ICHTHYOPLANKTON OF THE LOWER COLUMBIA RIVER ESTUARY IN RELATION TO ENVIRONMENTAL VARIABLES

By

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To the faculty of Washington State University:

The members of the Committee appointed to examine the thesis LISA MARIE MARKO find it satisfactory and recommend that it be accepted.

Chair

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Abstract

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The Lower Columbia River Estuary (LCRE) is thought to be an important nursery ground for young fish, but this issue has not been studied comprehensively in 25 years. Thus, we examined the community of larval fish in the LCRE, USA, in relation to environmental variables over a full annual cycle (January - December 2006). Larval fish collections occurred monthly from Tongue Pt., OR to the mouth of the river using 0.6 m diameter bongo nets of 335 µm and 500 µm mesh size. Thirty taxa were captured;, Eulachon (*Thaleichthys pacificus*) was the most abundant species, followed by Prickly Sculpin (*Cottus asper*), Butter Sole (*Isopsetta isolepis*) and English Sole (*Parophrys vetulus*), which together accounted for 94.6% of the total abundance. Peak larval fish abundance occurred in spring, between the months of March and June. Larval fish in the LCRE were absent or in low abundance during summer and fall, which coincide with warmer temperatures and higher salinities as freshwater outflow is reduced in the estuary. Larval fish of oceanic origin (e.g. pleuronectids) were distributed within estuary reaches nearer to the mouth in more saline waters, while estuarine dependant fish (e.g. cottids) were located upriver in brackish waters. Salinity, season and temperature were the environmental variables that best explained the variation seen in the LCRE larval fish assemblage and appear to structure the larval fish community in terms of their abundance, distribution and composition. Our findings, when compared with other studies, indicate that the LCRE assemblage has changed over the past 25 years and is substantially different from other larval fish assemblages in Northeast Pacific estuaries.

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CHAPTER 1

Introduction

Estuaries commonly exhibit high biological productivity and contain a wide variety of important lower trophic level species (Day and Yáñez-Arancibia, 1985; Mallin and Paerl, 1994; Gewant and Bollens, 2005). Due to this high productivity estuaries provide high quality habitat for numerous fish species during various life history stages. Many fish species use estuaries for feeding, but also for reproduction, growth and refuge. Specifically, estuaries are important for the rearing of early life stages of fish and are often referred to as fish nurseries (Frank and Legget, 1983; Ramos et al., 2006).

The Columbia River provides the largest freshwater input into the northeastern Pacific Ocean, where it mixes with ocean water to create an estuarine ecosystem (Simenstad et al., 1990). The ichthyoplankton assemblage of the Lower Columbia River Estuary (LCRE) is dominated mostly by marine fish species (Misitano, 1977; Bottom and Jones, 1990; Monaco et al., 1990). Many estuarine fish assemblages are marine fish dominated, as these species enter estuarine ecosystems to feed (Blaber and Blaber, 1980; Neira et al., 1992). Other estuarine residents include anadromous fish, entering the estuary to migrate to rivers for reproduction, and resident fish that spend their entire life cycle in the estuary. Occasionally freshwater fish species enter estuaries, but it is rare (Lenanton and Potter, 1987; Neira et al., 1992; Able, 2005; Ramos et al., 2006). Because larval fish are very vulnerable to both predation and starvation, estuary habitats are important to their survival (Frank and Legget, 1983; Ferron and Leggett, 1994; Ramos et al., 2006). Furthermore, survival of fish during these early life stages is thought to be important for the recruitment of fish populations (Cushing, 1975; Frank and Legget, 1983; Ferron and Leggett, 1994; Ramos et al., 2006).

Little research has been published on the community ecology of larval fish in the LCRE. Previous zooplankton surveys of the estuary generally detailed the overall community structure, which only secondarily included larval fish (Haertel and Osterberg, 1967; Haertel et al., 1969; Haertel, 1970). For instance, Haertel (1969) found most of the fish species in the estuary to be euryhaline and composed mainly of flatfish species, with Starry Flounder (*Platichthys stellatus*) the most abundant larval fish captured. However, many of the fish collected in these surveys were post-larval and juvenile fish (standard length > 50 mm) (Haertel and Osterberg, 1967; Haertel et al., 1969; Haertel, 1970).

The National Marine Fisheries Service (NMFS) conducted the most comprehensive survey to date of the larval fish assemblage in the LCRE (Misitano, 1977; Jones et al., 1990). The purpose of this survey was to study the productivity and seasonal variation of the entire zooplankton community in the estuary. Misitano (1977) showed that larval fish were most abundant in the estuary January through May, with no larval or post larval fish collected in summer months. The peak abundances of two species of Osmerid larvae (*Spirinchus thaleichthys* and *Thaleichthys pacificus*) occurred in March and May. Overall, early life history stages of fish collected in this survey comprised 22 species; 89% of these fish were the two Osmerids, 7% were Prickly sculpin (*Cottus asper*) and the remaining 19 species accounted for 1% of the total catch. Twenty-two species were captured at the mouth of the river (salinity range 29-32) versus less than five species captured upriver at Tongue Pt, OR (salinity range 0-4). Misitano (1977) concluded that the majority of larval fish were oceanic in origin due to their presence near the mouth of the river where salinities were highest (29-32).

The Columbia River Data Development Program (CREDDP) sampled the estuary from 1980-81 to understand the ecology, hydrology and sedimentology of the river (Simenstad et al., 1990; Jones et al., 1990). Part of the CREDDP study focused on the plankton in the Columbia River, which like the earlier NMFS survey (Misitano, 1977; Jones et al., 1990), included surveys of larval fish. Jones et al. (1990) found most of the larval fish captured to be of oceanic origin. The larval fish most commonly captured in this study were of the family Osmeridae, and *Cottus asper*. Both taxa were found throughout the entire salinity range of the estuary. Overall, larval fish were most abundant in the estuary in the spring (however, the authors noted that January through May was a poorly sampled time period in their study) and densities decreased through summer, with almost no fish present in August.

Many other studies conducted on fish in the Columbia River have targeted only salmon, or lower Columbia River reaches above the estuarine zone (e.g., Gadomski and Barfoot, 1998). Monaco et al.'s (1990) goal was to provide a comprehensive database of fish and invertebrates in West Coast estuaries, using information compiled from several previous publications (including the LCRE). Osmerid larvae were the only fish to be classified as 'abundant' or 'highly abundant,' with *Spirinchus thaleichthys* found in the LCRE year round and *Thaleichthys pacificus* in the winter/spring.

These earlier studies, while ranging in spatial and temporal scope, concluded that the LCRE is dominated by marine species, mainly of the Osmeridae family, with peak abundances occurring in the winter and spring. However, since there has not been a detailed study of the ichthyoplankton assemblage in the LCRE in 25 years, there is a need for an updated and comprehensive survey of larval fish populations in the LCRE. In addition, there is little published literature on how the physiochemical conditions (salinity, temperature) in the estuary influence the distribution, abundance and composition patterns of larval fish. The LCRE is known to be a very dynamic system physically, chemically and biologically (Simenstad et al.,

1990) and it is known that these characteristics influence the distribution, abundance and composition of fish species in other estuarine ecosystems (Gewant and Bollens, 2005; Blaber and Blaber, 1980). Thus, the objective of this study was to describe the community of larval fish in the LCRE in terms of their abundance, distribution, and composition over a full annual cycle (January-December 2006) in relation to environmental variables.

CHAPTER 2

Materials and Methods

Study Area

The LCRE is located at the border between the southwest corner of Washington State and the northwest corner of Oregon (46°218’ N, 123°763’ W; Figure 1). The drainage basin of the Columbia River covers 66,480 km^2 in total area and is the second largest river in the United States (Simenstad et al.,1990).

The coastal sub-basin, of which the LCRE is a part, accounts for only 8% of the total drainage basin of the Columbia River by area; however, it accounts for 24% of the total river flow due to high precipitation on the westward side of the Cascade and Coast Mountains. There are three major tributaries to this coastal sub-basin; the Cowlitz, Willamette and Lewis Rivers. These rivers have highest river flow during winter months, up to ten times the average flow (Simenstad et al., 1990). This freshwater influx results in very dramatic and rapid changes in salinity in the estuary (Haertel and Osterberg 1967). Hydroelectric, power and irrigation dams (primarily upstream) along the river have continued to alter the overall river flow and discharge in the Columbia River (Simenstad et al 1990).

The LCRE is a drowned river mouth, salt-wedge estuary that has a strong tidal influence (McCabe et al., 1983). The salt intrusion has been shown to extend as far as 20 to 50 km upriver from the mouth with tidal influence as far as 165 km upriver (Jay and Dungan Smith, 1990a). The major habitats located within the estuary are tidal marsh (low and high), tidal flats (mudflats), and swamp. The estuary is comprised mainly of fine silt or clay sediments in the tidal marsh and tidal flat regions and coarse sediments in the riverine sections of the estuary (Simenstad et al., 1990).

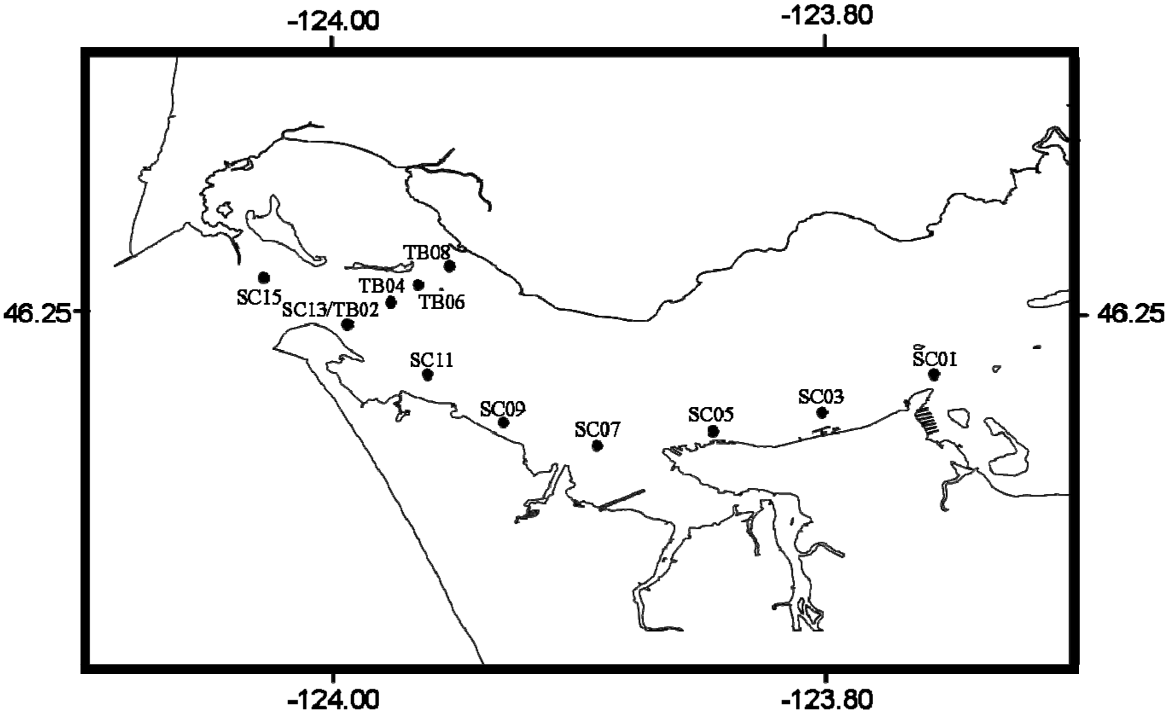

Figure 1. Map of the Lower Columbia River Estuary. Black circles indicate larval fish sampling stations located from Tongue Pt., OR seaward to the mouth of the river at buoy 10. Station numbers are located above black circles.

Sampling

Larval fish collections were made in the LCRE along and across the main channel of the estuary (Figure 1). Along channel collections were performed in the South Channel and across channel collections were performed along a transect that runs approximately south to north. Stations were located between Tongue Point, OR (46°218’ N, 123°763’ W) and the river mouth (46°256’ N, 124°026’ W) along channel and between Hammond, OR (46°236’ N, 123°997’ W) and Chinook, WA (46°261’ N, 123°965’ W) across channel. Monthly sampling was initiated in January 2006 and was terminated in December 2006 (Table 1).

Vertical profiles of salinity (measured using Practical Salinity Scale), temperature (ºC) and chlorophyll *a* fluorescence (mg m^3) were taken at all stations across and along channel using a Sea-Bird Electronics CTD. Fish collections occurred at odd numbered stations (e.g., SC01, SC03, etc.) along channel and at even numbered stations (e.g., TB02, TB04, etc.) across channel (on two occasions other stations were sampled, see Table 1). Larval fish were collected using 0.6 m diameter bongo nets towed obliquely off the side of the *M/V Forerunner* from surface to a depth of approximately 5m off the bottom, and then back to the surface. Two nets, 335 µm and 500 µm mesh sizes, were mounted on the bongo net frame. The nets were towed at a boat speed between 1.5-2 knots (0.77- 1.03 m s^{-1}). Flowmeters were mounted inside the mouth of the bongo nets to determine the volume of water filtered. Nets were retrieved, rinsed with seawater, and the contents immediately preserved in a 5-10% formalin-seawater solution. All samples were collected during daylight hours.

Back in the laboratory, larval fish were sorted from samples, enumerated and identified to the lowest taxonomic level possible following Matarese et al. (1989). In addition, fish were measured to the nearest millimeter using an optical micrometer (standard length (SL) for postflexion larvae; notochord length (NL) for preflexion and flexion larvae) (Duffy-Anderson et al., 2006). Larvae that were not identifiable, due to damage in collection, were not measured. Fish counts were then transformed to number of fish per cubic meter by dividing fish counts by volume of water filtered (m^3). All salinity, temperature and chlorophyll *a* data were collected and analyzed using SBE Data Processing, v. 7.12. Hydrographic river outflow data were obtained from the US Army Corps of Engineers, Northwest Division DART (data in real time) River Environment program online database (http://www.cbr.washington.edu/dart/river.html).

Table 1. Sampling the Lower Columbia River Estuary. Number of stations sampled between January and December 2006 on the Lower Columbia Estuary (LCRE). Larval fish collections = number of stations where bongo net tows were performed; CTD casts = the number of stations where CTD casts were performed in order to collect physiochemical and hydrographic data.

Month	Larval fish collections	CTD casts
January	12	22
February	20	46
March	22	46
April	20	48
May	20	48
June	22	28
July	22	48
August	24	48
September	22	48
October	22	48
November	20	46
December	20	46
Total	246	522

Statistical Analysis

To determine spatial and temporal relationships between environmental variables and larval fish abundance patterns, a non-metric multidimensional scaling (NMS) ordination technique was used. This multivariate analysis was executed using the computer software PC-ORD, version 4 (McCune and Mefford, 1999). A Pearson – Kendall correlation analysis was used to compare axis scores in multi-dimensional space to environmental variables sampled in order to interpret species abundance patterns (Gewant and Bollens, 2005). The variables included salinity, temperature, chlorophyll *a* (fluorescence), distance to river mouth (buoy 10), outflow, month and season. Samples were excluded that contained no individuals or rare occurrences (occurrence in < 2 samples) because these occurrences may not represent the true nature of the species' patterns. Analyses were performed on both nets together; however, species occurring in both nets were identified as different entities in order to avoid pseudoreplication.

A multi-response permutation procedure (MRPP) was used to test differences in groups defined categorically by environmental variables (Mielke and Berry, 2001; McCune and Grace, 2002). This analysis attempts to compare the species composition between defined groups within each environmental variable category. The environmental variables used were salinity, season and temperature. The groups defined within these categories were freshwater (0-5), estuarine (6-29) and oceanic (≥ 30) for salinity; winter (January – March), spring (April – June), summer (July – September) and fall (October- December) for season; and cold (≤ 9 °C), cool (10 – 14 °C) and warm (≥ 15 °C) for temperature. In addition, an indicator species analysis was used to determine one or more species that indicate different environmental conditions (Dufrêne and Legenre, 1997). Both analyses were executed using PC-ORD, version 4 software.

The spatial distribution of larval fish was also analyzed using a Kendall's Concordance test. This test was performed in order to determine if the species assemblage varied between stations. The Kendall's test provides both a correlation value (tau b) and a p-value when comparing species abundances across sites, with a correlation value of 1.0 and a $p \leq 0.05$ indicating similarities of assemblages between sites. For this analysis, we used mean annual abundances for the top ten most abundant taxa and analyzed each net separately. This analysis was performed using SAS, version 9.1 software.

CHAPTER 3

Results

Hydrography, Chlorophyll a, and Outflow

There was considerable variation in all environmental variables sampled, especially seasonally. Mean temperature in the LCRE during 2006 varied up to 10 ºC between the low in January (7 ºC) and the high in June (17 ºC) (Figure 2). Mean salinities were lowest during January and November (6) and highest during July (22) (Figure 2). Outflow peaked in the spring ($\geq$ 300 kfcs) and was at its lowest in the fall (< 150 kfcs) (Figure 2). Chlorophyll *a* concentrations peaked in April (12.8 mg m^{-3}), with smaller peaks occurring in March (9.3 mg m^{-3}) and July (8.2 mg m^{-3}) (Figure 2). Overall, the annual pattern of chl *a* showed higher concentrations in the spring and lowest in late fall and early winter (Figure 2).

There was also high spatial variability in most environmental variables (data not shown). For instance, mean annual salinity varied from a high of 26 closest to the mouth (station SC15) to a low of 2 furthest upstream (station SC01). Other environmental variables also exhibited high spatial variability, but with no clear patterns and trends. For instance, mean annual temperature was 11 °C at the mouth and 14 °C furthest upstream, whereas mean annual chlorophyll *a* peaked near the center of our sampling (SC09), but had secondary peaks both upstream (SC01) and downstream (TB06).

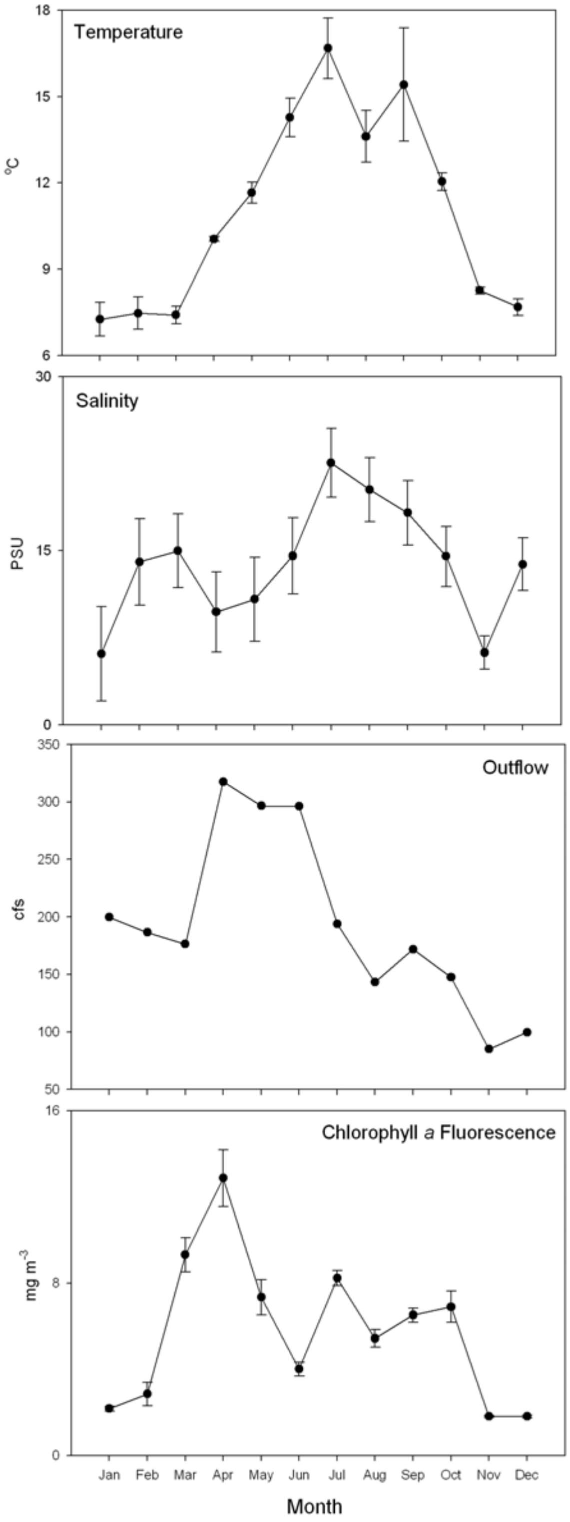

FIGURE 2. Annual Environmental Variable Patterns. LCRE-wide means (± SE) over an annual cycle for temperature, salinity, chlorophyll *a* fluorescence and outflow. cfs = cubic feet per second.

Community Composition

A total of 2,698 individual fish larvae representing 30 taxa (Table 2) were collected between January and December 2006 in the LCRE. The two most abundant species, *Thaleichthys pacificus* (Eulachon) and *Cottus asper* (Prickly sculpin), accounted for 90% of the total catch. The top ten most abundant taxa collected - *T. pacificus, C. asper, Isopsetta isolepsis* (Butter sole), *Parophrys vetulus* (English sole), Osmeridae, *Leptocottus armatus* (Pacific staghorn sculpin), *Glytocephalus zachirus* (Rex sole), *Psettichthys melanosticus* (Sand sole), *Clupea pallasi* (Pacific herring) and *Platichthys stellatus* (Starry flounder) - accounted for approximately 98% of the total catch (Table 2). The community composition differed only slightly between the two nets, with the 335 µm net containing more taxa (26) and higher abundances. The 500µm net contained only 20 taxa, five of which were not found in the 335 µm net (Figure 3).

Table 2. Composition of Larval Fish Assemblage. Rank, in terms of total year abundance, of ichthyoplankton collected from the Lower Columbia River Estuary (LCRE) between January and December 2006. n = total number of specimens collected, % = percentage of total species collected, month = month present in the estuary and net = mesh size of net used for collection.

Rank	Taxon	Common Name	Mean Abundance (#/m^3)	n	%	Cumulative %	Month Present	Net (μm)
1	*Thaleichthys pacificus*	Eulchon	0.0821	1611	59.7	59.70	1-5	335,500
2	*Cottus asper*	Prickly Sculpin	0.0418	821	30.4	90.10	1-6	335,500
3	*Isopsetta isolepsis*	Butter Sole	0.0034	66	2.45	92.55	2-4	335,500
4	*Parophrys vetulus*	English Sole	0.0028	54	2.00	94.55	3,4,6	335,500
5	*Unidentified (damaged)*	n/a	0.0015	29	1.08	95.63	1-4,12	335,500
6	*Osmeridae*	Smelt	0.0012	23	0.85	96.48	12	335,500
7	*Leptocottus armatus*	Pacific Staghorn Sculpin	0.001	19	0.7	97.18	2-4,10,11	335,500
8	*Glyptocephalus zachirus*	Rex Sole	0.0008	15	0.56	97.74	3	335,500
9	*Psettichthys melanosticus*	Sand Sole	0.0006	12	0.45	98.19	1-3,6,10	335,500
10	*Clupea pallasi*	Pacific Herring	0.0006	11	0.41	98.60	2-6	335,500
11	*Platichthys stellatus*	Starry Flounder	0.0005	9	0.33	98.93	3	335,500
12	*Hexagrammos lagocephalus*	Rock Greenling	0.0002	4	0.15	99.08	10	335,500
13	*Ammodytes hexapterus*	Pacific Sandlance	0.0002	3	0.11	99.19	3	335,500
14	*Artedius harringtoni*	Scalyhead Sculpin	0.0001	2	0.07	99.26	4	335
15	*Lumpenus sagitta*	Snake Prickleback	0.0001	2	0.07	99.33	2	335,500
16	*Anoplarchus spp.*	Cocksomb	0.0001	2	0.07	99.40	3	335,500
17	*Hexagrammos decagrammus*	Kelp Greenling	0.0001	1	0.04	99.44	10	335
18	*Oligocottus snyderi*	Fluffy Sculpin	0.0001	1	0.04	99.48	4	335
19	*Stellerina xyosterna*	Pricklebeast Poacher	0.0001	1	0.04	99.52	4	500
20	*Rhinogobiops nicholsi*	Blackeye Goby	0.0001	1	0.04	99.56	7	335
21	*Sardinops sagax*	Pacific Sardine	0.0001	1	0.04	99.60	3	335
22	*Liparis pulchellus*	Showy Snailfish	0.0001	1	0.04	99.64	5	335
23	*Clinocottus acuticeps*	Sharpnose Sculpin	0.0001	1	0.04	99.68	4	500
24	*Pholis sp.*	Gunnel	0.0001	1	0.04	99.72	4	335
25	*Hemilepidotus hemilepidotus*	Red Irish Lord	0.0001	1	0.04	99.76	9	500
26	*Artedius fenestralis*	Padded Sculpin	0.0001	1	0.04	99.80	2	335
27	*Scorpaenichthys marmoratus*	Cabezon	0.0001	1	0.04	99.84	2	500
28	*Lyopsetta exilis*	Slender Sole	0.0001	1	0.04	99.88	5	335
29	*Liparis sp.*	Sanilfish	0.0001	1	0.04	99.92	5	335
30	*Gobiesox maeandricus*	Northern Clingfish	0.0001	1	0.04	99.96	3	500
31	*Engraulis mordax*	Northern Anchovy	0.0001	1	0.04	100.00	9	335
	Total Number Species 30	Total Specimens	2698					

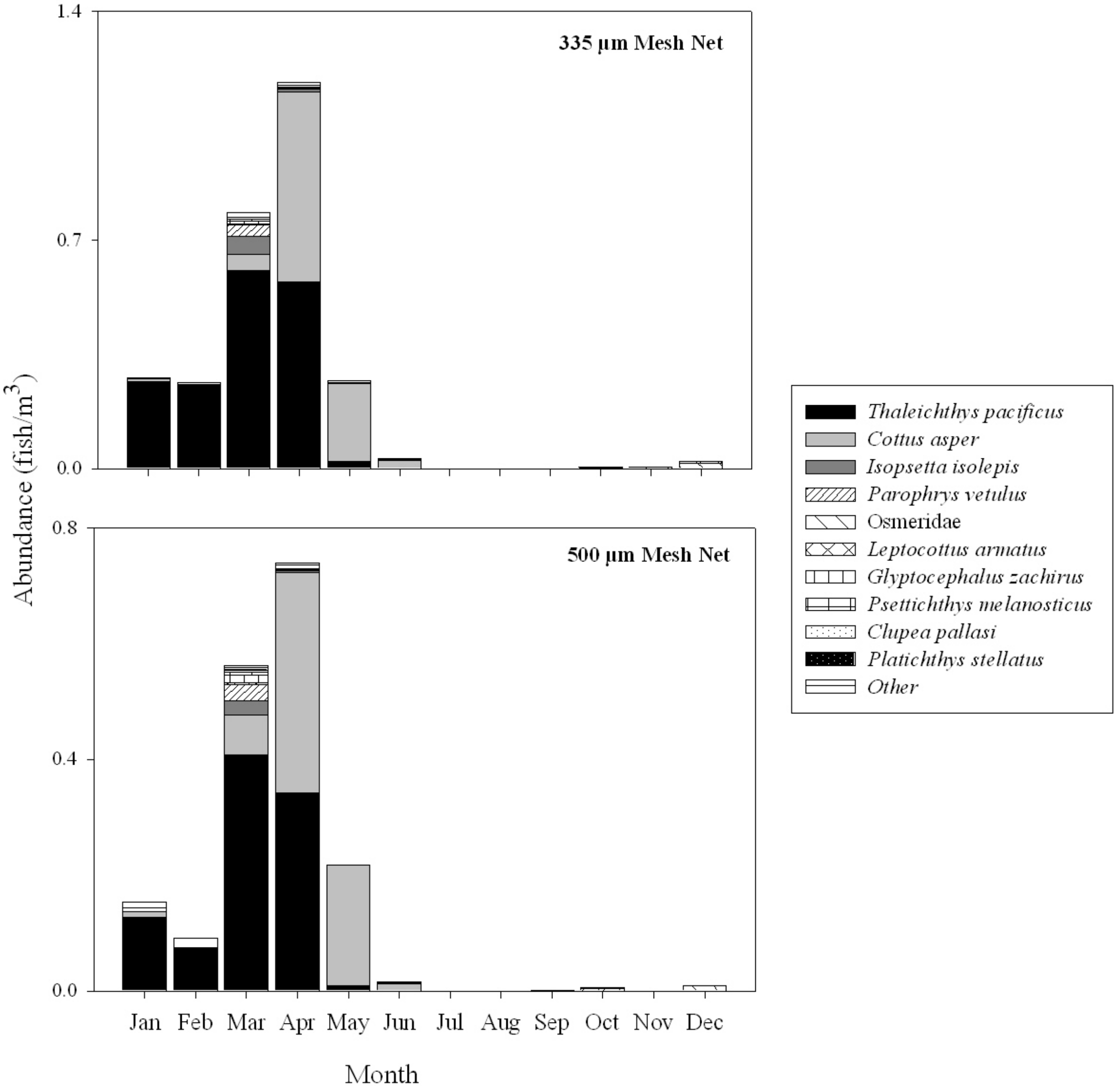

Figure 3. Seasonal Abundance and Composition. Composition and seasonal abundance of top ten most abundant larval fish taxa collected in the Lower Columbia River Estuary in 335µm mesh (a) and 500µm mesh (b) nets. Species are listed in order of highest to lowest mean abundance. "Other" refers to remaining twenty species not individually listed.

Seasonal Patterns of Abundance

The highest abundances occurred in late winter and early spring (March – May) (Figure 3). The peak abundance occurred in April with mean abundances of 1.2 individuals m^{-3} in the 335 µm net and 0.74 individuals m^{-3} in the 500 µm net. There were very few individuals collected in the summer months, with no individuals collected in August. A small increase in abundance was seen in the fall; but was still quite low ($< 0.016\ m^{-3}$).

The top ten most abundant species generally followed the same abundance pattern, except for the Osmerids (Figure 4), which were collected only in December. *Thaleichthys pacificus*, although a member of this family, was most abundant in late winter and early spring (March – May), with no individuals collected after May. *Cottus asper* was the most abundant species collected after the spring-time, community-wide peak in abundance, with mean abundances exceeding 0.02 individuals m^{-3} in June. *Leptocottus armatus* was the most abundant species collected in the early fall (October –November).

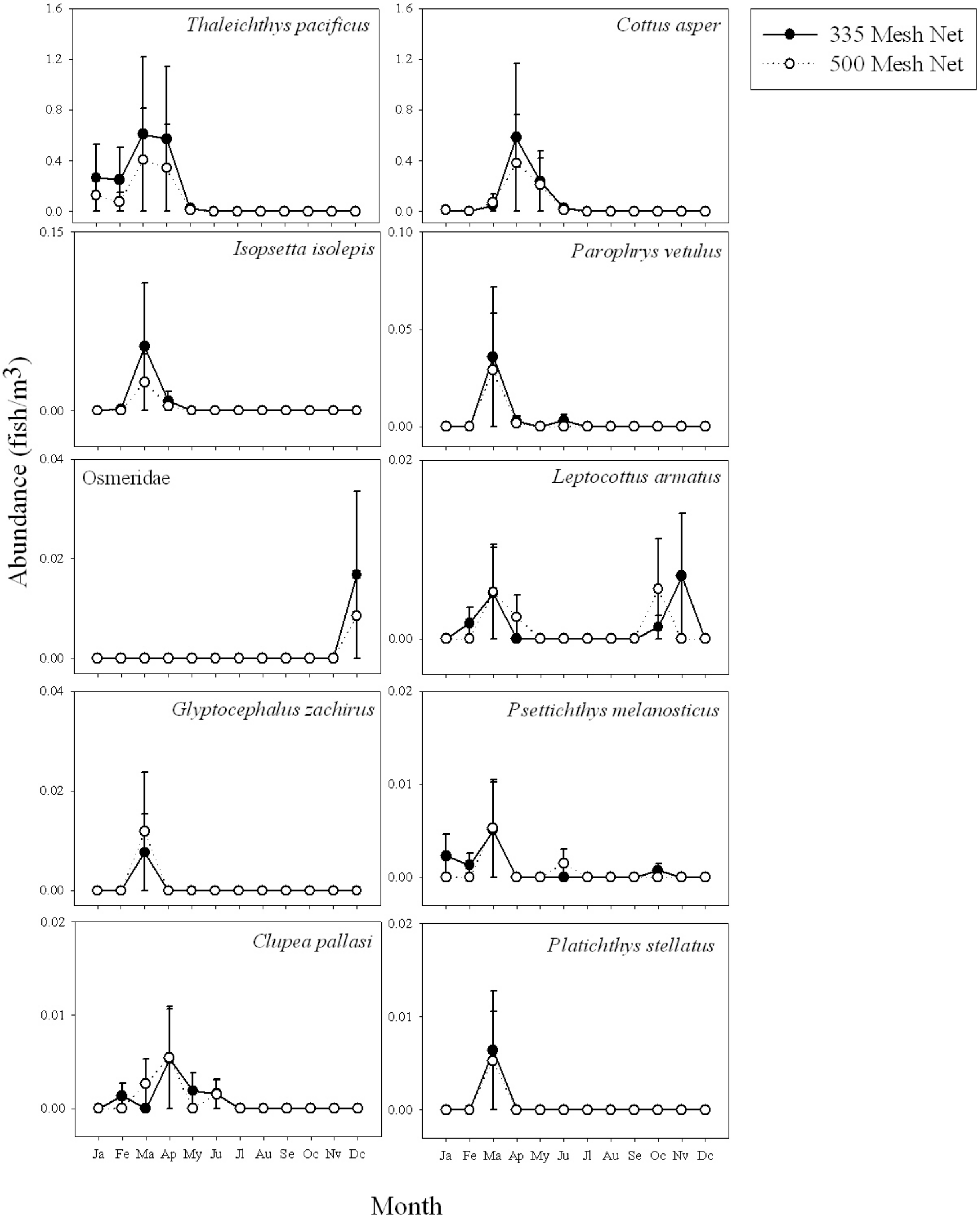

Figure 4. Individual Species Abundance (mean ±SE). Seasonal abundance patterns for *Thaleichthys pacificus, Cottus asper, Isopsetta isolepis, Parophrys vetulus,* Osmeridae, *Leptocottus armatus, Glyptocephalus zachirus, Psettichthys melanosticus, Clupea pallasi* and *Platichthys stellatus* in the Lower Columbia River Estuary between January and December 2006. Solid line and symbol = 335 µm mesh net; dashed line and open symbol = 500 µm mesh net.

Spatial Distribution

The stations with the highest average abundances for the entire sample period were those that occurred considerably upriver from the mouth (e.g., SC05; Figure 5). Station SC05, the deepest station located directly beneath the Astoria - Megler Bridge, had the highest abundance. Stations located just downstream of the Astoria - Megler Bridge had the next highest abundances (e.g., SC07, SC09, SC11). The stations with the lowest abundances were located near the mouth of the river (e.g., TB04, SC15).

The two most abundant species in the estuary, *Thaleichthys pacificus* and *Cottus asper,* were broadly distributed within the LCRE at all sites. Both species predominantly occurred in the upper reaches of the estuary, above station SC11, and were most abundant at stations SC09 and SC05, respectively. *T. pacificus* were also abundant along transect B and station TB06. Osmeridae larvae, the fifth most abundant taxon in the estuary, were primarily located in the lower reaches of the estuary, below station SC07, with peak abundance occurring at station SC11. Both *Isopsetta isolepis* and *Parophrys vetulus* were primarily located in the lower reaches of the estuary as well. *I. isolepis* had no presence in the estuary above station SC11 and was most abundant at station TB04. Similarly, *P. vetulus* was most abundant at station TB04, but rarely occurred in the upper reaches of the estuary (stations SC03 and SC05). The Kendall's Concordance test showed that station TB04 was dissimilar in assemblage in both the 335 and 500 μm mesh net in relation to the remaining stations ($p > 0.05$ for all pairwise comparisons). Excluding station TB04, all station assemblages were shown to be significantly similar ($p < 0.05$ for all pairwise comparisons). Thus, there was very little variation in assemblage at each station with the exception of station TB04.

In terms of spatial distribution in salinity and temperature, *T. pacificus* and *C. asper* were both distributed mainly within cool temperature waters and low to intermediate salinities (Figure 6). Specifically, *T. pacificus* was most abundant between 4 and 14 °C and 5 and 15. A few individuals were collected above 15, but no individuals were collected in waters above 14 °C. *C. asper* was most abundant between 9 and 14 °C and in salinities below 15. Very few individuals were collected above 15 and above 14 °C. The remaining species collected showed very little variation and/or range in temperature and salinity distribution; however, this may be due to the small number of specimens collected (Table 2).

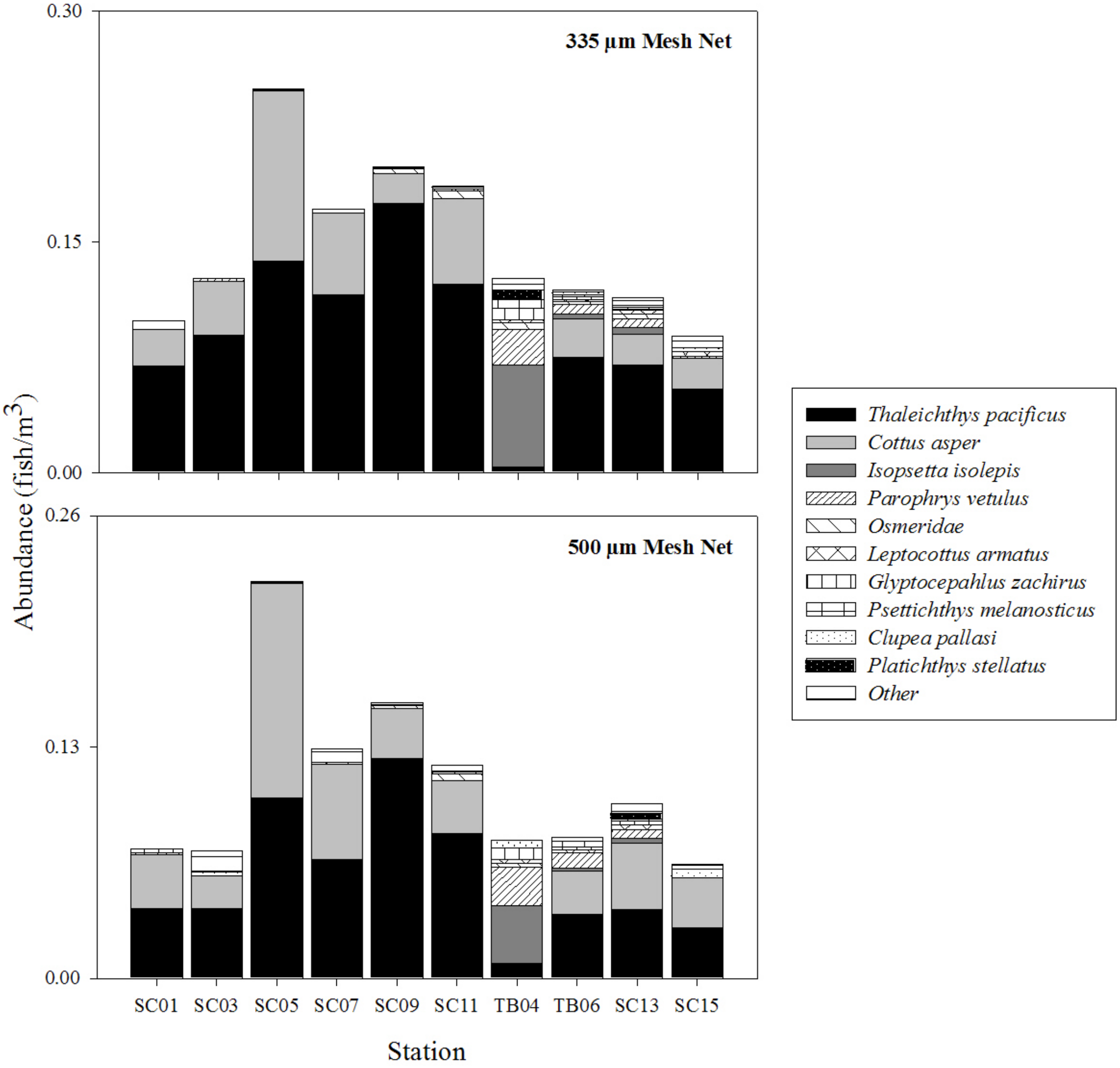

Figure 5. Community Spatial Distribution and Composition. Mean annual abundance and spatial distribution of top ten most abundant larval fish taxa collected in the Lower Columbia River Estuary from Tongue Pt., OR to mouth of the river at buoy 10. Each panel indicates a different mesh size (335 µm and 500 µm) used in sampling. Species are listed in order of highest to lowest abundance. "Other" refers to remaining twenty species not individually listed. Stations are listed from left to right in decreasing distance to the mouth.

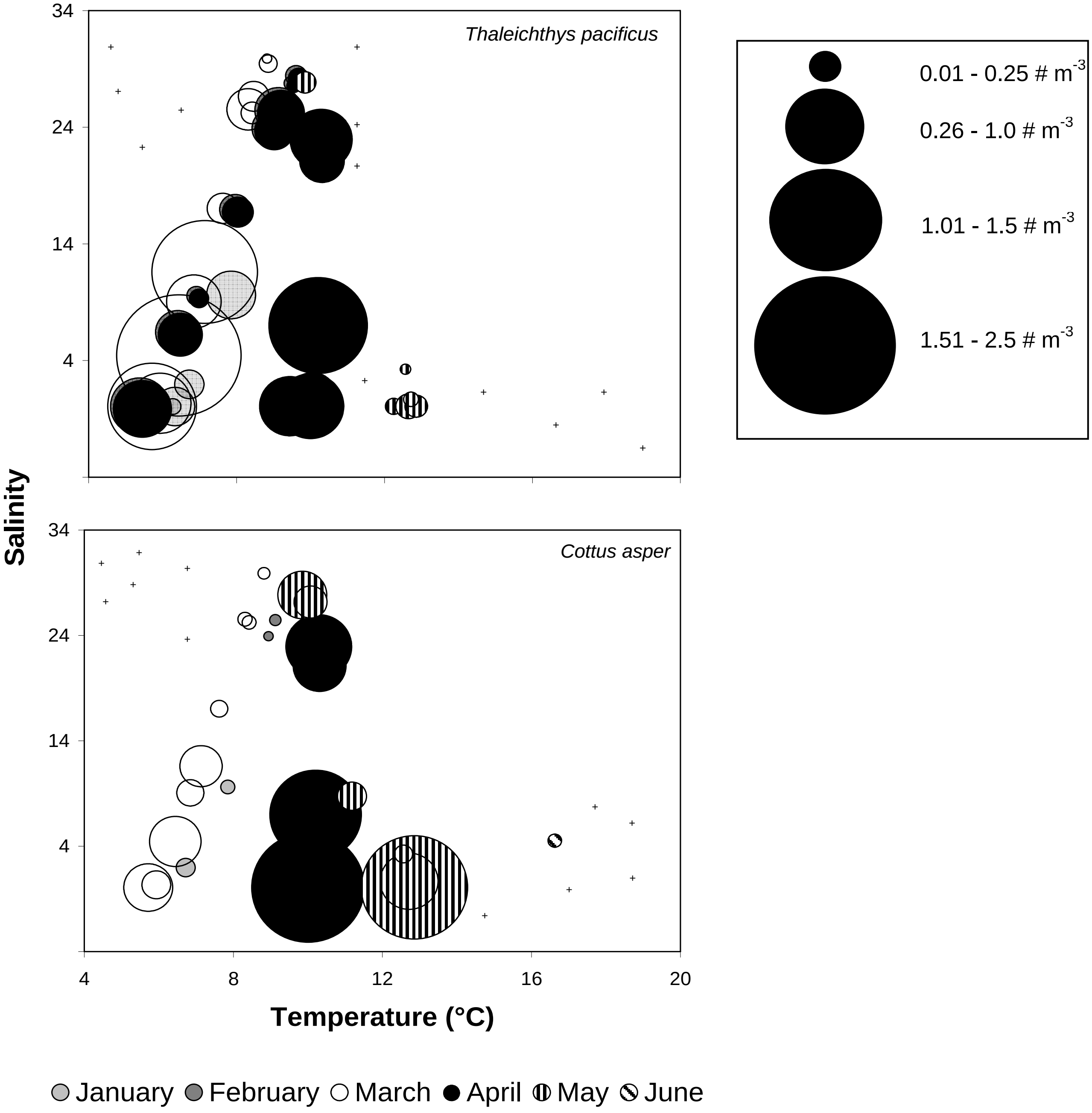

Figure 6. Salinity and Temperature Distribution of Individual Species. Temperature and salinity distribution of *Thaleichthys pacificus* and *Cottus asper* at each station collected within month present. Size of circle indicates abundance (not exceeding 2.4 individuals m^{-3}), color of circle indicates month and number of circles indicates number of stations. + indicates stations sampled with no fish present.

Relationship to Environmental Variables

Variation in abundance of ichthyoplankton in the LCRE was attributed to salinity, season/month (time) and temperature (Table 3). The coefficient of determination, as described by an r^2 value that expresses the proportion of variation explained by that variable as accounted for in the statistical model, for axis one was highest (most closely correlated) for salinity. Axis two scores were most closely correlated with both season and month (time). Finally, axis three scores were significantly correlated with temperature. P-values were not assigned due to the lack of independence between ordination scores and environmental variables. The coefficient of determination of the correlations between ordination distances and distances in the original *n*-dimensional space was 0.301 for axis one, 0.222 for axis two and 0.239 for axis three. Cumulatively, these axes account for 76% of the variation in these data. The final stress reported for the three-dimension solution was 14.22608.

When taxa are grouped by similar salinity range, seasonal occurrence and temperature gradient, the ordination of species scores shows that those species that scored low on axis one (below zero) were located in areas of low salinity, while those located around and above zero were located in estuarine and oceanic salinities (Figures 7, 8). Additionally, those species that scored high on axis two occurred in the summer, while those that scored low occurred in the fall. Intermediate values along axis two (around zero) indicate winter and spring occurrence (Figures 7, 9). Finally, those species that scored high on axis three occurred in warmer temperature waters, while the majority of species scored near zero at intermediate levels and occurred in cool temperatures (Figures 8, 9).

The MRPP analysis indicated a significant difference ($p = 0.001$) between groups of species in all three environmental variable categories. Osmerids were a strong indicator of season, salinity and temperature. More specifically, Osmerids occurred only in the fall, only in freshwaters and only in the coldest temperatures. *Glyptocephalus zachirus* was an indicator of season as well, occurring only in winter. *Clupea pallasi* was the strongest spring indicator, while *C. asper* and *L. armatus* were the strongest indicators of estuarine and oceanic water, respectively. *Cottus asper* was also the strongest indicator of intermediate water temperature, while none of the species were strong indicators of warm temperatures (Table 4).

Table 3. Coefficients of Determination. Expresses the proportion of variation that is explained by each environmental variable category when inputted into a correlation matrix against species abundance. Values are given as r^2. Bold indicates the environmental variables that are most strongly correlated with each axis.

	Distance	Month	Chl a	Outflow	Season	Temp	Salinity
Axis							
1	0.075	0.069	0.002	0.045	0.043	0.007	**0.132**
2	0.134	**-0.735**	0.226	0.678	**-0.707**	0.204	-0.392
3	0.045	0.354	0.094	0.065	0.325	**0.454**	0.015

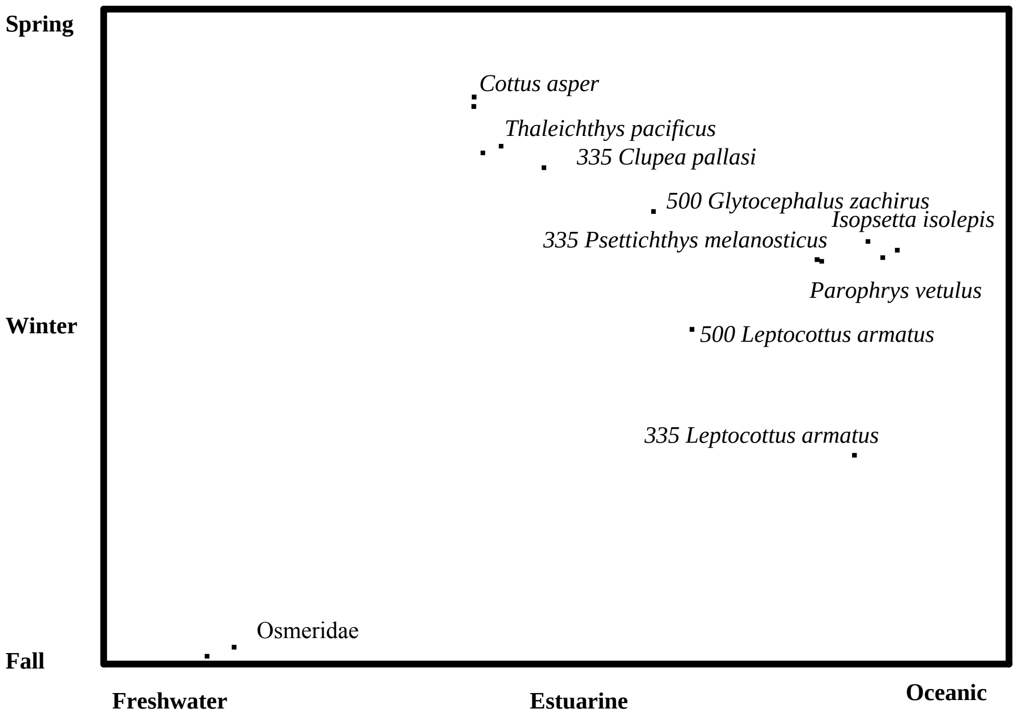

Figure 7. Salinity and Season Ordination. Non-metric multidimensional scaling (axes 1 and 2) of the fifteen most abundant ichthyoplankton species in the LCRE. Unless noted, the species location within ordination space represents species present in both the 335 and 500 µm mesh nets. Summer is not included in the ordination, as none of the most abundant species were captured in this season.

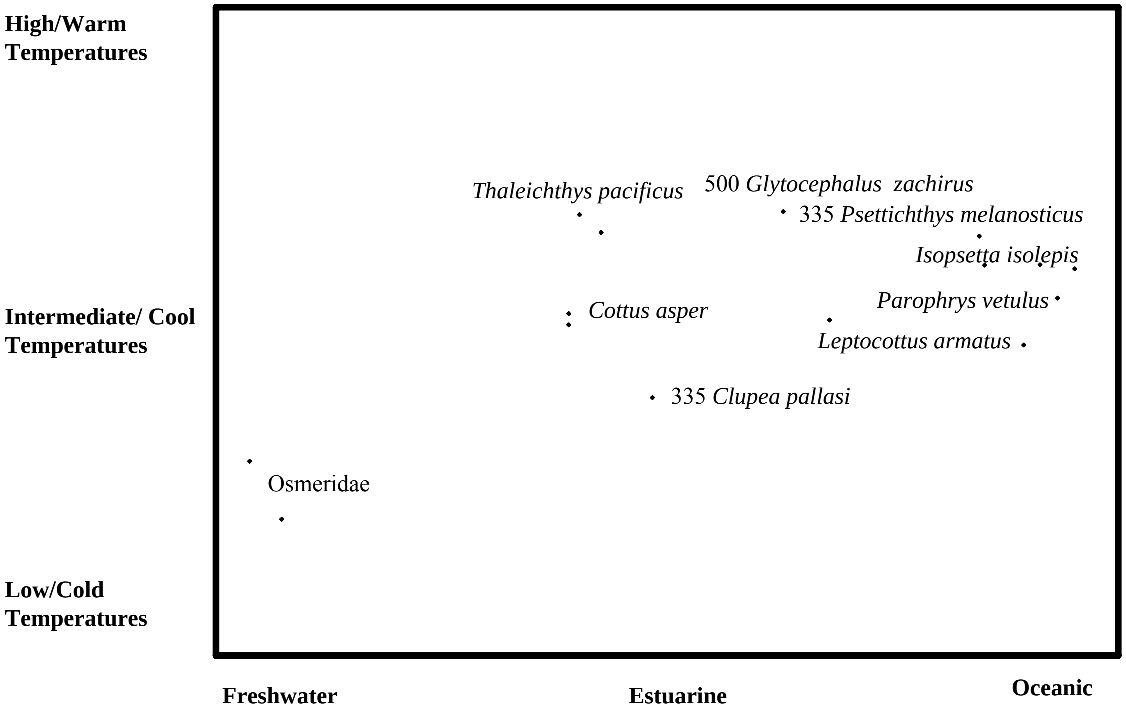

Figure 8. Salinity and Temperature Ordination. Non-metric multidimensional scaling (axes 1 and 3) of the fifteen most abundant ichthyoplankton species in the LCRE. Unless noted, the species location within ordination space represents species present in both the 335 and 500 µm mesh nets. Summer is not included in the ordination, as none of the most abundant species were captured in this season.

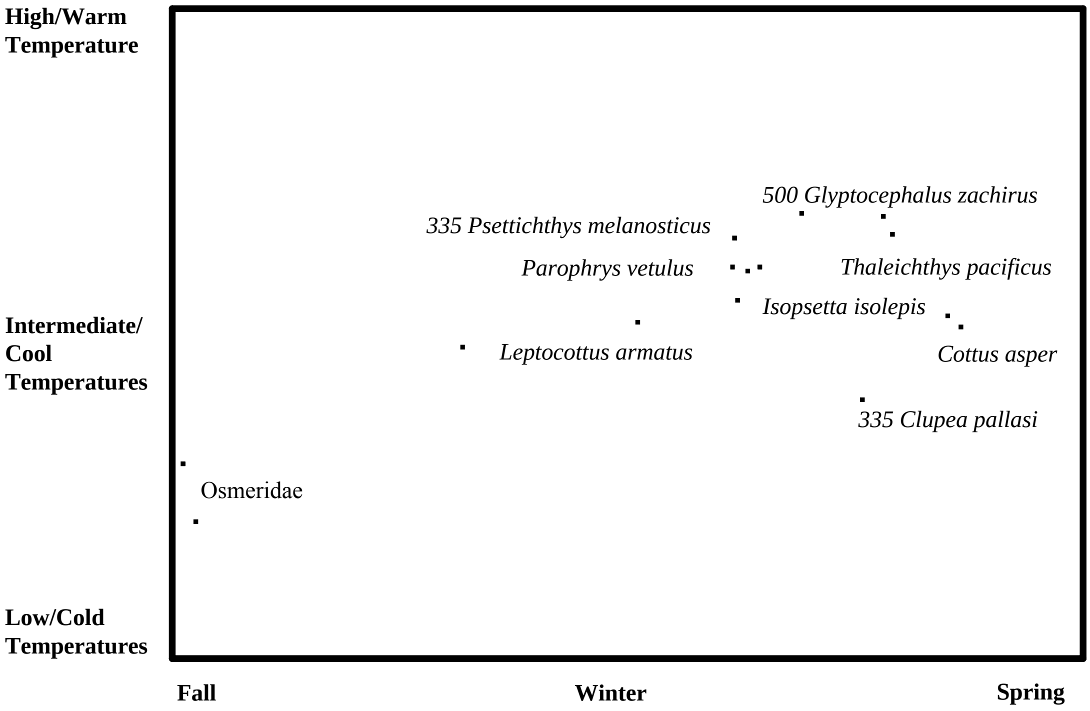

Figure 9. Season and Temperature Ordination. Non-metric multidimensional scaling (axes 2 and 3) of the fifteen most abundant ichthyoplankton species in the LCRE. Unless noted specifically, the species location within ordination space represents species present in both the 335 and 500 µm mesh nets. Summer is not included in the ordination, as none of the most abundant species were captured in this season.

Table 4. Indicator Species Analysis. An indicator species analysis was performed on the three environmental variables most closely correlated with ordination axes: salinity, season, and temperature. Groups are determined within each environmental category. These groups are defined as freshwater (0-5) estuarine (6-29) and oceanic (> 30) for salinity; winter (January – March), spring (April – June), summer (July – September) and fall (October – December) for season; cold (9 °C and below), cool (10-14 °C) and warm (> 15 °C) for temperature. Species listed are those collected in this study that best define each group within each environmental category. Indicator values are also given.

Environmental Variable		Indicator Value	Indicator Species/ Taxon
Salinity Zone			
	Freshwater	100	Osmeridae
	Estuarine	72	*Cottus asper*
	Ocean	87	*Leptocottus armatus*
Season			
	Winter	100	*Glyptocephalus zachirus*
	Spring	91	*Clupea pallasi*
	Summer	n/a	None
	Fall	100	Osmeridae
Temperature Zone			
	Cold	100	Osmeridae
	Cool	80	*Cottus asper*
	Warm	n/a	None

CHAPTER 4

Discussion

Community Composition and Dominant Taxa

Of the 30 taxa collected in the LCRE, two species, *T. pacificus* (Osmeridae) and *C. asper* (Cottidae) dominated the ichthyoplankton community (59.7 % and 30.4%, respectively). These two species were identified as present or dominant in previous studies of the LCRE in both their larval and adults stages (Haertel and Osterberg, 1967; Misitano, 1977; Jones et al., 1990; Monaco et al., 1990). Moreover, adult *C. asper*, which is an estuarine species, was found to be a major constituent of the adult fish community in the LCRE as determined by midwater and otter trawls (Haertel and Osterberg, 1967). In addition, Monaco et al. (1990) listed *T. pacificus*, an anadromous fish, as 'abundant' in the LCRE during their adult life history stage.

However, our results differ from those of previous authors in several ways. For instance, Misitano (1977) found *T. pacificus* and *C. asper* comprised 19% and 7%, respectively, of the ichthyoplankton assemblage of the LCRE, but that Longfin smelt (*Spirinchus thaleichthys)* comprised 67% (this species was completely absent in our study) and the remaining 22 taxa accounted for 1% of the total abundance. Moreover, Misitano (1977) found that of this remaining 22 taxa, four species occurred that did not occur in our study: Pacific tomcod (*Microgadus proximus*), Lingcod (*Ophidon elongates*), Buffalo sculpin (*Enophrys bison*) and Tidepool sculpin (*Oligocottus maculosus*). Jones et al. (1990) determined *T. pacificus* and *C. asper* to be abundant in the LCRE, and their remaining taxa, listed as 'abundant,' all occurred in relatively high abundance in our study.

Of the top ten most abundant species in our study, only *T. pacificus* and *C. asper* were found in similar abundances in previous studies (Haertel and Osterberg, 1967; Misitano, 1977;

Jones et al., 1990). The other eight "top-ten" species from our study were either in low abundance or did not occur at all in previous studies. For instance, the family Pleuronectidae (flat fish) were very abundant in our study; however, *P. stellatus* was not found in the LCRE by Misitano (1977). Similarly, *P. melanosticus* and *I. isolepis* were not found by Jones et al. (1990) and *G. zachirus* was not mentioned in either Misitano (1977) or Jones et al. (1990). These differing results may have occurred for several reasons. Both of these earlier studies were performed more than 25 years ago, and it is possible that the current environment (e.g., biotic and/or abiotic conditions) within the LCRE have changed. In addition, while the collection methods in these two previous studies were similar to ours, Misitano (1977) collected fish at fewer stations and used only the largest mesh size net (500 μm), while Jones et al. (1990) collected fish at stations farther upriver than our study and used a 254 μm mesh net in addition to a 335 μm mesh net. Also, Jones et al. (1990) noted that January through May was a poorly sampled period in their study, which was the period of highest abundances in our study. Finally, the taxonomy of some of the larval fish taxa has been revised (Matarese et al., 1990), such that *S. thaleichthys* may be included in our group of Osmeridae.

More recently, Parnel et al. (2008) found ichthyoplankton of the family Pleuronectidae in relatively high abundances in the Columbia River Plume (an area of low salinity water that extends up to 400 km offshore of Oregon). Specifically, *P. vetutlus*, *P. melanosticus* and *G. zachirus* were three of the top five most abundant species collected in the plume (Parnel et al., 2008). This substantially different rank order of abundance from our study is not surprising given the very different habitats sampled (estuarine in our case vs. coastal ocean plume by Parnel *et al.*, 2008).

Misitano (1977) suggested that the community composition of ichthyoplankton in the

LCRE differed from that of other Northwest estuaries and was comprised primarily of marine species. Our study has found the same to be true. For instance, in Dabob Bay, WA, Bollens et al. (1992) found Pacific hake (*Merluccius productus*), rockfish (*Sebastes* spp.), slender sole (*Lyopsetta exilis*) and Pacific sandlance (*Ammodytes hexapterus*) to be the most abundant species over a three-year study period. Elsewhere in Puget Sound, it has been reported that fish of the family Gadidae are most dominant (Waldron, 1972; Blackburn, 1973). In Yaquina Bay, OR, Pearcy and Myers (1974) found Pacific herring (*Clupea pallasi*) and bay goby (*Lepidogobius lepidus*) were the most abundant fish larvae over an 11-yr period, with Prickly sculpin (*Cottus asper*), pacific staghorn sculpin (*Leptocottus armatus*), Gobiidae and surf smelt (*Hypomesus pretiosus*) following in abundance. In Coos Bay, OR, Miller and Shanks (2005) found Northern anchovy (*Engraulis mordax)*, penpoint gunnel (*Apodichthys flavidus*), Pacific sardine (*Sardinops sagax*), rosylip sculpin (*Ascelichthys rhodorus*) and surf smelt (*Hypomesus pretiosus*) to account for greater than 70% of the catch. Further to the south, Meng and Matern (2001) found the Suisun Marsh in central California to be comprised mainly of shimofuri goby (*Tridentiger bifasciatus*), *C. asper*, and striped bass (*Morone saxatilis*). In a study of San Pablo Bay and Central Bay, San Francisco Estuary, CA, Bollens and Sanders (2004) found *E. mordax*, Gobiidae, and Pacific Staghorn Sculpin (*Leptocottus armatus*) to be the dominant larval fish species.

These differences between the LCRE and other Northeast Pacific estuaries could be attributed to a number of causes. A major factor may be estuary type. The LCRE is classified as a large salt-wedge estuary, while Dabob Bay, WA is classified as a temperate fjord (Bollens et al., 1992), Yaquina Bay, OR as a small well-mixed tidal estuary (Pearcy and Myers, 1974), Coos Bay, OR as a well-mixed tidal estuary (Miller and Shanks, 2005), Suisan Marsh, CA as a brackish water tidal bay (slough; Meng and Matern, 2001), San Pablo Bay, CA as a shallow, brackish water estuary (however can be heavily river-dominated in the spring thus creating a salt-wedge, Conomos, 1981) ; and Central Bay, CA as a largely marine, drowned river valley (Emmett et al., 2000; Feyrer et al., 2004). Although Emmett et al. (2000) described the LCRE as a drowned river valley, they mentioned its unusually high freshwater inflow compared to other West coast estuaries, as it is a river-dominated estuary. These classifications describe the salinity, freshwater flow, river velocity, vertical mixing and depth of each estuary type. Thus, it is not surprising that different types of estuaries would contain different fish assemblages.

Moreover, the published salinity and temperature ranges and averages in other Northeast Pacific estuaries differ from that of the LCRE. In Suisan Marsh, CA, salinity averaged 1.0 and temperature 16.0 °C (Meng and Matern, 2001). Bollens and Sanders (2004) found salinity to range between 8 and 30 and temperature to range between 10 ° and 18 °C in San Francisco Bay (higher salinities were found in Central Bay (23- 30) than in San Pablo Bay; however, salinities in San Pablo Bay were generally above 18). In the LCRE, high fish abundance was generally associated with lower salinity and temperatures than those that occurred in the studies of California. In addition, many of the collection methods varied between studies. Pearcy and Myers (1974) collected samples using a 12.5 cm Clarke-Bumpus (CB) Sampler with a 0.233 μm aperture nylon net (bongo nets were used in conjunction with the CB sampler at five stations). Light-trap collections were performed in Coos Bay, OR (Miller and Shanks, 2005), a tucker trawl was used in Dabob Bay, WA (Bollens et al., 1992) and in San Francisco Estuary (Bollens and Sanders, 2004) and Meng and Matern (2001) performed collections just below the water surface using a rectangular steel framed plankton net; however, all of these studies used nets with mesh sizes similar to ours.

Seasonal and Spatial Patterns of Occurrence

Estuarine fish communities tend to be characterized by the seasonal occurrence of a few dominant species (e.g., temporary residents, Neira et al., 1992; Gewant and Bollens, 2005). This pattern of seasonal occurrence can be seen in our data from the LCRE, with major peaks in larval fish abundance occurring between January and May. This is likely the result of winter and spring spawning by the dominant species. *Cottus asper*, for instance, are known to spawn between January and April (Matarese et al., 1989), which is consistent with their larval occurrence in the LCRE between January and June. Although there is little information available on the spawning patterns of *T. pacificus*, the co-occurrence of this species with *C. asper* may indicate a similar spawning pattern. Both species have freshwater and anadromous life histories and *C. asper* have been documented to migrate downstream for spawning regardless of residency type in the estuary (Matarese et al., 1989). Another fish of the Osmeridae family, *S. thaleichthtys,* also classified as anadromous, has been documented to migrate downstream to spawn in brackish water before migrating to neritic waters as juveniles (Gewant and Bollens, 2005).

The pleuronectid assemblage (e.g., *I. isolepis*) peaked between March and May, which is also likely the result of winter and spring spawning of species in this family (Matarese et al., 1989). *Isopsetta isolepis* and *P. vetulus* spawn between January and April in coastal and nearshore areas (Norcross and Shaw, 1984; Matarese et al., 1989). As a result of this nearshore spawning pattern, the offshore transport of eggs is less likely to occur, and instead transport into the estuary is more likely (Norcross and Shaw, 1984). In a salt-wedge estuary like the LCRE, many planktonic organisms are passively carried into the estuary in deeper saltwater currents moving upstream (Norcross and Shaw, 1984). This is likely the larval transport mechanism of the majority of the marine species in the LCRE. In addition, upwelling events occurring off the coast of the LCRE may be responsible for the transport of deeper spawning marine species (e.g., *G. zachirus*) into the estuary from the Astoria canyon, which is directly east of the LCRE and flows inshore during the upwelling season (Hickey, 1997; Parnel et al., 2008).

Past studies of the LCRE found similar seasonal patterns of larval fish abundance to our study. The most striking and interesting similarity is the almost complete absence of fish in the summer months (July-Sept). That is, Misitano (1977) found no larval fish in the estuary during the summer and Jones et al. (1990) saw a decrease in larval density as the summer progressed, with few individuals present in August. During our study period, larval fish densities decreased by an order of magnitude from May to June, with only a very few individuals captured later in the year. This pattern of abundance is consistent with the dominance of winter and spring spawning species in the LCRE, and has previously been hypothesized to maximize the use of the California Current for larval transport (Parrish et al., 1981). The California Current can, at times, impact the movement and transport of fish in the Northeast Pacific (Norcross and Shaw, 1984). In addition, many of these fish may be transported in the Columbia River plume in the summer. The plume flows both seaward and southward (off the Oregon coast) during summer months (Parnel et al., 2008), and is likely responsible for transporting species, especially of the family Pleuronectidae, away from the estuary, resulting in a reduced abundance of these fish in the LCRE in the summer, as seen in our study.

Our data, while inconsistent with compositional patterns, are consistent with the seasonal abundance patterns of ichthyoplankton seen in other Northeast Pacific estuaries as well. For instance, peak abundances in Dabob Bay, WA occurred in winter and spring, specifically in January - April (Bollens et al., 1992). In Yaquina Bay, OR, abundances peaked between

February and June with very few fish collected after June (Pearcy and Myers, 1974). In Coos Bay, OR, ichthyoplankton peaked during the downwelling season, defined as occurring between October and March, and occurred least frequently during the latter portion of the upwelling season, defined as June to September (Miller and Shanks, 2005). Of the most abundant species collected in Suisun Marsh, CA, the majority were captured between February and June (Meng and Matern, 2001). The peak of *C. asper* occurred in February and March, which is only a slightly earlier peak than was seen in our study. In San Pablo Bay and Central Bay, San Francisco, CA, peaks in larval fish abundance were seen in February – May and April, respectively, albeit in much higher densities than in the LCRE (Bollens and Sanders, 2004).

Our ordination and concordance results indicate that the larval fish assemblage in the LCRE varies very little in spatial distribution. The variation that can be seen (TB04) can possibly be attributed to life-history traits of species within the LCRE. Gewant and Bollens (2005) found distance to the Golden Gate bridge (thus the coastal ocean) to be a determining factor in the spatial distribution of macrozooplankton and micronekton in the San Francisco Estuary. Specifically, they found estuarine dependant species to be broadly distributed within the estuary, anadromous or occasional estuarine resident species to be in Central and North Bay (near to the Golden Gate) and resident estuarine species to be in South Bay (farthest from the Golden Gate). In the LCRE, *T. pacificus* is broadly distributed within the estuary and is considered to be estuarine dependant, while many of the pleuronectids, which are of marine origin, are located upriver at stations farther from the mouth. The station with a unique assemblage (TB04) was located nearer to the mouth, was very shallow and was comprised mainly of species from the pleuronectid family. Pleuronectids tend to exhibit diel migration (low in water column during daytime and high in water column during nighttime) and tend to remain below the thermocline in a stratified system like the LCRE (Frank et. al., 1992). However, it should be noted that our results indicate that the physical environment plays more of a role in spatial distribution than the proximity to the coastal ocean.

Relation to Environmental Variables

In addition to seasonality, salinity and temperature also played major roles in structuring the community of larval fish in the LCRE. Salinity and temperature tolerances have been determined to structure many of the estuarine fish communities in West coast estuaries (Emmett et al., 2000). These environmental factors are generally related to the strong seasonal patterns seen in temperate estuarine ecosystems (Day and Yanez-Arancibia, 1985; Horn and Allen, 1985; Cloern, 1996; Gewant and Bollens, 2005). Specifically, larval fish may be geographically and seasonally distributed in areas and during times when salinity and temperature are physiologically favorable to individual species. This can be seen in the San Francisco Estuary, where distinct larval and post-larval fish assemblages occurred seasonally during both dry/warm and wet/cold seasons (Gewant and Bollens, 2005). Observed variation of the fish assemblage in a New Jersey estuary was attributed mainly to salinity (Martino and Able, 2003), i.e., the Mullica River, Great Bay and the adjacent continental shelf were each found to have distinct fish assemblages and salinities.

Salinity was significantly correlated with axis one scores in our ordination analysis and temperature with axis three scores. Similarly, Bottom and Jones (1990) found salinity and temperature to be defining factors of the ichthyoplankton assemblage in the LCRE. This interpretation is supported by the clear separation of species (e.g., family Osmeridae) within temperature and salinity gradients used in our ordination. It has been suggested that salinity patterns in the LCRE, as a result of riverflow, influence the distribution (due to physiological constraints) of larval fish and also other zooplankton species (Jones et al., 1990). The average salinity in the LCRE is higher, as a result of reduced riverflow, during summer and fall than during high-flow spring (Bottom and Jones, 1990).

Estuaries are defined, in part, by the flow of freshwater into the system (e.g., Alber, 2002). In our study, while the outflow of freshwater was not found to be the most closely correlated variable with any one axis, it was very highly correlated with axis two. High freshwater flow is often associated with higher abundances of fish in an estuary (Kimmerer, 2002; Whitfield, 2005) and transportation of larval fish (Dew and Hecht, 1994). The inflow and outflow of freshwater to an estuarine ecosystem influences the delivery of nutrients, sediments and other organic materials to the estuary, the salinity of the estuary, the tidal influence, the flushing time in the estuary (i.e., for pollutants, sediments, etc.) and thus can impact the biological organisms in an estuary (Alber, 2002; Kimmerer, 2002; Whitfield, 2005). Dew and Hecht (1994) found high freshwater flow to be related to seaward movement of Atlantic tomcod larvae in the Hudson River. This seaward displacement from freshwater flow may act as a co-variable in explaining the observation of high abundances of larval fish within the LCRE during winter and spring, high flow seasons. Gewant and Bollens (2005) found freshwater flow in the San Francisco Estuary to directly impact the salinity and temperature; South Bay, an area of low freshwater inflow and thus higher salinity and less flushing, had the lowest abundances.

Temperature, the variable related to axis three, can also play a role in the variability of larval fish abundance. Meng and Matern (2001) found unique warm and cool larval fish assemblages in Suisan Marsh, CA. The mean summer temperature in the LCRE is almost twice that of the spring (17 and 9 °C, respectively), however, we did not find a distinct “warm assemblage” in the LCRE. This may be in part due to the impact of freshwater outflow. The changes in temperature and salinity in the LCRE correspond with the seasonal patterns of abundance of larval fish in the estuary (e.g., lack of abundant species occurring in summer/fall). It is likely that these environmental factors are creating physiological "barriers" within which larval fish are limited in their survival and distribution. It should be mentioned, however, that our ordination showed some fish species occurring in estuarine and oceanic salinities as well as in intermediate temperatures. However, most species in our study are occurring in seasons when LCRE temperature and salinity are at their lowest.

Many of our findings may be attributed to the origin of these species (e.g., marine) and their respective life-history (e.g., estuarine resident). For instance, Neira et al. (1992) found that marine - spawned fish in Swan Estuary, Australia were located only in the lower and middle reaches of the estuary, whereas, estuarine - spawned fish occurred throughout the entire estuary. They determined that marine - spawned fish were restricted from the upper reaches of the estuary based on the physical characteristics of the Australian coast. In our study, the same types of patterns can be seen. Those species clustered in oceanic salinities are marine in origin (e.g., pleuronectids), while those species clustered in estuarine salinities are either estuarine residents (e.g., *C. asper*) or anadromous fish (e.g., *T. pacificus).*

Tides are an important force in estuarine circulation (Dyer, 1973; Kjerfve, 1978; Norcross and Shaw, 1984). The LCRE is longitudinally stratified into three distinct salinity zones (Simenstad et al., 1990; Jay and Dungan Smith, 1990a), which were used in our analyses. It is likely that the circulation of the estuary and the resulting salinity zones are restricting marine fish to the lower and middle reaches of the estuary. The circulation in the LCRE has been described as being closely correlated with tidal currents, density field and river flow (Jay and Dungan Smith, 1990a; Jay and Dungan Smith, 1990b). The LCRE has a high outward flow and short flushing time as a result of tidal influence (Jay and Dungan Smith, 1990a; Jay and Dungan Smith, 1990b) and this may be responsible for concentration of larval fish in the lower reaches (e.g., station SC05 and below) of the estuary and within specific temperature and salinity zones. In Coos Bay, OR, Miller and Shanks (2004) found that abundance and distribution of larval and juvenile fish were related to tidal stage. Spring tides were associated with peaks in abundance of several species and the authors hypothesized that selective tidal-stream transport was a driving mechanism behind these patterns. Sampling in relation to the tides was unfortunately beyond the scope of our study.

Larval fish are both actively and passively distributed throughout aquatic systems, with transport mechanisms often dependent upon physical conditions (Norcross and Shaw, 1984). These physical conditions may result in the transport or retention of larvae into geographical areas of high food densities. Spawning is hypothesized to occur annually during times of high food abundance in order to enhance offspring survival (e.g., the match-mismatch hypothesis; Cushing, 1975; Norcross and Shaw, 1984; Cushing, 1990; Bollens et al., 1992). Parnel et al. (2008) suggested that fish species in the Columbia River plume in the coastal ocean have adapted their life histories to take advantage of nutrient-rich upwelling. The upwelling season and temperatures are suggested by Parnel et al. (2008) to determine the ichthyoplankton assemblage of the plume. Bottom and Jones (1990) found adult fish assemblages of the LCRE to be correlated with season, salinity and also density of potential prey. Specifically, Jones et al. (1990) found potential larval fish prey items to be concentrated in certain salinity zones of the estuary and to be present at similar times of the year (spring); they suggest that zooplankton (e.g., larval fish) may be retained in these same salinity zones and seasons. An explicit test of the food limitation and match-mismatch hypothesis in the LCRE is recommended for future study.

Conclusions

In conclusion, the LCRE had distinct patterns of abundance, composition and distribution of ichthyoplankton during 2006. We identified 30 taxa of ichthyoplankton within the LCRE, the top ten of which accounted for over 98% of the total abundance. Individuals were most abundant during winter and spring, which corresponded with known adult spawning patterns. The majority of species collected were oceanic in origin; however, these species occurred in relatively low abundances. Species of non-oceanic origin (e.g., estuarine residents) were the most abundant species collected. Our ordination analysis showed that variation in the ichthyoplankton community in the LCRE was correlated with salinity, season and temperature. It is evident from our results that the ichthyoplankton community of the LCRE is structured to a significant degree by physical conditions. Larval fish were of low abundance or did not occur during seasons in which salinities and temperatures were high. Instead, peak abundances were observed during seasons of intermediate salinities and temperature. In addition to these physical constraints, further research is needed into biological processes (e.g., food limitation and predation), which would also be expected to affect the larval fish assemblage of the LCRE.

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