We know of no data concerning swimming speeds of the species examined, but an individual moving completely across one depth zone would cover 6-35 km in southern and up to 20-90 km in northern Texas coastal waters.

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PETER F. SHERIDAN
DAVID L. TRIMM

Southeast Fisheries Center Galveston Laboratory
National Marine Fisheries Service, NOAA
4700 Avenue U
Galveston, TX 77550

LIFE HISTORY OF SPLITTAIL (CYPRINIDAE: *POGONICHTHYS MACROLEPIDOTUS*) IN THE SACRAMENTO-SAN JOAQUIN ESTUARY[1]

The Sacramento-San Joaquin estuary is the largest on the west coast of North America. Because of its comparatively young geologic age, <8,000 yr (Atwater 1979), its fish fauna is a mixture of native freshwater and marine species, to which numerous exotic species have been added in the past 100 yr (Moyle 1976). The ranges of two extant species, the delta smelt, *Hypomesus transpacificus*, and the splittail, *Pogonichthys macrolepidotus*, are restricted to the estuary. Both species are abundant but their biology is nevertheless poorly known, since most fisheries research in the estuary has concentrated on species of major economic importance, especially the introduced striped bass, *Morone saxatilis* (Stevens 1980; Collins 1982).

The fish communities of the estuary are changing, however, as new species are introduced and as conditions change in response to upstream water projects, water diversions, such as increased use of the water for cooling power plants, and pollution. Given the restricted ranges and habitats of these two species (Moyle 1976), their abundance could decline rapidly if environmental conditions become unfavorable for them, possibly making them candidates for listing as threatened species. This paper is concerned with the life history of the splittail, a species of

[1]Contribution No. 351 from the New York State Museum, Albany, N.Y.

interest for reasons besides its status as a potentially threatened endemic: 1) It is consistently one of the most abundant species in many of the brackish sloughs of the estuary (Moyle and Daniels unpubl. data; Caywood 1974), 2) most other cyprinids are exclusively freshwater species, rarely found in brackish waters, 3) its life history patterns reflect adaptation to an environment in which drought and flood occur episodically, and 4) it supports a small but locally important hook-and-line fishery (Caywood 1974).

Methods

Fishes were collected in the Suisun Marsh between January 1979 and January 1982, using 2.5 m otter trawls (mesh at cod end 6 mm bar) and 3 mm bar beach seines. The Suisun Marsh is the largest contiguous tidal marsh on the eastern Pacific coast (Fig. 1). It comprises 34,000 ha of marshland, sloughs, and shallow bays (Moyle et al. 1982a). At each locality, salinity (‰), water temperature (°C), secchi depth, and turbidity were recorded. Standard length (SL) was measured on all fish captured; for most months a random sample of splittail was preserved in 4% formaldehyde solution. In the laboratory, preserved specimens were measured and weighed. Scales were removed from 210 randomly selected fish, from the area above the lateral line, caudad to the posteriormost point of the pectoral fin. These scales were mounted on glass slides and projected on a microfiche reader screen. Measurement and back-calculation follow Tesch (1968). A condition factor ($K = \text{wt}/\text{SL}(3 \times 10^6)$) was calculated for each fish (Tesch 1968). Gonads were removed and weighed; fecundity was determined by weighing three subsamples from each prespawning ovary, counting the number of ova present in each subsample, averaging, and multiplying by total gonad weight. Stomachs were removed; contents were separated, identified, and weighed. When possible, the total length of prey items was measured. In April 1979, fish were collected over a 24-h period for a feeding habit study. Fullness indices (Windell 1968) were calculated for each fish as an indirect measure of activity.

Several statistical techniques were used. One-sided t-tests were used to compare means between two groups; one-way analysis of variance was used to

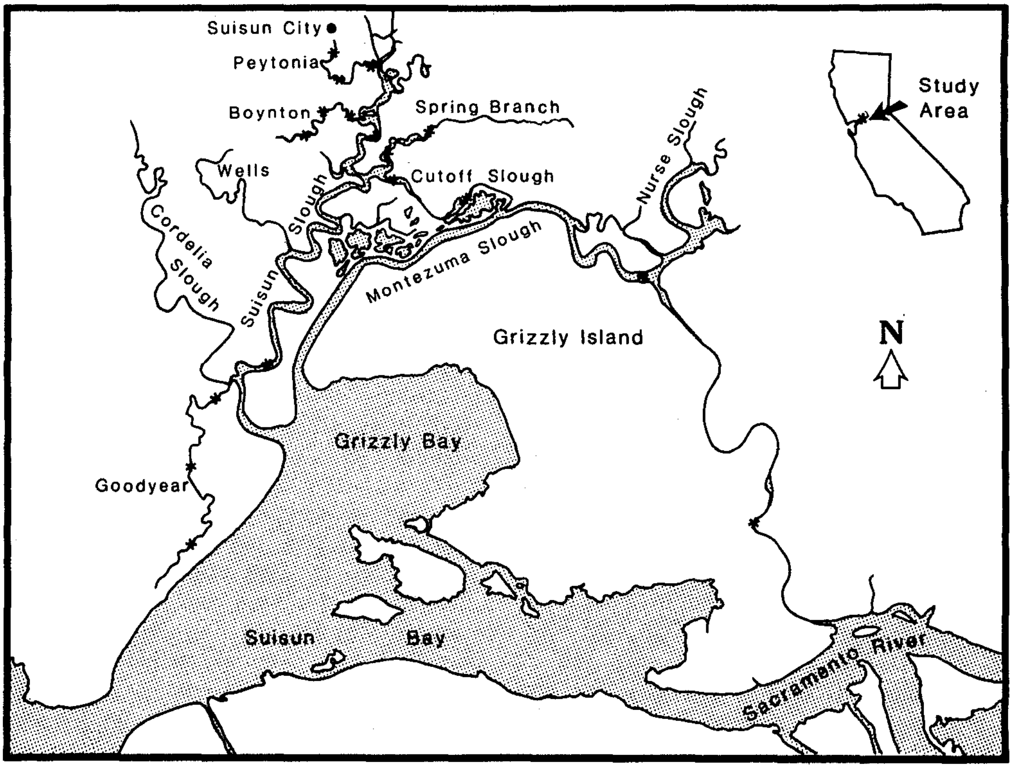

FIGURE 1.—Suisum Marsh, Sacramento-San Joaquin Estuary, Calif. Samples were taken from all sloughs identified. Monthly (1979) or bimonthly (1980-81) sample sites are designated (*). Each site represents two tows.

compare means among three or more groups (Remmington and Schork 1970). Wilcoxon sum of ranks or Kruskal-Wallis tests were used to compare indices (Sokal and Rohlf 1981). Regression lines were compared using techniques in Neter and Wasserman (1974).

Results and Comparisons

Age, Growth, and Condition

Young-of-the-year splittail appeared in samples in late May 1980 and early June 1981 with a mean of 32 mm SL in both years (Fig. 2). Lengths ranged from 23 to 54 mm. The back-calculated length for scale formation was 22 mm. Splittail grew at about 20 mm/mo through September, then that rate decreased to <5 mm/mo through February. In March fish began to grow again and added about 10 mm/mo during the next growing season. During the remaining 3 yr, fish added 5-7 mm/mo in length. These results were corroborated by back-calculating fish length from scales (Table 1). Annuli were formed in March 1979 and in late February 1980 in most specimens. Back-calculated growth rates were similar within the first and second age groups in 1979 and 1980 [age group 0: $F = 2.78 < F_{(0.95;2,12)}$; age group 1: $F = 0.8 < F_{(0.95;2,18)}$] but differed in the third age group [$F = 20.7 > F_{(0.95;2,16)}$]. Growth increments determined from back-calculation also were not significantly different between drought years (1976-77) and wet years (1978-80) in the first two age groups (age group 0: $t = 0.2 < t_{0.95}$; age group 1: $t = 1.0 < t_{0.95}$). These growth rates are similar to those found by Caywood (1974) in the upper Delta. The largest fish encountered in this study was 387 mm SL, which is approximately the

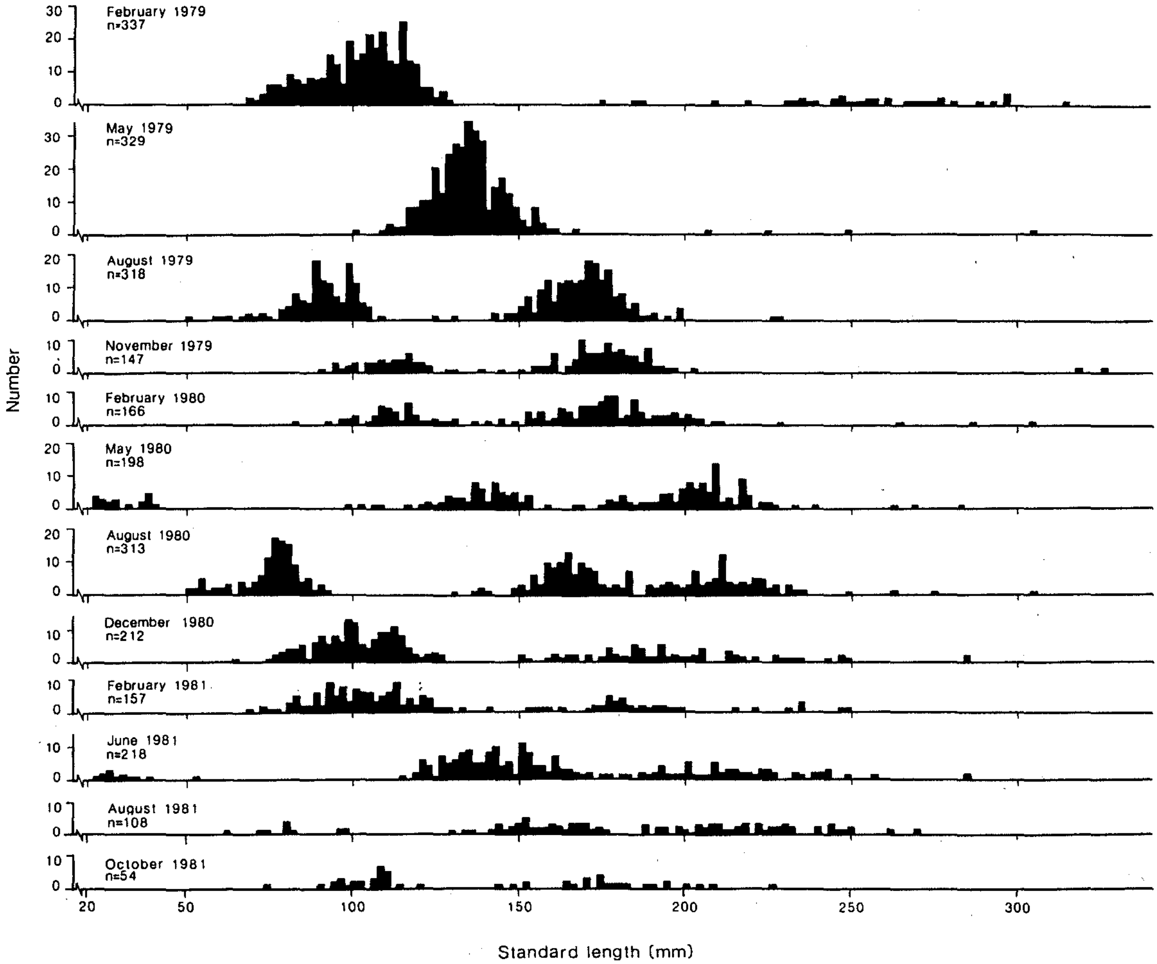

FIGURE 2.—Length (SL) frequency histograms of splittail samples, Suisun Marsh, Calif., 1979-81.

TABLE 1.—Mean back-calculated standard length (mm) and 95% confidence intervals at successive annuli for splittail taken in the Suisun Marsh, Calif., 1979-80.

Age group	n	I	II	III	IV	V
0	11					
1	86	111.8±2.7				
2	56	109.6±4.1	175.3±5.0			
3	29	110.8±4.5	170.2±5.3	218.9±5.0		
4	20	115.7±8.3	162.4±9.0	211.1±6.4	249.7±6.2	
5	8	109.4±12.2	167.3±15.2	213.4±12.4	253.1±14.1	286.8±12.4
Total	210					
$\bar{x}$		111.4	171.2	215.4	250.6	286.8
Increment			59.8	44.2	35.2	36.2

same maximum size encountered by Caywood (1974). No sex-related differences in growth were detected (t-test, $\alpha = 0.05$).

Monthly mean condition factors of mature fish varied little throughout the year (Table 2). Mean condition factors were significantly higher in females during the months preceding spawning (t-tests, $\alpha = 0.05$); sex-related differences were not significant in other months. The condition factors of immature fish generally were not significantly different from those of mature fish (t-tests, $\alpha = 0.05$). Between-year differences in mean condition factors were not significant in mature fish. However, immature fish of the 1978 year class (immediately postdrought) had mean condition factors significantly higher than those of the 1979 year class in March ($t = 4.81 > t_{0.99}$) and April ($t = 1.73 > t_{0.95}$).

TABLE 2.—Mean monthly condition factors of splittail from Suisun Marsh, Calif., 1979-80. No data are available for December.

Month	Female	Male	Immature
January	23.0	20.4	19.9
February	22.1	21.5	19.7
March	20.5	19.1	20.9
April	20.7	19.6	20.4
May	20.1	17.7	19.5
June	19.2	19.6	19.2
July	19.5	19.9	21.2
August	20.8	19.1	20.2
September	19.8	19.9	19.4
October			18.7
November	21.0	20.5	21.5

Reproductive Biology

Sacramento splittail were mature by their second winter, at minimum lengths of 180-200 mm; both males and females matured at the same age. Caywood (1974), however, noted that a small percentage of the males became sexually mature at the end of their first year and a small percentage of the females did not become mature until their third year. Gonadal growth began to increase in the autumn at about the same time somatic growth declined. Ovaries increased in size until April when they account for 18% of the body weight; testes reached their greatest size in March, April, and May, but never accounted for more than 2% of body weight. Splittail spawned in late April or early May in the marsh. Caywood (1974) found that spawning in the upper Delta occurred between early March and mid-May (in 1973 and 1974). Young-of-the-year fish appeared in our collections in late May or early June at 22-40 mm SL; at this size they had absorbed the yolk sac and were free swimming.

The fecundity (F) of 20 fish >175 mm SL collected from January through March ranged from 17,500 to 266,000 ova. Mean number of ova per gram body weight (Wt) was 408; in this sample the relationship between number of ova and body weight was $F = 457 (Wt)^{0.91}$ (log-log transformation $r = 0.546$; $F = 7.64 > F_{1,18}$ at $P = 0.05$). They averaged 600 ova/mm SL. The relationship between fecundity and SL was $F = 0.01 (SL)^{2.92}$ (log-log transformation $r = 0.536$; $F = 7.25 > F_{1,18}$ at $P = 0.05$). Fecundity increases with length and weight; both adequately predict fecundity.

The onset of spawning appears to be associated with increasing water temperatures and increasing day length; during the spawning period there were no changes in turbidity or salinity. The success of the spawn was correlated with river outflow (Table 3). Caywood (1974) captured ripe splittail in the upper end of a freshwater slough, in association with recently flooded vegetation. It is possible that splittail spawn on vegetation.

Year Class Strength

The percent of each year class in the catch varied (Fig. 3). The 1978 year class was extremely strong and dominant through the 1980 summer. The 1979 year class was never strong and never clearly dominated a monthly sample. Instead it remained

TABLE 3.—Splittail reproductive success, outflows of the Sacramento River at Chipps Island, Calif., and the correlations between them (* = $P < 0.05$, ** = $P < 0.01$). Abundance index is based on the strength of the year class, by percentage of sample (1 = weak, 3 = strong). The index is derived from the collection data of this study, from California Department of Fish and Game unpublished records, and Caywood (1974).

Year	Abundance index	Monthly mean flows at Chipps Island (in cubic feet per second × 10^3) Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sept.	Annual total
1969	3	5	11	26	123	159	94	69	65	47	13	12	20	644
1970	2	19	20	46	193	111	56	11	11	6	5	8	15	501
1971	2	13	26	85	64	34	32	37	26	21	12	13	20	383
1972	1	14	14	24	21	22	18	7	5	3	6	6	10	150
1973	2	12	26	27	11	102	77	22	12	7	5	6	11	318
1974	3	14	60	76	139	59	78	109	26	17	9	13	21	621
1975	2	19	24	28	17	57	67	35	29	23	11	10	13	333
1976	1	17	18	20	9	7	8	9	4	4	4	5	3	108
1977	1	4	4	4	4	5	3	3	4	3	3	3	3	43
1978	3	2	4	9	64	54	84	60	41	9	4	6	12	349
1979	2	10	11	9	30	44	37	14	13	5	5	4	5	187
1980	3	8	12	19	118	122	99	29	21	15	11	4	10	468
1981	1	6	5	12	13	20	21	10	9	5	5	2	4	112
Correlation of flow with index		−0.215	0.316	0.285	0.655*	0.720**	0.924**	0.786**	0.765**	0.600**	0.553*	0.511	0.682*	0.864**

relatively constant, representing 30-50% of the catch. The 1980 year class did not begin to dominate monthly samples until the disappearance of the 1978 year class in November 1980. The 1980 year class remained dominant from that date to the end of the study. The importance of the 1978 year class was indicated by the significant negative correlation ($P < 0.01$) between catch per minute and number of months that had elapsed since the beginning of our study.

Data for 1969 through 1974 from Caywood (1974) and for 1972 through 1978 from the California Department of Fish and Game (CDFG) (D. Kohlhorst unpubl. data) also show strong and weak year classes in splittail. These data sets are not strictly comparable with ours because different methods were used to capture the fish and because Caywood's samples were not from the Suisun Marsh. However, the consistency of the patterns in the data from two sources on the same years (1972-74, 1977-78) allowed us to rank year class strength from weak to strong, on a 1 to 3 scale (Table 3). Although the use of such a scale is likely to bias an analysis against finding significant correlations (Thorndike 1978), strong positive correlations ($P < 0.01$) were nevertheless found between year class strength and outflows in February, March, April, and May, as well as with total outflows. Splittail may spawn on flooded vegetation in March and April. Thus, wet years, such as 1974 and 1978, show extremely large year classes that remained abundant for several successive years. During drought years, such as 1976 and 1977, nearly complete year class failures occurred. CDFG collected only one young-of-the-year in 1976 and none in 1977. Our samples in January-March of 1978 yielded only large adults, none of which was from the 1976 or 1977 year classes.

Feeding

Splittail prey upon a variety of organisms but detritus dominates gut contents (Table 4). A small part of the gut content was unidentifiable animal matter. *Neomysis mercedis* was the dominant prey item, and crustaceans accounted for almost 85% by volume of the animal portion of the diet. *Neomysis mercedis* dominated the diet seasonally and through a diel cycle. Annelids, molluscs, insects, and fish completed the prey list; all were relatively unimportant components. These results are in contrast to those of Caywood (1974) who analyzed three collections of splittail from the upper Delta. He found the dominant animal matter in the stomachs to be clams (*Corbicula manilensis*), amphipods (*Corophium* spp.), copepods, and dipteran larvae and pupae. In a sam-

TABLE 4.—Prey items taken by 635 splittail collected from the Suisun Marsh, Calif., 1979-80.

Item	Frequency of occurrence (%)	Volume (%)	Volume less detritus/substrate (%)
Detritus/substrate	74	57	—
Polyclads	1	<1	<1
Polychaetes	3	2	3
Oligochaetes	1	<1	1
Molluscs	1	<1	<1
Crustaceans		35	
Harpacticoid copepods	15		7
Other copepods	7		2
Ostracods	6		<1
Cladocerans	1		1
Corophium	8		9
Other amphipods	1		2
Isopods	<1		1
Neomysis	37		59
Crangon	3		1
Palaemon	<1		<1
Insects		1	
Collembola	1		<1
Coleoptera	1		<1
Diptera	1		<1
Fish	1	2	3
Unidentified	6	3	7

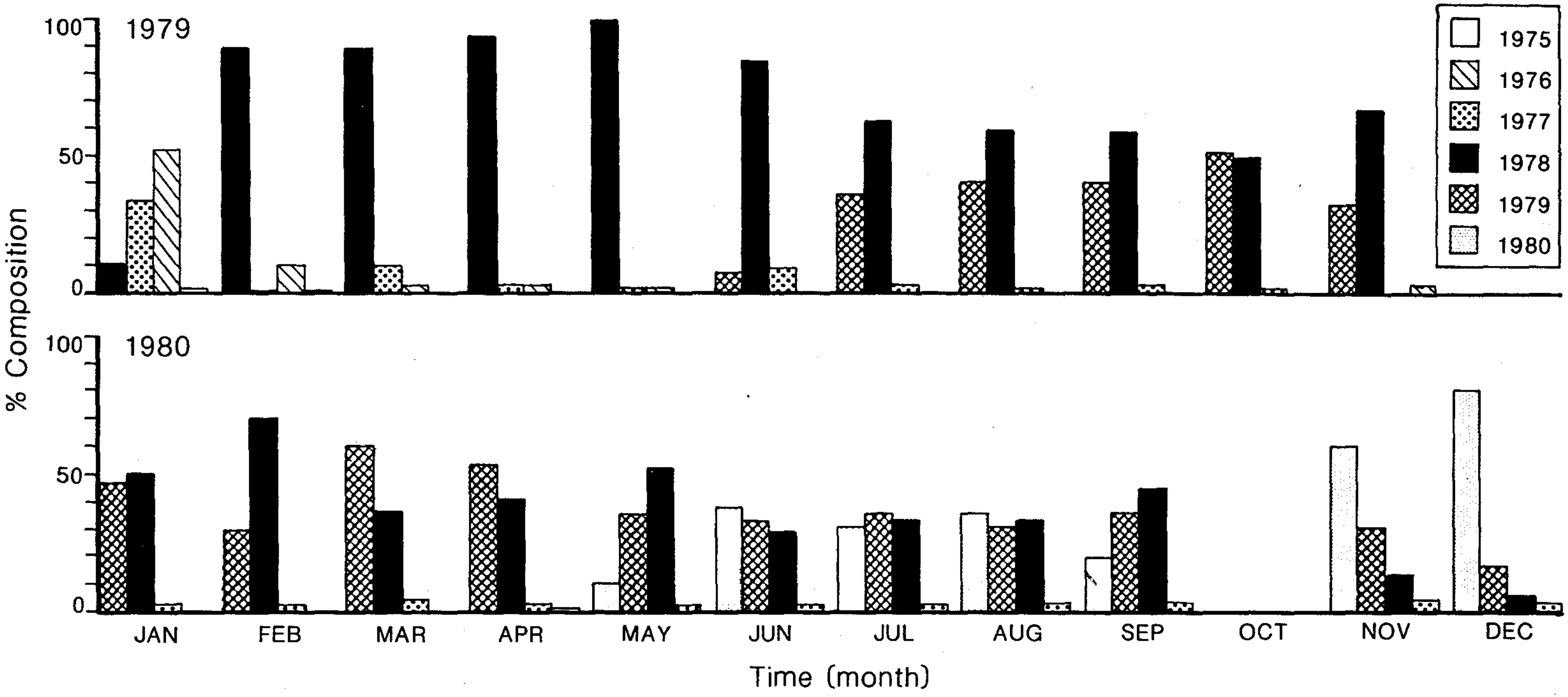

FIGURE 3.—Year class strength of splittail as percentage of sample, Suisun Marsh, Calif., 1979-80.

ple of splittail taken in a flooded pond, however, the main food was earthworms (*Lumbricus* sp.). The types of prey consumed indicate that splittail are bottom feeders. Feeding activity, inferred from fullness indices, was greatest during morning and early afternoon. The mean fullness index for fishes collected from 0600 to 1400 was 5.4, the mean index for fishes collected at 1800 and 2200 was 2.3. There was a seasonal difference in fullness indices of fishes collected midday (Kruskal-Wallis $\chi^2 = 28.9 > \chi^2_{0.99}$). The greatest mean index (2.8) was calculated from fishes collected during the summer. Mean autumn, winter, and spring indices ranged from 1.3 to 1.8.

Discussion

Sacramento splittail is a major component of the Sacramento-San Joaquin estuary fish association. Although abundant within its range, Sacramento splittail is now confined to the lower Delta and the main channel of the Sacramento River, a fraction of its former distribution (Moyle 1980). Population size fluctuates drastically from year to year and year class strength varies annually.

Within the Suisun Marsh, Sacramento splittail is dominant, by number, in the small cul-de-sac sloughs where it is associated with other native fishes (Moyle et al. 1982b). It is a benthic feeder with a limited range of prey types. *Neomysis mercedis*, the primary, nondetritus/substrate component of its diet, is abundant throughout the marsh and serves as a major food source of most other fishes in the marsh as well (Moyle and Daniels unpubl. data).

Sacramento splittail grows to moderate size, lives a relatively long life, and produces a large number of eggs per year. This is typical of native California cyprinids, particularly those found in the larger rivers and lakes (Moyle et al. 1982b). Such a pattern allows this annual spawner to fail to reproduce during environmentally unfavorable years. Unfavorable conditions, which, in the case of splittail, may include high salinities, low water levels, and/or high temperatures, are (or were) periodic and predictable. Particularly dry years occurred in 1972, 1976, and 1977. During these years splittail either failed to spawn or the spawn failed to develop; however, adults were present in the sloughs. A similar relationship between year class strength and outflows has been demonstrated for striped bass for the years 1959-76, although since then the relationship has not been as strong (Stevens 1980).

The small shallow sloughs lined with emergent vegetation inhabited by splittail offer protection from larger piscivorous fish and provide abundant sources of food. The periodic fall in water level simultaneously concentrates prey in the remaining shallow water and excludes large predatory fishes. Avian and mammalian predators are thwarted in all but the most shallow water by its turbidity.

Tolerance to relatively high salinities is unusual in cyprinids although tolerances similar to that of splittail have been recorded for carp, *Cyprius carpio*, and peamouth, *Mylocheilus caurinus* (Scott and Crossman 1973). It is likely that salinity tolerance in splittail increases somewhat with size, as many large (200 mm SL +) adults were collected from the more saline areas (>8‰).

Acknowledgments

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ROBERT A. DANIELS

New York State Museum
Biological Survey
Cultural Education Center, Room 3132
Albany, NY 12230

PETER B. MOYLE

Department of Wildlife and Fisheries Biology
University of California
Davis, CA 95616

LIFE HISTORY AND EXPLOITATION OF *MACROBRACHIUM FAUSTINUM* IN A TROPICAL HIGH-GRADIENT RIVER

Macrobrachium spp. are widely distributed in tropical freshwaters where they often support commercial or artisanal fisheries (Holthuis and Rosa 1965; Holthuis 1980). Studies of exploited *Macrobrachium* stocks have been carried out in large, low-gradient rivers in Liberia (Miller 1971), India (Rajyalakshmi and Ranadhir 1969), and the Philippines (Rasalan et al. 1969), but do not provide the bionomic information necessary for a quantitative assessment of the response of the stocks to exploitation. We know of no such study of a wild population of *Macrobrachium* species.

Macrobrachium faustinum inhabits freshwaters throughout the Caribbean area and in Florida (Chace and Hobbs 1969). In Jamaica it is the most common, eurytopic, freshwater shrimp, inhabiting both slow-flowing rivers and marshes in low lying areas, and fast-flowing streams in hilly regions (Hunte 1978). In the former, *M. faustinum* supports trap fisheries; in the latter it is fished either by hand or by turning over stones and allowing the shrimps to be washed into baskets. Although this fishery is pursued part time by children and men after work, these and other shrimps from small rivers are an important dietary component in an area where protein is scarce and expensive. In this paper we describe the bionomics of *M. faustinum* in a high-gradient stream (Cane River, Jamaica), and assess the effects of fishing on yield and population fecundity.

Description of Study Area

Cane River (lat. 17°58'N, long. 76°44'W) flows into the Caribbean Sea on an exposed south shore (Fig. 1). There is no protected bay at the river mouth, and the estuary is small. Altitude at the source is about 650 m, total length about 10.2 km, overall mean width 2.3 m, and mean depth about 9.4 cm. The width and depth vary markedly with seasonal rainfall. Cane River is a characteristic high-gradient stream in Jamaica. The water is clear and fast-flowing with a high oxygen content and a rocky bottom devoid of macrovegetation. Mean oxygen concentration along the river was 8.5 mg/l, mean pH 7.3. Mean temperature at the extreme lower limit of the river was 25.4°C with a mean daily range of 8.6°C and a mean seasonal range of 4.2°C. Corresponding temperature values at the extreme upper limits were overall mean 21.7°C, mean daily range 3.7°C, and mean seasonal range 3.4°C. The river bed consisted of stones, pebbles, gravel, sand, and mud over rock.

Materials and Methods

Shrimps were collected using a combined Surber sampler (Moffett 1936; Surber 1936) and Box sampler (Berg 1938). It consisted of a square frame of 0.25 m^2 with four legs protruding 5 cm below the frame and 40 cm above it. Net (1 mm square mesh) enclosed the sampler on three sides. Flaps of net under all four sides of the frame served as a seal between the frame and the substrate. On the fourth (downstream) side, there was a detachable collecting net 80 cm long with a mouth 50 × 40 cm (1 mm square mesh).