

Assessing nursery habitat quality for native smelts (*Osmeridae*) in the low-salinity zone of the San Francisco estuary

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Habitat quality was assessed for two native osmerids, delta smelt *Hypomesus transpacificus* and longfin smelt *Spirinchus thaleichthys*, between two distinct nursery areas located in the low-salinity zone of the San Francisco estuary. The relationship between several variables was investigated including fish density, fish size, feeding success and the general condition of larvae as well as juveniles for both species. The nursery habitats that were evaluated included the North and South Channels of Suisun Bay. The results showed higher densities of zooplankton and decreased water velocities for the North Channel when compared to the South Channel. The dominant prey item was calanoid copepod *Pseudodiaptomus forbesi* for both species although longfin smelt residing in the North Channel also included another copepod in their diets, *Acanthocyclops* spp. In both locations, delta smelt fed predominantly during daytime flood tides, while longfin smelt feeding appeared to continue into the night hours. When both locations were compared, delta smelt in the North Channel exhibited higher densities, larger sizes, increased somatic condition and larvae <15 mm standard length demonstrated greater feeding success. Longfin smelt, exhibited similar densities, feeding success and size distributions between both channels, but generally showed poorer somatic condition for the South Channel, potentially due to energetic costs associated with documented vertical migration behaviour. Overall, the physical conditions of the North Channel provided superior habitat for both species, while the South Channel afforded only marginal habitat for longfin smelt and very poor habitat for delta smelt. Therefore, the North Channel of Suisun Bay acts as critical nursery habitat by providing better feeding and growing conditions leading to increased health and survival for both species.

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INTRODUCTION

Estuaries have long been thought to harbour vital nursery habitats for young fishes by providing abundant prey resources, while affording protection from predators (Bruton, 1985; Boehlert & Mundy, 1988; Day *et al.*, 1989). Evidence for the role of estuarine nurseries is implied in numerous studies describing

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complex behaviours exhibited by larvae to locate and maintain position within estuaries (Laprise & Dodson, 1989; Bennett *et al.*, 2002), as well as accounts of higher biomass or densities within these habitats as compared to nearby areas. To fully evaluate the role of nursery habitats in fish recruitment, however, the benefit of increased growth, survival and connectivity to adult populations must also be taken into consideration (Beck *et al.*, 2001). Accurate assessment of nursery habitats is crucial for the protection of these habitats for threatened and endangered species as well as for the management of fisheries.

The landward margin of an estuary is often a location of high biological productivity and physical entrainment of sediments; this region is called the estuarine turbidity maxima (ETM) or low-salinity zone (LSZ, salinity 2–6). The role of the ETM as nursery habitat for young fishes has been recognized for several major estuaries. In the Chesapeake Bay estuary, striped bass *Morone saxatilis* (Walbaum) and white perch *Morone americana* (Gmelin) larvae are retained within the ETM by actively maintaining their vertical position near the bottom of the estuary (North & Houde, 2001). Similarly, larval rainbow smelt *Osmerus mordax* (Mitchill) exhibited tidally oriented vertical migrations in the St Lawrence River, to maintain their position at the landward margin of the estuary, where they also showed increased feeding success, growth rates and survival (Laprise & Dodson, 1989; Davin & Dodson, 1990; Sirois & Dodson, 2000a, b).

In the San Francisco estuary (SFE), zooplankton and young fishes are found in relatively high abundances in the LSZ (Bennett *et al.*, 2002; Kimmerer *et al.*, 2002). The native longfin smelt *Spirinchus thaleichthys* (Ayres) and introduced striped bass *M. saxatilis* larvae have been shown to undergo tidally oriented vertical migrations within the LSZ, presumably for position maintenance (Bennett *et al.*, 2002). Moreover, longfin smelt exhibited the ability to modify migration behaviour in different areas under different hydrodynamic conditions, thus highlighting the role of larval behaviour in the retention strategies of young fishes (Bennett *et al.*, 2002). Zooplankton in the LSZ have also been shown to undergo reverse-diurnal vertical migrations along with delta smelt *Hypomesus transpacificus* McAllister in the North Channel of Suisun Bay (Bennett *et al.*, 2002; Kimmerer *et al.*, 2002). Thus, the ability to migrate is a conspicuous characteristic of fishes utilizing the LSZ habitat, however, the mechanisms responsible for variability in migration behaviours remains unclear as well as the potential benefits gained by maintaining position in this area.

Seasonal and interannual variability in freshwater outflow regulates the position of the LSZ, such that it can occur as far landward as the lower Sacramento River and delta and as far west as the Carquinez Strait under high outflow. The seasonal mean position of the LSZ within Suisun Bay is currently used as a management tool to enhance the recruitment success of numerous fish species because annual abundances of several macro-zooplankton and fishes are associated with a seaward position of LSZ and moderate to high outflow (Stevens & Miller, 1983; Jassby *et al.*, 1995; Kimmerer, 2002). For example, the recruitment success of longfin smelt and striped bass is associated with higher freshwater outflow and thus seaward position of the LSZ during spring. Delta smelt, however, do not exhibit this relationship (Jassby *et al.*, 1995). Although their recruitment is successful only in years of moderate outflow when

shallower, slower water habitats like those of the North Channel in Suisun Bay are accessible, the factors determining delta smelt year-class success remain unclear (Bennett, 2005). Nevertheless, there does appear to be a link between the recruitment success for delta smelt and the availability of shallow-water habitats rather than freshwater outflow alone (Aasen, 1999; Bennett *et al.*, 2002; Kimmerer, 2002).

In this study, the importance of two different subregions in the LSZ as nursery habitat is assessed for two native osmerids in the SFE. To assess the nursery habitat hypothesis, stomach fullness index, general somatic condition and density are compared in relation to physical condition and migration strategies employed by longfin smelt and delta smelt between the North and South Channels of Suisun Bay in the SFE (Fig. 1). Observations on the feeding ecology of delta smelt and longfin smelt in the LSZ are also provided. The data indicate that fishes exhibit significant differences in these characteristics between the two subregions allowing for the identification of critical nursery habitat for the two species within the LSZ.

METHODS

The SFE, one of the most morphologically diverse and dynamic estuaries in the U.S., is formed by the Sacramento and San Joaquin Rivers, which create a large delta at their confluence. Throughout the year, huge volumes of fresh water are exported from the delta to support significant agriculture and the growing human population in California. This is largely a result of climatic conditions where *c.* 80% of the precipitation occurs during the winter months and north of the SFE, whereas *c.* 80% of the demand for fresh water occurs south of this system. Moreover, there is high annual variability in

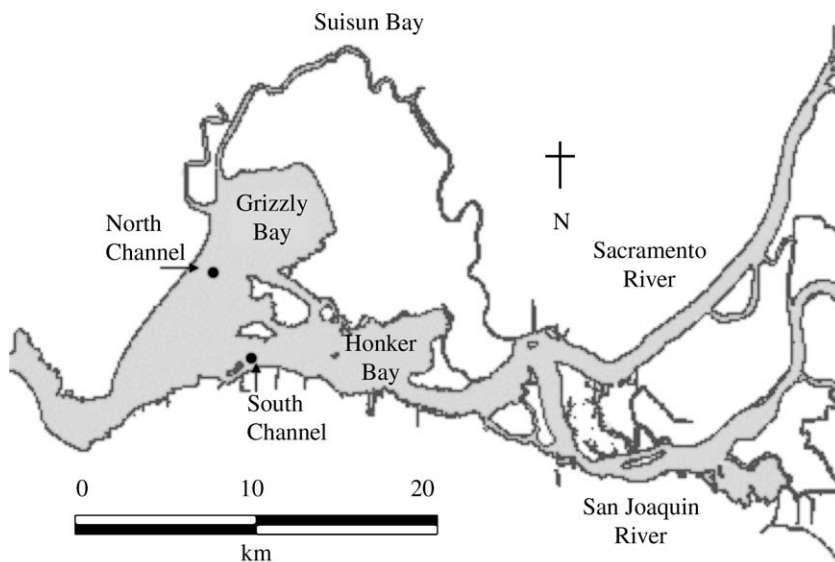


FIG. 1. Northern San Francisco estuary–Suisun Bay and location of the stations sampled in June 1996 cruises in the North and South Channels.

the amount of precipitation and thus freshwater outflow. Together, these conditions result in an estuary that is hydrologically irregular (Nichols *et al.*, 1986; Monismith *et al.*, 1996). Within the greater SFE, Suisun Bay is located c. 15 km west of the confluence of the Sacramento and San Joaquin Rivers, and c. 65 km east from the entrance to the estuary at the Golden Gate Bridge, San Francisco. Suisun Bay is characterized by moderate tidal currents (c. 1 m s^{-1}), a tidal range of 1.75 m and variable bathymetry. During the spring and summer months under moderate outflow conditions, the LSZ is typically located in Suisun Bay where it forms multiple estuary turbidity maxima of various origins (Schoellhamer, 2001). Due to the variable bathymetry, tidal forcing and freshwater outflow, the North and South Channels within LSZ appear to be distinct habitats.

PHYSICAL CONDITIONS

A complete description of the prevailing conditions for the North and South Channels during sampling is provided by Bennett *et al.* (2002). The South Channel, located along the southern end of Suisun Bay, generally exhibited swifter and colder water conditions than the North Channel. Depths between the two sites were similar; in the South Channel, depths ranged from 8–12 m, while in the North Channel depths ranged from 7–11 m. Unlike the South Channel, however, the North Channel site was adjacent to a large, warm and shallow bay: Grizzly Bay. Gravitational circulation was not detected during the study at either location.

SAMPLING

Sampling was carried out for larval and juvenile delta smelt and longfin smelt as well as physical variables in the LSZ during three cruises in June 1996 (Bennett *et al.*, 2002). Sampling took place at two fixed stations. The R/V Turning Tide was located in the North Channel at station M during cruise A (3–4 June) as well as station S during cruise B (13–14 June) and cruise C (20–21 June); the R/V San Carlos was located at station A3 in the South Channel (Fig. 1). A detailed description of the sampling programme and physical characteristics of each station is provided by Bennett *et al.* (2002) and Kimmerer *et al.* (2002). Sampling occurred hourly over an entire tidal cycle (c. 30 h) using 75 cm diameter, 200 μm mesh net. The net was placed at three intervals, 1 m below the surface, at mid-depth and near bottom. Each net was fitted with a flow-meter for measuring the volume of water sampled. With this sampling design, the two isohaline advected tidally past each station allowing for samples of larval fishes to be collected within and at the margins of the LSZ. Vertical profiles of salinity and temperature were monitored with a Seabird SBE-19 CTD before and after each deployment of the nets. Currents were continuously monitored with fixed acoustic doppler current profilers at stations M and S in the North Channel and at station A3 in the South Channel (Fig. 1).

Contents of the nets were fixed in 5–10% formaldehyde and subsequently stored in 70% ethanol. All fishes were removed from the samples, identified (J.C.S. Wang, unpubl. data) and measured with a dissecting scope fitted with an ocular micrometre (standard length, L_S , $\pm 0.1 \text{ mm}$). As a quality control measure, all larval smelt ($<15 \text{ mm}$) were verified for species (J.C.S. Wang, pers. comm.). Samples of delta smelt and longfin smelt were sub-sampled for gut content analysis from each cruise. For delta smelt $<20 \text{ mm } L_S$, the entire gut was extracted as the digestive tract was not fully formed. Zooplankton contents from the entire digestive tract were counted and identified to species where possible. For individuals $>20 \text{ mm } L_S$, only the stomach was dissected and again, zooplankton were counted and identified (Lott, 1998). All longfin smelt in this study were juveniles $>20 \text{ mm } L_S$, with developed stomachs; therefore, stomach contents were quantified as above. In addition, a sub-sample of 50 longfin smelt and delta smelt from each sampling location were dried for 48 h in a convection oven and weighed to the nearest mg (M_D) with a Mehtler 4500 balance.

ANALYTICAL METHODS

The gut fullness index was calculated as the ratio of individual gut fullness (number of prey items) in relation to the maximum gut fullness per L_S group (mm). This allowed for standardization of fullness over ontogenetic stages (Knight & Margraf, 1982; Herbold, 1986). After sorting and identifying zooplankton from the gut contents, the gut fullness index was calculated and the feeding incidence was quantified (individual with at least one prey item in the gut) as a measure of feeding success for $n = 347$ delta smelt from cruises (A to C) and for $n = 307$ longfin smelt from cruises A and C. Delta smelt were separated into two groups based on their ontogenetic stage. Delta smelt <15 mm L_S , or pre-swimbladder inflation, were distinguished from fish >15 mm L_S , or those having a developed swimbladder. All longfin smelt were similar in size and ontogenetic stage and were thus not classified into distinct groups. Diet composition for each species was quantified by reporting the per cent for each prey item consumed as a percentage of the total number of prey items (%M). Condition factor (K) was calculated as $K = M_D L_S^{-1}$ and used as a proxy to growth (Busacker *et al.*, 1990). Indices of zooplankton and detritus abundance were also calculated by quantifying the volume of zooplankton and detritus material sampled during each tow per litre of water sampled (1 m^{-3}) and then standardized to $10\,000 \text{ m}^3$ of water.

The distribution of all measured variables was examined by first plotting frequency distributions and then applying transformations where appropriate to achieve normality. The t -tests were employed to compare environmental conditions and K on non-transformed data. A two-way ANOVA was used to examine density differences between the North and South Channels for lifestages (<15 mm and >15 mm L_S) and cruises (A to C) for delta smelt and a one-way ANOVA for longfin smelt density for each cruise. To evaluate gut fullness for delta smelt, an ANOVA was conducted using general linear models (GLM) in SYSTAT 10.0 comparing the main effects; channel (North and South), cruises (A to C), lifestages (<15 mm and >15 mm), depth (surface and bottom) and the interaction terms of all main effects. Bonferroni corrections were applied to examine significance of interaction terms. For longfin smelt, gut fullness was analysed by ANOVA in GLM with main effects; channel (North and South), cruises (A to C), lifestages (<15 mm and >15 mm), depth (surface and bottom) and the interaction terms of all main effects. Bonferroni corrections were applied to examine significance of interaction terms. A two-way ANOVA was used to examine K for delta smelt with lifestages (<15 mm and >15 mm L_S) and cruises (A to C), and a one-way ANOVA for longfin smelt comparing K between cruises A and C only. Mean L_S between the North and South Channels were analysed with t -tests on $\log_{10}$ -transformed data. A two-way ANOVA was then used to evaluate the influence of photoperiod and tide stage on the feeding rhythm for delta smelt and longfin smelt for both regions combined.

RESULTS

Salinity ranged from 0.1 to 6.0 in the North Channel and from 0.0 to 5.0 in the South Channel. Mean daily water temperatures were also similar, fluctuating from 17.9 to 21.0°C in the South Channel and from 18.5 to 22.0°C in the North Channel (Table I). Slight differences in salinity and temperature, although statistically significant, did not seem to be biologically important for the two smelt species. Turbidity, as measured by volume of detrital material, ranged from 2.55 to 4.47 l per $10\,000 \text{ m}^3$ in the North Channel and from 1.94 to 3.88 l per $10\,000 \text{ m}^3$ in the South Channel but were not significantly different ($P > 0.05$). Mean water velocities ranged from 18 to 69 cm s^{-1} in the North Channel and from 26 to 94 cm s^{-1} in the South Channel. Each site was primarily dominated by ebb tides with residual currents being primarily seaward throughout the study period (J. R. Burau, unpubl. data). Tidal flows

TABLE I. Comparison of environmental conditions in the North and South Channels of Suisun Bay (means from cruise A, 3–4 June 1996; cruise B, 13–14 June 1996; cruise C, 20–21 June 1996) in the San Francisco estuary low-salinity zone

Variable	North Channel		South Channel		<i>P</i>
	Mean $\pm$ S.D.	<i>n</i>	Mean $\pm$ S.D.	<i>n</i>	
Detritus (l per 10 000 m ³)	3.51 $\pm$ 0.96	69	2.91 $\pm$ 0.97	81	0.132
Zooplankton (l per 10 000 m ³)	2.53 $\pm$ 0.87	71	1.48 $\pm$ 0.84	51	<0.001
Temperature (°C)	20.17 $\pm$ 0.70	86	19.49 $\pm$ 0.91	86	<0.001
Salinity	0.73 $\pm$ 0.45	82	0.56 $\pm$ 0.47	82	0.017
Water velocity (cm s ⁻¹)	43.78 $\pm$ 25.13	85	59.84 $\pm$ 44.62	85	0.001

in the North Channel flushed between the shallow subembayment of Grizzly and the Honker Bays through the Suisun Cutoff (Fig. 1) (Bennett *et al.*, 2002). Cross-channel circulation occurred only minimally between each region of the LSZ (Schoellhamer, 2001).

DENSITY AND SIZE DISTRIBUTION

Longfin smelt density was generally similar between the North and South Channels (ANOVA, $P > 0.05$) (Table II). Although they decreased in density from cruises A to B, longfin smelt densities increased again during cruise C (ANOVA, $P \leq 0.001$). Mean L_S for longfin smelt were also similar between the North and South Channels (*t*-test, $P > 0.05$) (Fig. 2). Delta smelt, however, showed a more distinctive pattern with higher densities in the North Channel

TABLE II. ANOVA results for density comparisons for longfin smelt, larval delta smelt (<15 mm) and juvenile delta smelt (>15 mm) between the North and South Channels of Suisun Bay

Source	SS	d.f.	MS	<i>F</i>	<i>P</i>
Longfin smelt density					
Channel	1.500	1	1.500	3.410	0.067
Cruise	11.426	2	5.717	12.993	<0.001
Channel $\times$ cruise	0.550	2	0.275	0.625	0.54
Error	71.28	162	0.82		
Delta smelt <15 mm density					
Channel	2.862	1	2.862	133.542	<0.001
Cruise	0.569	2	0.284	13.268	<0.001
Channel $\times$ cruise	0.542	2	0.371	12.657	<0.001
Error	3.47	162	0.02		
Delta smelt > 15 mm density					
Channel	29.901	1	29.901	152.691	<0.001
Cruise	1.385	2	0.693	3.537	0.031
Channel $\times$ cruise	16.267	2	8.133	41.534	<0.001
Error	31.72	162	0.11		

than the South Channel (ANOVA, $P \leq 0.001$) and were also larger in the North Channel (t -test, $P < 0.001$) (Fig. 2). Similarly, mean zooplankton volume in the North Channel was greater than the South Channel (t -test, $P \leq 0.001$) (Table I). During cruise B, a second larval cohort of delta smelt and longfin smelt arrived in the LSZ, however, by cruise C this second cohort had either dramatically declined or were missed by the sampling gear (Fig. 3).

DIET, FEEDING SUCCESS AND CONDITION

The diversity of prey items in the fishes diets was generally low. In the North Channel, delta smelt diets were composed of the exotic calanoid copepod

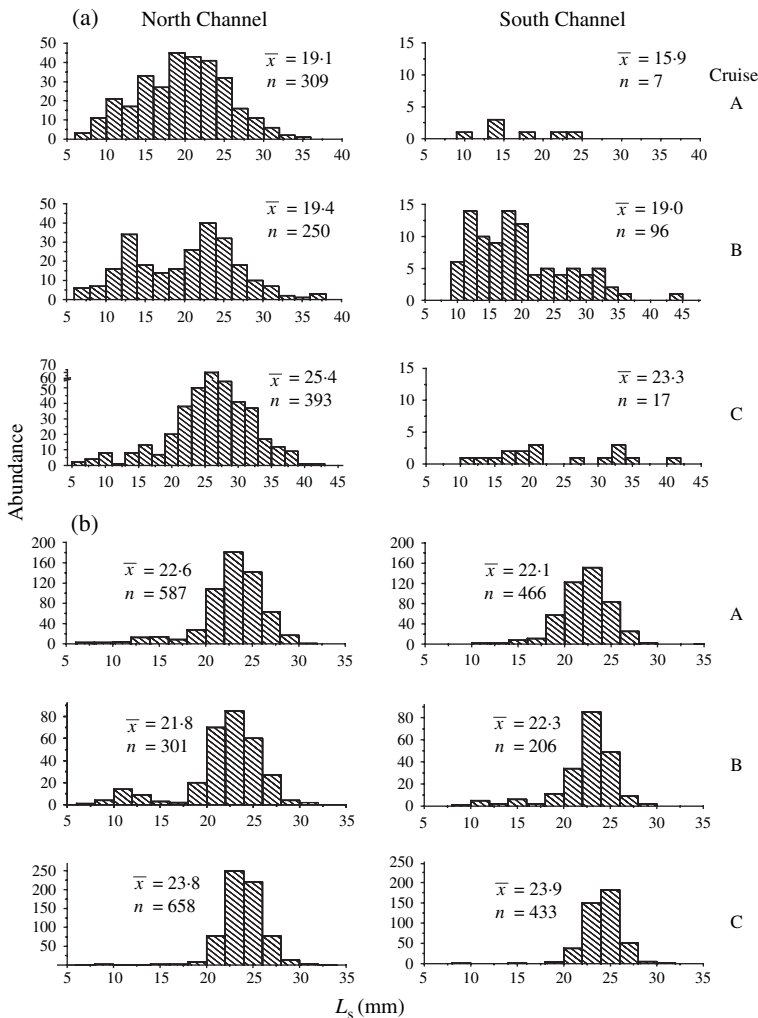


FIG. 2. (a) Delta smelt and (b) longfin smelt standard length frequencies from the North and South Channels of Suisun Bay for cruise A (3–4 June), B (13–14 June) and C (20–21 June 1996). $\bar{x}$ = mean L_S ; n = sample size.

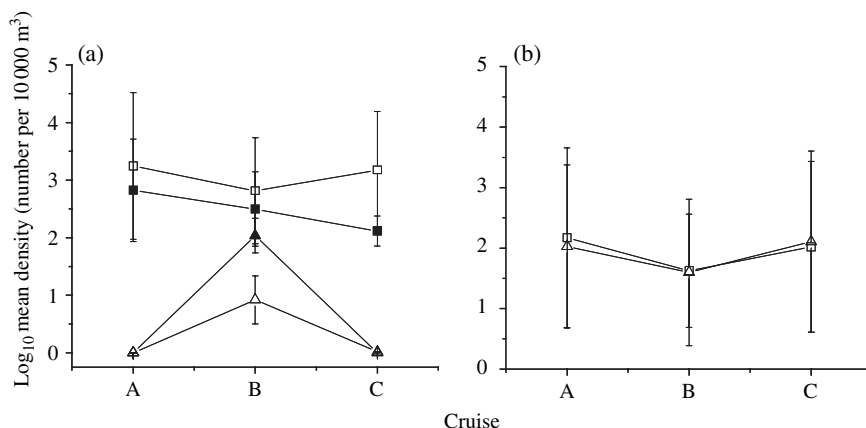


FIG. 3. Plots of mean $\pm$ s.d. $\log_{10}$ density for (a) larval (<15 mm) in the North (■) and South (▲) Channels, and juvenile delta smelt (>15 mm) in the North (□) and South (△) Channels and (b) longfin smelt from the North (□) and South (△) Channels of Suisun Bay during cruises A to C in June 1996.

Pseudodiaptomus forbesi (58%) and other calanoid copepodids (31%), probably *Pseudodiaptomus* sp., while longfin smelt diets consisted of the exotic cyclopoid copepod *Acanthocyclops vernalis* (93%). In the South Channel, delta smelt diets consisted of mostly *P. forbesi* (78%) and other calanoid copepodids (21%), whereas longfin smelt diets were similar including *P. forbesi* (76%), but also included *Acanthocyclops vernalis* (11%) (Table III).

The gut fullness index for delta smelt <15 mm was significantly lower in the South than in the North Channel (ANOVA, $P = 0.001$) (Table IV), however, this pattern was driven primarily by gut fullness values during cruise C (Bonferroni corrected $P \leq 0.001$) (Fig. 4). The pattern for delta smelt >15 mm was similar, with cruise C gut fullness index significantly greater in the North Channel (Bonferroni corrected $P \leq 0.05$) (Table IV). Longfin smelt gut fullness index was similar across cruises and between sites (Fig. 4). Sampling depth had no effect on gut fullness index for delta smelt or longfin smelt (ANOVA, $P > 0.05$) (Table V).

The K values increased from cruises A to C for delta smelt (ANOVA, $P \leq 0.001$) (Table VI) with cruises A and B having higher K values in the North Channel relative to the South Channel for both size classes (Bonferroni

TABLE III. Per cent prey composition in the stomachs of delta smelt and longfin smelt

	North Channel		South Channel	
	Delta smelt	Longfin smelt	Delta smelt	Longfin smelt
<i>Pseudodiaptomus forbesi</i>	58	4	78	77
<i>Acanthocyclops vernalis</i>	4	93	—	11
<i>Sinocalacus doerrii</i>	—	—	—	6
<i>Limnoithona tetraspina</i>	—	—	1	—
<i>Daphnia</i> sp.	2	1	—	—
Calanoid copepodids	31	—	21	4
Cyclopoid copepodids	5	2	—	2

TABLE IV. ANOVA results for gut fullness index comparisons for delta smelt and longfin smelt

	SS	d.f.	MS	<i>F</i>	<i>P</i>
Delta smelt					
Source ¹					
Channel	4.326	1	4.320	13.825	<0.001
Cruise	14.242	2	7.120	22.759	<0.001
Lifestage	0.229	1	0.229	0.734	0.392
Depth	0.002	1	0.002	0.008	0.930
Channel × cruise lifestage × depth	1.735	2	0.867	2.773	0.064
Error	107.00	342	0.31		
Longfin smelt					
Source ²					
Channel	0.152	1	0.152	0.499	0.48
Cruise	0.365	1	0.365	1.196	0.27
Depth	0.301	1	0.301	0.987	0.32
Channel × cruise	0.013	1	0.013	0.043	0.83
Error	83.51	274	0.30		

¹Main effects: Channel (North and South), Cruise (A, B and C), lifestage (larvae <15 mm and juveniles >15 mm) and depth (surface and bottom tows).

²Main effects: Channel (North and South), cruise (A and C only) and depth (surface and bottom tows).

corrected $P \leq 0.001$) (Fig. 5). The K values for cruise C, however, were not significantly different between the North and South Channels (Fig. 5). Longfin smelt K values increased from cruises A to C ($P \leq 0.001$) and were greater in the North Channel (Bonferroni corrected $P \leq 0.001$) (Fig. 5).

Temporal variation in gut fullness for delta smelt and longfin smelt showed that feeding rhythm was associated with tidal stage and photoperiod (delta smelt: ANOVA, tide stage $P < 0.05$ and photoperiod $P < 0.01$; longfin smelt: ANOVA, tide stage $P < 0.01$ and photoperiod $P < 0.001$) (Fig. 6 and Table VII). At both sites, delta smelt gut fullness index increased during periods of daylight hours and flooding tides, and decreased during ebbing tides and darkness. Longfin smelt gut fullness increased slightly during daylight and ebb tides, but gut fullness during hours of darkness was higher than daylight. Minimums in the gut fullness index were associated with slack tides. Mean gut fullness indices were similar for both species among depths at each site, although delta smelt >15 mm had a greater gut fullness index at the surface in the South Channel during cruise C (t -test, $P < 0.05$) (Table V).

DISCUSSION

Beck *et al.* (2001) suggests that by evaluating the nursery habitat hypothesis, the mechanisms underlying spatial variability within apparent nursery areas can be better understood, thus allowing for the identification of critical nursery habitat. In this study, nursery habitat quality was spatially variable for delta smelt and longfin smelt, with the North Channel providing superior habitat

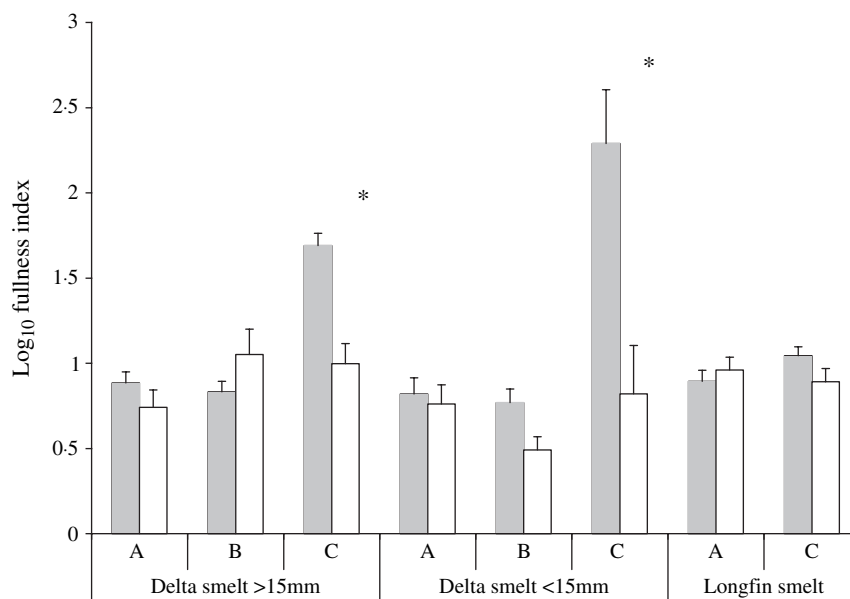


FIG. 4. Mean + s.e. log₁₀ fullness index for larval (<15 mm) and juvenile delta smelt (>15 mm) and longfin smelt in the North (■) and South (□) Channels of Suisun Bay for cruises A, B and C for delta smelt and A and C for longfin smelt. *, $P < 0.001$.

for both species. In the North Channel, delta smelt exhibited greater densities and larger size, with larvae <15 mm demonstrating greater feeding success. Overall, delta smelt K were higher in the North Channel when compared to the South Channel. Longfin smelt, however, exhibited similar densities, feeding success and size distributions between the two channels, but demonstrated reduced K in the South Channel. These data suggest that the North Channel of Suisun Bay acts as critical nursery habitat for both species by providing better feeding and growing conditions, which may promote higher survival. The South Channel, however, appears to provide only marginal habitat for longfin smelt and very poor habitat for delta smelt. Moreover, the mechanisms responsible for the apparent higher habitat quality of the North Channel are probably due to the availability of shallow-water habitat as well as the migration behaviour of each species. Previous studies in the St Lawrence estuary have also shown a link between migration strategies and position maintenance at the landward margin of the LSZ, which had higher prey abundance and resulted in greater feeding success, growth and survival for rainbow smelt (Dauvin & Dodson, 1990; Sirois & Dodson, 2000a, b). Thus, within the St Lawrence estuary, the landward margin of the LSZ functioned as critical nursery habitat relative to seaward regions.

Habitat-specific migration behaviours employed by longfin smelt and delta smelt, emphasizes the role that larval behaviour can play in assessing nursery habitats (Bennett *et al.*, 2002). In the North Channel, both species appeared to undergo reverse diel migrations, remaining near the surface during the day and at depth during the night, whereas in the South Channel longfin smelt

TABLE V. Comparison of the delta smelt and longfin smelt gut feeding index at depth (surface and bottom)

			Mean $\pm$ S.D.		
Channel	Lifestage	Cruise	Surface	Bottom	<i>P</i> *
North	Delta smelt <15 mm	A	0.831 $\pm$ 0.49	0.787 $\pm$ 0.42	0.299
		B	0.752 $\pm$ 0.51	0.824 $\pm$ 0.59	0.743
		C	2.290 $\pm$ 1.31	N/A	N/A
	>15 mm	A	0.810 $\pm$ 0.66	1.013 $\pm$ 0.60	0.543
		B	0.735 $\pm$ 0.41	0.868 $\pm$ 0.42	0.396
		C	1.636 $\pm$ 0.53	1.715 $\pm$ 0.24	0.879
	Longfin smelt				
		A	0.810 $\pm$ 0.65	0.958 $\pm$ 0.57	0.110
		C	1.019 $\pm$ 0.48	1.053 $\pm$ 0.56	0.342
South	Delta smelt <15 mm	A	0.763 $\pm$ 0.51	0.743 $\pm$ 1.05	0.500
		B	0.537 $\pm$ 0.43	0.331 $\pm$ 0.43	0.665
		C	0.821 $\pm$ 0.56	N/A	N/A
	>15 mm	A	0.862 $\pm$ 0.56	0.726 $\pm$ 0.32	0.634
		B	0.984 $\pm$ 0.76	1.079 $\pm$ 0.73	0.224
		C	1.240 $\pm$ 0.50	0.574 $\pm$ 0.74	0.031
	Longfin smelt				
		A	0.933 $\pm$ 0.53	0.971 $\pm$ 0.47	0.858
		C	0.937 $\pm$ 0.51	0.862 $\pm$ 0.55	0.519

*, Bonferroni corrected multiple comparisons from GLM ANOVA. N/A, not available.

underwent tidally oriented vertical migrations occurring near the surface during flood tides and at depth on ebb tides (Bennett *et al.*, 2002). Relatively, fewer delta smelt were sampled in the South Channel, possibly obscuring a similar pattern of migration. Reverse diel migration employed by both species in the North Channel may enhance horizontal exchange with the shallow Grizzly Bay (Wooldridge & Erasmus, 1980; Bennett *et al.*, 2002). Similarly, surface orientation of zooplankton in the North Channel during flood tides also implies horizontal exchange (Schoellhamer, 2001; Kimmerer *et al.*, 2002). Such a mechanism of exchange would promote higher residence time for both species where prey were more abundant, resulting in higher feeding success and somatic condition. These observations are consistent with those of Aasen (1999), who also observed that delta smelt were more abundant and larger in shallow-water habitats, such as Grizzly Bay, relative to the adjacent deeper channels. Although, increased stomach fullness was only observed for delta smelt larvae <15 mm, higher feeding success and increased growth rate of fish in habitats, such as the productive Grizzly Bay would promote higher survival rates and year-class success for both species.

Both longfin smelt and *P. forbesi*, the dominant prey item, underwent tidal-vertical migrations in the South Channel (Bennett *et al.*, 2002; Kimmerer *et al.*,

TABLE VI. ANOVA results for condition factor comparisons of delta smelt and longfin smelt

Source*	SS	d.f.	MS	<i>F</i>	<i>P</i>
Delta smelt					
Channel	99.590	1	99.589	18.076	<0.001
Cruise	510.228	2	255.114	46.305	<0.001
Lifestage	242.251	1	242.251	43.970	<0.001
Channel × cruise × lifestage	5.968	2	2.983	0.542	0.584
Error	512.38	93	5.51		
Longfin smelt					
Channel	9.222	1	9.222	11.207	<0.001
Cruise	85.718	1	85.718	104.165	<0.001
Channel × cruise	0.171	1	0.171	0.208	0.65
Error	78.18	95	0.82		

*, See Table IV for main effects.

2002). Despite their ability to vertically migrate with their prey, longfin smelt in the South Channel exhibited poorer somatic condition than the longfin smelt that occurred in the North Channel. While longfin smelt diets varied considerably between channel habitats, feeding success was similar between the sampling sites and the depths, implying different migration behaviours help them to maintain position in the LSZ and maximize feeding success (Bennett

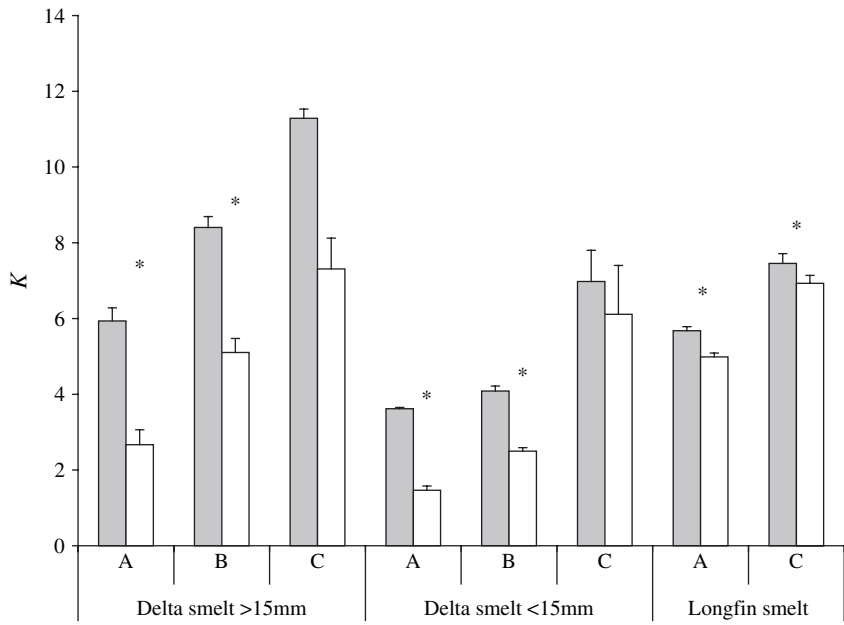


FIG. 5. Mean + s.e. condition factor for larval (<15 mm) and juvenile delta smelt (>15 mm) and longfin smelt in the North (■) and South (□) Channels of Suisun Bay for cruises A, B and C for delta smelt and A and C for longfin smelt. *, *P* < 0.001.

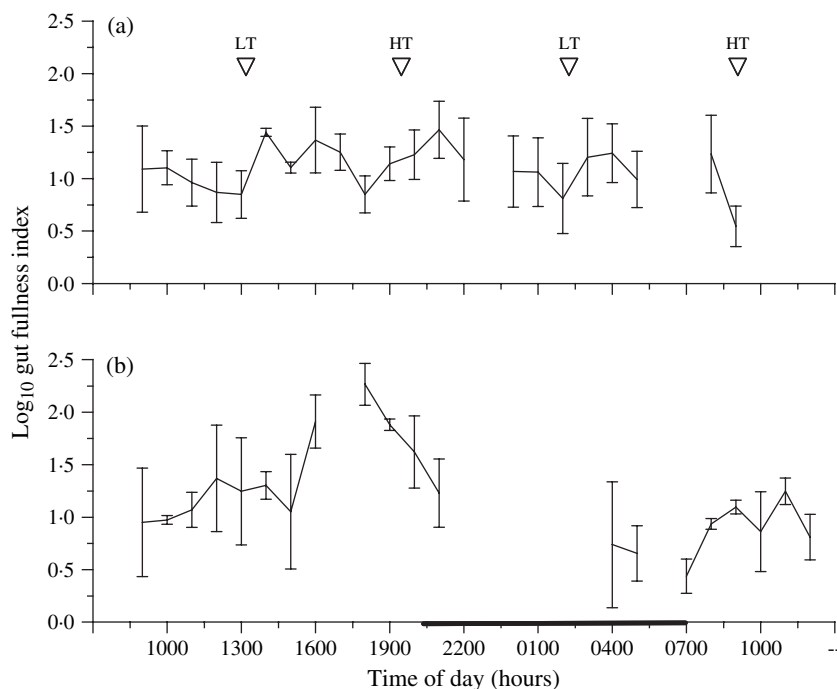


FIG. 6. Temporal variability of the $\log_{10}$ -transformed mean $\pm$ s.d. per cent gut fullness index for the North and South Channels combined for (a) delta smelt and (b) longfin smelt. Dark horizontal bars, night-time; HT, high tide; LT, low tide.

et al., 2002; Kimmerer *et al.*, 2002). The reduced condition exhibited by longfin smelt in the South Channel, however, may have been a consequence of the potentially higher energetic cost required to maintain position and find food in this dynamic habitat (Bevelhimer & Adams, 1993). Potentially, lower energetic costs and higher residence time in a more benign habitat may account for the higher somatic condition observed for both smelt species in the North Channel. The increased energetic costs of vertical migration in a deeper and more dynamic habitat may also explain the decreased somatic condition of delta smelt in the South Channel.

TABLE VII. ANOVA results for feeding rhythm for delta smelt and longfin smelt

Source	SS	d.f.	MS	<i>F</i>	<i>P</i>
Delta smelt					
Tide stage	2.147	2	1.073	3.130	0.045
Photoperiod	3.165	1	3.165	9.235	0.003
Error	117.56	343	0.34		
Longfin smelt					
Tide stage	3.326	2	1.664	5.934	0.002
Photoperiod	3.640	1	3.640	12.983	<0.001
Error	84.96	303	0.28		

Differences in the feeding ecology between these species also suggest delta smelt may be more susceptible to food shortages. Delta smelt larvae and juveniles fed only during daylight hours with gut fullness increasing when daylight hours coincided with flood tides, while longfin smelt exhibited a similar feeding rhythm, their feeding appeared to continue at night. Sirois & Dodson (2000*a, b*) showed a similar feeding pattern for rainbow smelt within the St Lawrence estuary; rainbow smelt were shown to feed only during daylight hours with stomach fullness also increasing with the occurrence of a flood tide. Unlike delta smelt, however, rainbow smelt demonstrated the ability to vertically migrate, thus possibly lessening their susceptibility to food shortages. Laboratory experiments have further documented that the feeding incidence of larval delta smelt increased when higher light levels were coupled with high turbidity thus illustrating the sensitivity of visual foragers to photo-conditions (Hunter, 1981; Baskerville-Bridges *et al.*, 2004). By comparison, other studies have observed that longfin smelt were less sensitive to light levels and do feed at night (Chigbu & Sibley, 1998). Therefore, these data suggest that the lower stomach fullness during slack tides may be associated with active tidal-vertical migrations during these periods (Bennett *et al.*, 2002).

Overall, these findings highlight the complex role of migration behaviours for position maintenance and foraging in the low-salinity regions of estuaries (Boehlert & Mundy, 1988). The differences in somatic condition and migration behaviours displayed by both smelt species between the habitats sampled within the LSZ demonstrates that fishes residing in the North Channel have a greater potential for survival and health than those in the South Channel, suggesting this area of the LSZ serves as the primary nursery habitat for young fishes in the LSZ of the San Francisco Bay estuary (Bennett *et al.*, 2002). This study highlights the intricate relationship between the feeding ecology and the migration behaviours employed by smelts in the LSZ regions. Finally, understanding the complex interactions of larval fish behaviour, habitat conditions and fish condition are imperative for assessing the quality of estuarine nursery habitats for commercial, recreational and protected fish species.

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