functions are postulated (Guillette et al., 1983): (1) to absorb solar radiation and thereby protect the testis from damage, or (2) to warm the testis with absorption of solar radiation. Since any warming would be quickly dissipated in water, the protective function only should be pertinent to fishes.

Precipitous coastlines where lagoons do not form at stream mouths define three presumably natural gaps in distribution noted previously. The Los Angeles Plains area of southern California (Culver and Hubbs, 1917) is a fourth hiatus not explainable by steep shorelines. No specimens exist to verify early published records from San Pedro and artesian wells in Santa Monica (Eigernann and Eigernann, 1892). This break also exists in the distribution of the freshwater *Gasterosteus aculeatus microcephalus*; only *G. a. williamsoni*, another freshwater stickleback, occurred on the Los Angeles Plain (Miller and Hubbs, 1969). Given extensive habitat modification and few early fish collections, some credence can be given to each of the four scenarios possibly involving *Eucyclogobius* and *G. a. microcephalus*: (1) both existed on the plain and disappeared, either historically or prehistorically; (2) and (3) only one or the other occurred and disappeared; or (4) neither ever lived in the area. The habitat must have been ideal for both taxa, and the negative evidence of lack of collections is not a strong argument against their original presence. Bell (1978) also discussed the equivocal nature of negative historical data in records of southern California freshwater fishes.

Barlow (1963) suspected that populations of *Eucyclogobius* were somewhat isolated from each other. Genetic differentiation between populations (Crabtree, 1985) supports the idea that interchange between populations is restricted. Our life history data also indicate that the complete life cycle is spent in lagoons or upper bays. Larvae provide at least a possibility of dispersal, but in San Francisco Bay and southern California, where many populations have disappeared, no case of recolonization is known. Today, populations are separated more widely, further isolating them. Brackish-water animals often show more morphological variability than freshwater or marine ones (Rasmussen, 1973; Wolff, 1983), perhaps due to such isolation.

The present distribution of *Eucyclogobius* may be a relict one from a time when brackish-water conditions were more widespread. Such distribution of several gobies in Mediterranean brackish coastal lagoons has been explained by alternating Pleistocene incursions of fresh and brackish water from the east (Zenkevitch, 1963; Miller, 1973). These taxa provide the closest ecological analog to *Eucyclogobius*. During the late Miocene and Pliocene, much of California was covered with large, occasionally connected, embayments and inland seas that were obliterated by the rapid Plio-Pleistocene uplift of the coastal ranges (Cole and Armentrout, 1979). Intraspecific phylogenetic analyses of *Eucyclogobius* (in progress by Swift and C.B. Crabtree) may help interpret the sequence of these changes.

**CONSERVATION**

The disappearance of populations and the vulnerability of those that remain indicate *Eucyclogobius* should be carefully monitored to avoid its complete loss. This is particularly true south of Point Conception where only 15 populations remain: three on Camp Pendleton, one each in the Santa Clara and Ventura rivers, and 10 between Santa Barbara and Point Conception. Today *Eucyclogobius* occurs with a full complement of close relatives (*Clevelandia, Gillichthys, Quietula, Ilypnus, and Lepidogobius*) only in Morro Bay, San Luis Obispo County, and Santa Margarita River, San Diego County.

Consideration should be given to restocking lagoons from adjacent populations if habitat conditions seem to have recovered sufficiently to accommodate the species. This means little or no channelization, and allowing lagoons to close off to the ocean for much of the year so that tidal fluctuation is absent or minima. Fresh unconsolidated sand seems optimal for reproductive burrows and should be available each year. The quality of inflowing water should be kept high. Anecdotal evidence indicates that enrichments from agricultural and sewage effluents cause algal blooms and deoxygenation that restrict the habitat area of lagoons in summer. Little is known of actual tolerances to factors other than salinity. A low-salinity environment (0–15%) will normally be maintained if the physical integrity of the lagoon remains. Sudden draining of a lagoon in late spring or summer allows marine water to dominate the lagoon for months until winter rains return. Non-native predators should be excluded since circumstantial evidence indicates that they adversely impact *Eucyclogobius*. This applies most to those species tolerant.
of brackish water such as striped bass, largemouth bass, white catfish, and *Tilapia*, as well as small species such as mosquitofish.

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APPENDIX

Museum records and locality data (listed north to south) for Eucyclogobius newberryi: Localities where fish are apparently rare, but may still occur, are preceded by a +. Sixty-three localities still holding the species in mid-1984 are marked with an asterisk. Distances are straight line (or airline) from point to point as determined from U.S. Geological Survey 7/8 minute quadrangle maps.

Del Norte County. *(1) Tillas Slough, about 3.2 km SE of mouth of Smith River, LACM 42683-2, about 500 m W mouth Rittner Creek, seaward of tide gate on Tillas Slough, 19 June 1981; *(2) Lake Earl, 3–6 km N Crescent City, LACM 42669-1, on NE shore at end Buzinian Road, 13 June 1981.

Humboldt County. +(3) Freshwater Lagoon, 3–4 km SW Orick on U.S. Hwy. 101, CAS Acc. 1932x:30, "near shore on highway," 22 August 1951; *(4) Stone Lagoon, 3.5–6.5 km S Orick, LACM 35342-3, vicinity of McDonald Creek on SE shore of lagoon, 31 July 1975; *(5) Big Lagoon, 8.5–13 km S Orick, LACM 35341-1, vicinity of inlet stream and boat ramp (Big Lagoon County Park), 31 July 1975; *(6) Humboldt Bay, LACM 42667-6, NE shore, vicinity oxidation ponds and Radio Station KATA, 13 June 1981, and LACM 35335-9.

Medocino County. *(7) Ten Mile River, LACM 35331-1, 0.75 km upstream Hwy. 1 bridge, 29 July 1975; *(8) Virgin Creek, about 2 km N Fort Bragg, LACM 35329-2, 28 July 1975; *(9) Pudding Creek, N edge Fort Bragg, LACM 35328-1, 28 July 1975; *(10) Manchester State Beach, 0.75 km N Manchester, two unnamed lagoons, LACM 42666-2, 12 June 1981.

Sonoma County. *(11) Salmon Creek, about 1.5 km N Bodega Bay, LACM 35317-3, S shore in Salmon Creek State Beach, 26 July 1975; *(12) Cheney Gulch, SE corner Bodega Lagoon, CAS 25512, 12 August 1948; *(13) Estero Americano, 1–1.5 km W Hwy. 1 on Valley Ford–Franklin School Road, LACM 37380-1, 12 October 1977.

Bridge, 28 October 1961; (19) Novato Creek at Hwy. 101 crossing, 2.5 km SE of Novato, CAS 12995; 19 July 1945.

**Alameda County.** (20) Aquatic Park, west edge of Berkeley, CAS Acc. 1964-xx:13, summer, 1930.

**San Francisco County.** (21) Lake Merced, CAS 12483, 1 November 1895.

**San Mateo County.** *(22) San Gregorio Creek about 16 km S Halfmoon Bay, LACM 35297-2, 22 July 1975; *(23) Pescadero Creek, CAS (uncataloged), 24 September 1923; *(24) Arroyo de los Frijoles (Bean Hollow), about 6.5 km N Pigeon Point, LACM 35293-2, 21 July 1975.

**Santa Cruz County.** (25) Waddell Creek, about 11.5 km NW Davenport, CAS 28670, 1939-1942; (26) Scott Creek, about 5 km NW Davenport, CAS 20896, 31 August 1939; *(27) Laguna Creek, about 13 km WNW Santa Cruz, LACM 35286-2, 20 July 1975; *(28) Baldwin Creek, about 5.0 km NW Santa Cruz, LACM 35284-1, 20 July 1975; *(29) Meder Creek, about 0.8 km W Santa Cruz, LACM 35285-2, 20 July 1975; *(30) Moore Creek, Natural Bridges State Beach, N edge Santa Cruz, LACM 43763-1, 3 October 1984; *(31) Twin Lakes (Woods Lagoon) between Santa Cruz and Capitola, LACM 35281-2, eastern lake of two, 19 July 1975; *(32) Rodeo Gulch, Corcoran Lagoon, in Capitola, LACM 35279-1, 19 July 1975; *(33) Aptos Creek, Aptos, LACM 37577-2, 23 July 1977; *(34) Pajaro River, CAS 31894, 3 August 1949.

**Monterey County.** *(35) Elkhorn Slough, 250 m W tidegate in Bennett Slough, LACM 42656-2, 8 June 1981; (36) Salinas River, CAS 48290, at Hwy. 1 crossing, 22 August 1951.

**San Luis Obispo County.** *(37) Arroyo del Oso, about 3 km N Piedras Blancas Light, LACM 35257-2, 14 July 1975; *(38) Arroyo del Corral, about 2.2 km N Piedras Blancas Light, LACM 42349-1, 30 June 1981; *(39) Arroyo Laguna (Oak Knoll Creek), 3-4 km N San Simeon, LACM 36195-1, 22 January 1975; *(40) unnamed canyon, 2.2 km NW San Simeon Point, LACM 36663-2, 15 June 1977; *(41) Arroyo del Puerto, 0.5 km ESE San Simeon Post Office, LACM 42351-1, 31 January 1981; *(42) Broken Bridge Creek, 1.0 km SE San Simeon Post Office, LACM 42352-1, 31 January 1981; *(43) Little Pico Creek, 2.6 km ESE San Simeon Point, LACM 36662-6, 15 June 1977; *(44) Pico Creek, 3.8 km SE San Simeon Point, SIO 72-88, 14 May 1972; *(45) San Simeon Creek, 6.2 km SE San Simeon Point, SIO 72-87, 13 May 1972; *(46) Lefingwell Creek, 7 km SE San Simeon Point, LACM 42353-1, 31 January 1981; *(47) Santa Rosa Creek, Cambria, LACM 36667-1, 15 June 1977; *(48) Villa Creek, 13.5 km NW Morro Rock, LACM 42355-1, 31 January 1981; *(49) Cayucos Creek, 9.5 km NNW Morro Rock, LACM 36669-1, 15 June 1977; *(50) Old Creek, 7.0 km NNW Morro Rock, LACM 36670-2, 15 June 1977; *(51) Chorro Creek, trib. Morro Bay, LACM 35573-1, 19 January 1976; *(52) Los Osos Creek, trib. Morro Bay, Tumri Road, LACM 42348-2, 28 January 1981; *(53) San Luis Obispo Creek, 2.3 km ENE Point San Luis, CAS SU 633, 1894; *(54) Pismo (Price) Creek, Pismo Beach, LACM 36673-3, 16 June 1977; *(55) Santa Maria River, 7.2 km N Point Sal, 0.5 km up from Ocean, S shore, LACM 42345-1, 28 January 1981.

**Santa Barbara County.** *(56) Shuman Canyon, 8 km SE Point Sal, LACM 36197-1, 3 November 1976; *(57) San Antonio Creek, 14.5 km SSE Point Sal, LACM 36200-1, 18 July 1975; *(58) Santa Ynez River, S shore, 150 m E railroad tracks, LACM 42434-1, 28 January 1981; *(59) Jalama Creek, 8 km NNW Point Conception, LACM 31425-2, 22 May 1970; *(60) Canada di Cojo, 5.0 km E Point Conception, SBMNH 00956, 27 February 1984; *(61) Arroyo St. Augustine, 10.5 km E Point Conception, SBMNH 00015, 25 May 1965; *(62) Canoa de las Agujas, 11.7 km E Point Conception, SBMNH 00957, 21 March 1984; *(63) Arroyo Bulito, 10.2 km W Gaviota Creek, LACM 36658-1, 14 June 1977; *(64) Canoa de Santa Anita, 7.5-8.0 km W mouth Gaviota Creek, SBMNH 00959, 21 March 1984; *(65) Canoa de Alegría, 4.1 km W mouth Gaviota Creek, SBMNH 00961, 21 March 1984; *(66) Canoa de Agua Caliente, 2.5 km W mouth Gaviota Creek, LACM 42340-1, 27 January 1981; *(67) Gaviota Creek, Gaviota, LACM 1693, 9 December 1961; *(68) Arroyo Hondo, 6.8 km E Gaviota, UMMZ 130666, 23 August 1934; *(69) Arroyo Queulado, about 9.5 km E Gaviota, LACM 36193-1, 27 December 1974; *(70) Tecomote Canyon, about 6.5 km W Goleta, LACM 42339-1, 27 January 1981; *(71) Bell (Ellwood) Canyon, about 6 km W Goleta, SBMNH 1077, 25 September 1984; *(72) Devereaux Slough, 3.2 km W Goleta Point at Coal Oil Point, SBMNH 00592, 1 March 1968; (73) El Estero, Carpenteria, UMMZ 63285, 17 May 1923; (74) Carpenteria Creek, Carpenteria, UMMZ 133067, 8 July 1940.

**Ventura County.** *(75) Ventura River at N edge Ventura, LACM 36216-1, 12 December 1974; *(76) Santa Clara River, between Ventura and Oxnard, LACM 34071-1, 22 September 1974; (77) Calleguas Creek, upper end Mugu Lagoon near Oxnard, UMMZ 133072, 8 June 1940.

**Los Angeles County.** *(78) Malibu Creek, 17 km W Santa Monica, UCLA (CAS) W55-272, 12 October 1955.

**Orange County.** *(79) Aliso Creek, 0.5 km NW Aliso Point, SW edge Laguna Beach, LACM 42372-1, 7 December 1976; *(80) San Juan Creek, 3.3 km E Dana Point, UMMZ 131650, 7 August 1940.

**San Diego County.** *(81) San Mateo (San Diego) Creek, N edge Camp Pendleton, LACM 36189-2, 26 December 1974; *(82) San Onofre Creek at San Onofre, LACM 42692-2, 3 December 1981; *(83) Las Flores (Las Pulgas) Creek, about 13 km NNW Oceanside, LACM 42691-2, 3 December 1981; *(84) Santa Margarita River, 3.3 km N Oceanside, 5-6 km inland of ocean, LACM 36191-3, 26 December 1974; *(85) San Luis Rey River, N edge Oceanside, UCLA W58-1, 10 April 1958; *(86) Buena Vista Lagoon, Carlsbad Bird Sanctuary, UCLA 53-235, 10 April 1953; *(87) Aquia Hedionda Lagoon, upper (E) end, UMMZ 131809, 29 June 1940.

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