

ACKNOWLEDGMENTS

We thank R. Colby; D. Davis; M. Henry; D. McBride; M. McBride; G. Moor; and, especially, T. Jackson, of the CDFG Wildlife Protection Division, for making daily activity reports available to us. R. Anthes, T. Evans, L. Goehring, J. Santana, and P. Symons, of the CDFG Air Services Branch, assisted in conducting aerial counts of vehicles. R. Vernoy, of the CDFG Wildlife Management Division, was diligent in maintaining several decades of important records. C. Milliron, T. Jean Bleich, and T. John Bleich assisted with the figures and proofreading. M. Oehler, D. Yparaguire, and 2 anonymous referees provided helpful comments on the manuscript. This investigation was funded by the CDFG Game Bird Heritage Program. This is a contribution from the CDFG Upland Game Conservation Program, and is Professional Paper 003 from the Eastern Sierra Center for Applied Population Ecology.

LITERATURE CITED

- Beattley, J.C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856-863.
- Bleich, V.C., R.T. Bowyer, and J.D. Wehausen. 1997. Sexual segregation in mountain sheep: Resources or predation? *Wildlife Monographs* 134:1-50.
- Bleich, V.C., L.J. Coombes, and G.W. Sudmeier. 1982. Volunteer participation in California wildlife habitat management projects. *Desert Bighorn Council Transactions* 26:56-58.
- Bleich, V.C. and A.M. Pauli. 1990. Mechanical evaluation of artificial watering devices built for mountain sheep in California. Pages 65-72 *in*: G.K. Takamoto and S.J. Silver, editors. *Wildlife water development*. Nevada Department of Wildlife, Reno, Nevada, USA.
- Chambers, W.T. 1995. California Desert Plan 1976-1980. Pages 569-592 *in*: J. Laiting and P. G. Rowlands, editors. *The California desert: An introduction to natural resources and man's impact*. June Laiting Books and University of California Press, Riverside, California, USA.
- Conover, W.J. and R.L. Inman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* 35:124-129.
- Jaeger, J.R., J.D. Wehausen, and V.C. Bleich. 1991. Evaluation of time-lapse photography to estimate population parameters. *Desert Bighorn Council Transactions* 35:5-8.
- Thorne, R.F. 1982. The desert and other transmontane plant communities of southern California. Also 10:219-257.
- Torres, S.G., V.C. Bleich, and A.M. Pauli. 1993. An analysis of hunter harvest of mountain sheep in California, 1987-1992. *Desert Bighorn Council Transactions* 37:37-40.
- Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Received: 29 September 1998
Accepted: 5 November 1999

LIBRARY

Jones & Stokes Assoc., Inc.
2800 V St.
Sacramento, CA 95818
(916) 737-3000
FAX (916) 737-3030

JUVENILE DELTA SMELT USE OF SHALLOW-WATER AND CHANNEL HABITATS IN CALIFORNIA'S SACRAMENTO-SAN JOAQUIN ESTUARY

GEIR A. AASEN

California Department of Fish and Game
4001 North Wilson Way
Stockton, California 95205-2486
e-mail: gaasen@delta.dfg.ca.gov

Juvenile delta smelt, *Hypomesus transpacificus*, densities were significantly greater in shallow water in Honker Bay and Sherman Lake than in adjacent channels in 1993, indicating that they used shallow areas in bay and flooded island environments as nursery habitats. Densities and lengths were significantly greater on high than low tides in shallow water in Honker Bay, but not in the adjacent channel, suggesting that delta smelt moved tidally between Honker and Grizzly bays. Delta smelt densities did not differ between Honker and Grizzly bays. Delta smelt riverine environments of Montezuma Slough, the lower San Joaquin River, and Cache Slough, presumably because shallow areas were smaller and no embayments existed to retain delta smelt. Delta smelt may be larger in shallow water in Honker Bay and Sherman Lake because 1) fish in shallow water were older and consequently larger or 2) residence time was longer and foraging success was better, resulting in increased growth rates. Availability of shallow habitats to delta smelt increases in high-outflow years when hydrodynamic transport locates the delta smelt population downstream in Suisun, Grizzly, and Honker bays.

INTRODUCTION

The delta smelt, *Hypomesus transpacificus*, is a small planktivorous fish endemic to California's Sacramento-San Joaquin Estuary, where it ranges from San Pablo Bay upstream at least as far as the confluence of the American and Sacramento rivers and to Mossdale on the San Joaquin River (Moyle 1976). It is found from freshwater to 10‰ salinity, but is most abundant in brackish water near the 2‰ isohaline (Moyle 1976, Moyle et al. 1992). Delta smelt spawn from February to May in the lower Sacramento and San Joaquin rivers, including Cache Slough, and most larvae are carried downstream to the 2‰ isohaline, although some larvae remain upstream. Depending on river outflow, the 2‰ isohaline moves between different environments, including bays, flooded islands, and river channels (Moyle et al. 1992). Consequently, the characteristics of delta smelt nursery habitat change between dry and wet years (Moyle et al. 1992). In low-outflow years, most juvenile delta smelt inhabit channelized riverine environments close to upstream spawning areas in the lower Sacramento and San Joaquin rivers and Cache Slough. In high-outflow years, many

7 25900003C



Arranged by Stokes & SaunJ

juveniles are transported downstream from riverine environments to Suisun, Grizzly, and Honker bays.

Delta smelt populations declined in the mid-1980s and remained low thereafter, resulting in federal and state listing as a threatened species in 1993. Moyle et al. (1992) listed the causes of the decline as 1) drought conditions during the mid-1980s which relocated delta smelt from highly productive shallow habitats in Suisun, Grizzly, and Honker bays upstream to less productive and deeper river channel habitats and 2) high mortality rates due to entrainment by the State Water Project and the Central Valley Project in the south delta where water is diverted into the California Aqueduct and the Delta-Mendota Canal for municipal and agricultural use. Moyle et al. (1992) hypothesized that delta smelt sustain high populations in high-outflow years when their preferred salinities are located in Suisun Bay due to increased shallow-water habitat area. They supported their hypothesis by comparing shoal and channel delta smelt catches by the California Department of Fish and Game (CDFG) midwater trawl survey (MWT). Sixty-two percent of MWT delta smelt catch occurred at 3 stations <4 m deep in Suisun Bay; the remaining 38% was at 6 deep channel stations.

The objective of this study was to compare juvenile delta smelt use of shallow-water habitat in bay, flooded island, and riverine environments with adjacent channels to identify potential nursery habitats. Length distributions; water quality variables, including temperature and salinity; and tidal stage were also analyzed relative to use of these habitats. Habitat characteristics of bay and riverine environments were also contrasted.

METHODS

A 31.5 x 6.1-m miniature purse seine with 1.6-mm stretch mesh was used to capture juvenile delta smelt because it reduces net avoidance common to towed nets. Similar purse seine designs have effectively sampled postlarval northern anchovies, *Engraulis mordax* (Murphy and Clutter 1972). The purse seine was deployed off the bow of a 7-m boat, while backing in a circle at a speed of 1-1.5 m/s. Once deployed, the 2 ends were joined and the bottom of the net was pursed to form a bag. An optimal purse seine set sampled 471 m², although water currents and wind conditions made sets less than optimal. Seine sets per station varied from 1 to 4, depending on weather.

Five areas were sampled monthly during May, June, and July 1993, a high-outflow year. Shallow-water (<4 m deep) and adjacent channel (>4 m deep) sites were paired. Sampling occurred in Honker Bay and adjacent channel stations in the Suisun Bay channel, Sherman Lake and adjacent channel stations in the Sacramento and San Joaquin rivers, Montezuma Slough, the lower San Joaquin River, and Cache Slough (Fig. 1). Honker Bay is a shallow bay and Sherman Lake is a flooded island. Montezuma Slough, the lower San Joaquin River, and Cache Slough (MSJC) are riverine environments. Shallow-water sites and channels were sampled equally, although the number of stations sampled per area was sometimes limited by inclement weather.

All fishes collected were identified and fork length (FL) measured to the nearest millimeter. Fish >100 mm were immediately released, but all fish <100 mm were

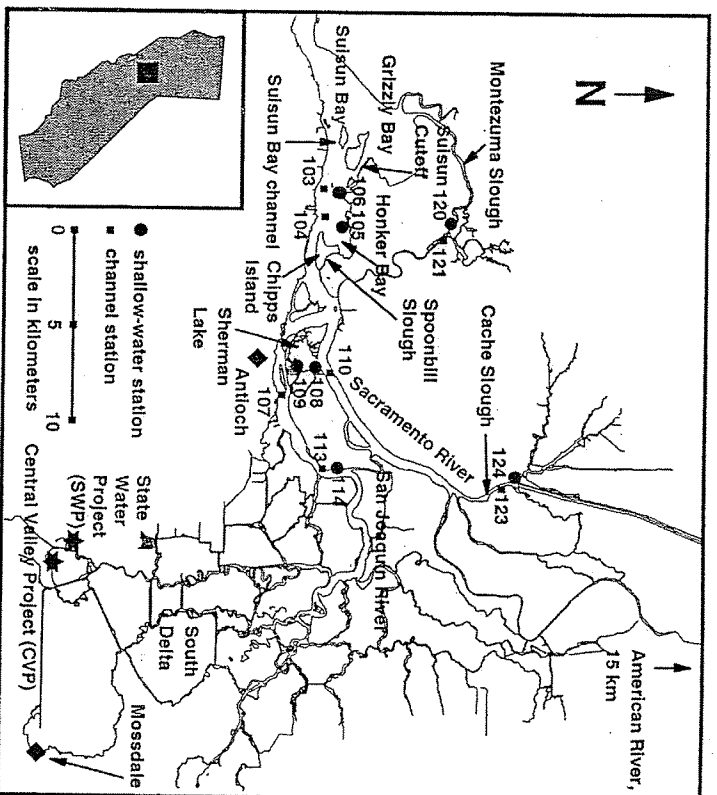


Figure 1. Delta smelt purse-seining stations in the Sacramento-San Joaquin Estuary.

preserved in sodium borate-buffered 10% formalin and returned to the laboratory for identification. Surface water temperature (°C) and electrical conductivity (EC, mS/cm) were recorded. Tidal stage and water depth were also recorded.

Delta smelt density was computed as the number of delta smelt per 1000 m³ of purse seine volume. Seine volume was recomputed when water depth was less than seine depth. No attempt was made to adjust seine volume for sub-optimal sets.

Differences in mean delta smelt density and fork length for sub-optimal sets between shallow-water and channel habitats were tested separately for each area sampled. Differences in mean delta smelt density and fork length between high (3 hours before and after high tide) and low tides (3 hours before and after low tide) were also tested for each sampling area. Density and length data from individual areas in MSJC were pooled to increase sample size if shallow water vs channel comparisons indicated that differences were not significant. Before comparisons, normality was tested with a Kolmogorov-Smirnov test. If log transformation did not normalize data, a nonparametric Mann-Whitney test was used. A t-test was used for normally distributed data. The significance level was 0.05. Statistical analyses were limited to 100 samples and samples where catch was >0.

RESULTS

A total of 893 juvenile delta smelt (18–49 mm FL) was caught from May to July in 180 purse seine sets. Mean delta smelt density was highest in Honker Bay (36.9/1000 m³), followed by Sherman Lake (28.5/1000 m³); density was lowest in MSJC (6.2/1000 m³).

Mean delta smelt densities were significantly greater in shallow water in Honker Bay ($U = 278.0$, $df = 1$, $P < 0.01$) and Sherman Lake ($U = 190.0$, $df = 1$, $P < 0.01$) than in adjacent channels, but not in MSJC ($U = 1288.0$, $df = 1$, $P = 0.15$) or any of its individual areas (all $P > 0.05$) (Table 1).

Delta smelt mean lengths also were significantly greater in shallow water in Honker Bay ($U = 12319.0$, $df = 1$, $P < 0.001$) and Sherman Lake ($t = 2.44$, $df = 21$, $P < 0.01$) than in adjacent channels, but in Cache Slough lengths were greater in the adjacent channel than in shallow water ($U = 1126.0$, $df = 1$, $P < 0.001$) (Table 1). Delta smelt mean lengths were not significantly different between shallow-water and channel areas in Montezuma Slough ($t = -0.96$, $df = 30$, $P = 0.35$). In the lower San Joaquin River, lengths could not be compared between shallow water and the adjacent channel because no delta smelt were caught in shallow water (Table 1).

Length frequencies for Sherman Lake and adjacent channels and Montezuma Slough were normally distributed, but length frequencies for Honker Bay and adjacent channels and Cache Slough were not. The length frequency for Honker Bay was negatively skewed by larger fish and the length frequency for Cache Slough was positively skewed by smaller fish (Fig. 2).

Surface temperature was not significantly different between shallow water and channels in any of the sampling areas (all $P > 0.05$) (Table 1). Surface EC was

Table 1. Comparison of mean shallow-water and channel delta smelt density and fork length, water temperature, and EC separately for each sampling area. Standard errors are in parentheses. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Bay		Riverine			
	Honker Bay	Flooded island Sherman Lake	Cache Slough	San Joaquin River	Montezuma Slough	
Density (no./1000 m ³)						
Shallow	71.1(29.1)**	46.9(9.0)**	6.8(3.8)	16.9(11.3)	0.0(0.0)	2.5(0.8)
Channel	5.7(2.7)	3.1(1.2)	5.6(1.7)	4.3(1.4)	1.3(0.8)	9.8(4.2)
Length (mm)						
Shallow	41.4(0.3)***	32.1(0.6)**	26.7(0.7)	No fish	29.7(1.1)	
Channel	37.9(0.8)	27.7(1.7)	32.7(1.7)***	30.0(2.0)	30.9(0.5)	
Temperature (°C)						
Shallow	20.0(0.6)	19.4(0.2)	19.6(0.3)	22.2(0.2)	20.0(0.3)	
Channel	20.5(0.5)	19.3(0.4)	19.3(0.3)	21.8(0.1)	20.5(0.2)	
EC (mS/cm)						
Shallow	1472.8(174.1)488.9(78.3)*		237.7(14.4)*	176.0(6.5)	1600.3(97.4)	
Channel	1497.6(215.4)241.4(36.4)		182.0(14.3)	197.5(14.2)	1757.5(146.6)	

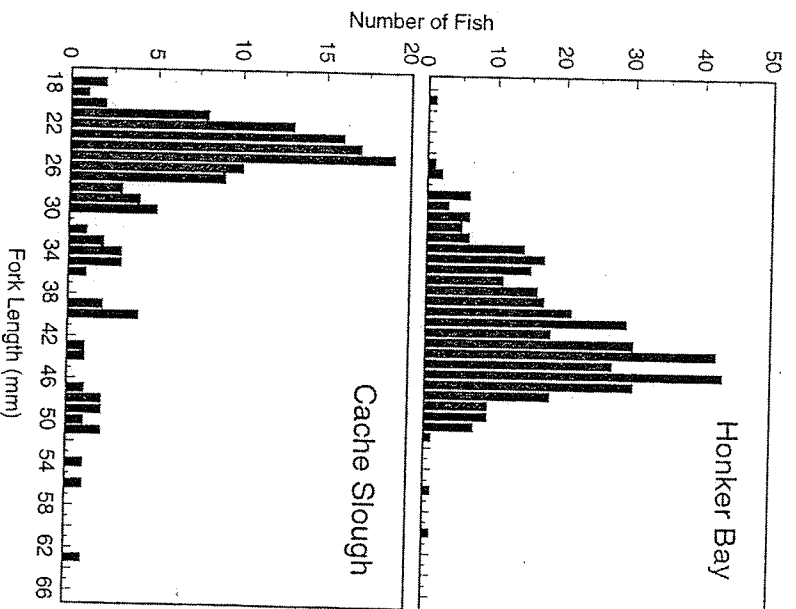


Figure 2. Length frequencies of delta smelt in Honker Bay and adjacent channels and Cache Slough. The length frequency for Honker Bay was negatively skewed by larger fish and the length frequency for Cache Slough was positively skewed by smaller fish.

significantly greater in shallow areas than in adjacent channels at Sherman Lake ($U = 169.0$, $df = 1$, $P < 0.05$) and Cache Slough ($U = 378.0$, $df = 1$, $P < 0.05$), but no significant differences were detected at the other areas (all $P > 0.05$). Surface temperature and EC for individual areas in MSJC were not pooled because of the distance between areas.

Mean delta smelt densities were significantly greater at high tide than at low tide in shallow water in Honker Bay ($U = 64$, $df = 1$, $P < 0.01$) and Sherman Lake ($U = 56$, $df = 1$, $P < 0.01$) (Table 2). Density differences associated with tidal stages were not statistically significant at shallow-water MSJC sites or any channel sites (all $P > 0.05$). As the channels adjacent to Sherman Lake were not sampled at low tide and some individual sites at MSJC were not sampled on either tide, no comparisons of delta smelt density at different tidal stages were possible at these 2 locations.

Delta smelt mean lengths were significantly greater at high tide than at low tide in shallow water in Honker Bay ($U = 1321.5$, $df = 1$, $P < 0.001$) and MSJC ($U = 343.0$,

Table 2. Comparison of high and low tide mean shallow-water and channel delta smelt density and fork length separately for sampling areas. Standard errors are in parentheses. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Density (No./1000 m ³)	Bay		Flooded Island		Riverine	
	Honker Bay	Sherman Lake	Combined (MSJC)	MSJC	MSJC	MSJC
Shallow	High	288.5(78.9)**	60.0(8.6)**	2.6(0.6)		
	Low	17.5(6.9)	0.0(0.0)	11.9(8.4)		
Channel	High	6.1(3.5)	3.1(1.2)	7.2(2.8)		
	Low	5.8(3.3)	No sample	3.2(0.9)		
Length (mm)	Shallow					
	High	43.1(0.2)***	32.1(1.2)	36.3(2.1)***		
	Low	95.2(1.0)	No fish	25.2(0.4)		
	Channel					
High		40.3(1.7)	27.7(1.7)	34.7(1.7)*		
	Low	38.7(1.0)	No sample	30.2(0.5)		

df = 1, $P < 0.001$) and in channels in MSJC ($t = -2.48$, df = 34, $P < 0.05$) (Table 2). Delta smelt in the channels adjacent to Honker Bay showed no tidal-associated differences in length ($U = 109.5$, df = 1, $P = 0.43$). As the channels adjacent to Sherman Lake were not sampled at low tide and some individual sites at MSJC were not sampled on either tide, no comparisons of delta smelt density at different tidal stages were possible at these 2 locations.

DISCUSSION

The difference in delta smelt use of shallow water between bay (Honker Bay), flooded island (Sherman Lake), and riverine (MSJC) environments may best be explained by tidal flux and flow patterns being modified by geomorphological features (Weinstein et al. 1980, Miller 1988). The greater mean density and length of delta smelt in shallow Honker Bay than in the adjacent Suisun Bay channel and the greater mean density and length at high than low tide in Honker Bay, but not the channel, suggest that delta smelt moved in and out of Honker Bay with the tide, but not from the Suisun Bay channel. Hydrodynamics studies of this area have found that Honker Bay fills and drains through Suisun Cutoff (from and to Grizzly Bay) and that water in Honker Bay on an ebb tide is replaced with water from the lower Sacramento and San Joaquin rivers through Spoonbill Slough and around the tip of Chipps Island (J. Burau, U.S. Geological Survey, personal communication). Also, the water mass in the adjacent Suisun Bay channel moves upstream and downstream with the tide in the channel and little exchange occurs with Honker Bay (J. Burau, personal communication). Thus, delta smelt in Honker Bay likely move with the ebb tide through Suisun Cutoff

into Grizzly Bay and are carried back into Honker Bay with the flood tide. This explains why the large concentration of delta smelt sampled at high tide in Honker Bay was not found there or in the adjacent channel at low tide. Higher densities of delta smelt in Honker Bay may be related to the geomorphology of the bay, so that more fish come into the bay from upstream on the ebb tide than leave it with the flood tide. Thus, delta smelt are "trapped" in Honker Bay.

To further investigate the hypothesis that high densities of delta smelt are exchanged between Honker and Grizzly bays with the tide, delta smelt abundance data from the 1993 summer townet survey, designed to measure annual delta smelt and striped bass abundance indices in June and July (Stevens 1977; CDFG, unpublished data), were examined. Townet sampling in Honker and Grizzly bays in 1993 always occurred at low tide. Townet estimates of delta smelt density at low tide in Grizzly Bay were high (mean catch/low = 11.2, SE = 4.6), whereas delta smelt density estimates in Honker Bay at the same tidal stage were low (mean catch/low = 3.0, SE = 1.6). This supports the hypothesis that water with high delta smelt density moves with the ebb tide into Grizzly Bay and the previously described hydrodynamic studies indicate that much of that water flows back into Honker Bay with the flood tide.

Delta smelt were likely transported into Sherman Lake from the Sacramento and San Joaquin rivers by the flood tide and became concentrated there in higher densities by the enclosure of the breached island; some were transported out of the lake with the ebb tide. However, drifter studies from this area have shown complex flow patterns between Sacramento and San Joaquin rivers and Sherman Lake (J. Burau, personal communication) and, consequently, it would be difficult to track fish movement without simultaneous hydrodynamic studies.

These results are consistent with other studies that have shown that estuarine fishes, particularly juveniles, commonly use tidal flux to move between habitats (Miller and Dunn 1980). Flood tides transported spot, *Leiostomus xanthurus*, and flounders, *Paralichthys* spp., to nursery areas in tidal creeks and over shoals in the Cape Fear Estuary, North Carolina (Weinstein et al. 1980). Pacific coast fishes, including chinook salmon, *Oncorhynchus tshawytscha*, and chum salmon, *O. keta*, also use flood tides to move to nursery areas (Healey 1982).

In the riverine environment, densities were not significantly different between shallow water and channels. I hypothesize that delta smelt move with tides in the channel and across shallow areas, and are not retained in shallow water due to the lack of embayments. Also, shallow areas in Cache Slough, Montezuma Slough, and the San Joaquin River are considerably smaller than in Honker Bay or Sherman Lake, which could affect retention rates of fish.

Temperature and salinity had no apparent effect on use of shallow and deep water by delta smelt as values were within tolerance limits and, except for EC in Sherman Lake and Cache Slough, were not significantly different between shallow-water and channel sites.

Delta smelt were larger in shallow water in Honker Bay and Sherman Lake than in adjacent channels, but were larger in the channel than shallow areas in Cache

Slough. Delta smelt in the shallow water of Honker Bay and Sherman Lake may be larger than in the channels because 1) entrapped fish may stay longer in shallow-water areas and consequently be older and larger or 2) fish in shallow water had a more abundant food supply, resulting in greater growth. Grimaldo et al.¹ (1998) reported that delta smelt in Suisun Bay in 1996 were older and larger than individuals in the Sacramento and San Joaquin rivers. Moyle et al. (1992) hypothesized that delta smelt growth rates are higher in Suisun Bay than the Sacramento and San Joaquin rivers due to the use of highly productive shallow-water areas resulting in increased feeding. Foraging success (percent stomachs with food) for 25-mm delta smelt in 1995 and 1996 was higher in shallow water in Grizzly and Honker bays than in the Suisun Bay channel (Lott² 1998). Future studies will examine age structure of delta smelt as an aid in understanding age and growth relative to area and chemical-physical parameters.

The larger size of delta smelt in the channel than in shallow water in Cache Slough is difficult to explain. Larger delta smelt migrating downstream from their early nursery area in the Cache Slough region in June and July may have increased mean size in the channels. Larger delta smelt downstream in Honker Bay are consistent with this explanation.

A significant increase in the availability of shallow habitats occurs in high-outflow years when the population is located in the Suisun Bay area (including Grizzly and Honker bays). Some estuarine species increase in high-outflow years due to a greater area of nursery habitat and larger populations of zooplankton available for forage (Sutcliffe 1973). Only 33% of potential delta smelt nursery habitat, mostly located in channelized riverine environments, is available during a typical low-outflow year (Moyle et al. 1992; CDFG, unpublished data). Thus, a significant relationship exists between the number of days the 2‰ isohaline is located in Suisun Bay from February through June and delta smelt abundance in the fall (Herbold³ 1994). In 1993, the 2‰ isohaline was located in Suisun Bay during the entire period from February through June, resulting in the 6th highest delta smelt abundance observed during 1967-1993.

In conclusion, shallow-water areas in Honker Bay and Sherman Lake are important delta smelt nursery habitats. Delta smelt were larger in Honker Bay and Sherman Lake than adjacent channels, although it is uncertain if they were older fish or had greater growth rates. Delta smelt use of shallow-water nursery habitats in Montezuma Slough, the San Joaquin River, and Cache Slough was not as apparent as in Honker Bay and Sherman Lake.

¹ Grimaldo, L., B.S. Ross, and D. Sweetnam. 1998. Preliminary results on the age and growth of delta smelt (*Hypomesus transpacificus*) from different areas of the estuary using otolith microstructure analysis. Interagency Ecological Program for the Sacramento-San Joaquin Estuary Newsletter, Winter 1998:25-28.

² Lott, J. 1998. Feeding habits of juvenile and adult delta smelt from the Sacramento-San Joaquin River Estuary. Interagency Ecological Program for the Sacramento-San Joaquin Estuary Newsletter, Winter 1998:14-20.

³ Herbold, B. 1994. Habitat requirements of delta smelt. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary Newsletter, Winter 1995:18-19.

ACKNOWLEDGMENTS

I thank R. Farrell, Z. Harris, R. Hagins, and K. Malchow for their reliable field work. Valuable help in developing the sampling design was provided by D. Sweetnam. I thank J. Orsi, D. Stevens, D. Kohlhorst, L. Miller, B. Herbold, and L. Smith for providing their helpful comments on the manuscript. Special thanks to L. Lynch for her accurate lab work.

LITERATURE CITED

- Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: The life support system. Pages 315-342 in: V.S. Kennedy, editor. Estuarine comparisons. Academic Press, New York, New York, USA.
- Miller, J.M. and M.L. Dunn. 1980. Feeding strategies and patterns of movement in juvenile estuarine fishes. Pages 437-448 in: V.S. Kennedy, editor. Estuarine perspectives. Academic Press, New York, New York, USA.
- Miller, J.M. 1988. Physical processes and the mechanism of coastal migrations of immature marine fishes. American Fisheries Society Symposium 3:68-76.
- Moyle, P.B. 1976. Inland fishes of California. University of California Press, Berkeley, California, USA.
- Moyle, P.B., B. Herbold, D.E. Stevens, and L.W. Miller. 1992. Life history and status of delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67-77.
- Murphy, G.I. and R.I. Clutter. 1972. Sampling anchovy larvae with a plankton purse seine. Fishery Bulletin 70:789-798.
- Stevens, D.E. 1977. Striped bass (*Morone saxatilis*) monitoring techniques in the Sacramento-San Joaquin Estuary. Pages 91-109 in: W. Van Winkle, editor. Proceedings of the conference assessing the effect of power-plant-introduced mortality on fish populations. Pergamon Press, New York, New York, USA.
- Sutcliffe, W.H., Jr. 1973. Correlations between seasonal river discharges and the local landings of American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence. Journal of the Fisheries Research Board of Canada 30:856-859.
- Weinstein, M.P., S.L. Weis, R.G. Hodson, and L.R. Gerry. 1980. Retention of three taxa of postlarval fishes in a intensively flushed tidal estuary, Cape Fear River, North Carolina. Fishery Bulletin 78:419-436.

Received: 22 January 1999

Accepted: 3 February 2000