Ichthyoplankton community in the Columbia River plume off Oregon: effects of fluctuating oceanographic conditions

Maria M. Parnel

Robert L. Emmett (contact author)

Richard D. Brodeur

Email address for Robert L. Emmett: Robert.Emmett@noaa.gov

National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Hatfield Marine Science Center
2030 S. Marine Science Drive
Newport, Oregon 97365

Abstract—Ichthyoplankton samples were collected at approximately 2-week intervals, primarily during spring and summer 1999–2004, from two stations located 20 and 30 km from shore near the Columbia River, Oregon. Northern anchovy (*Engraulis mordax*) was the most abundant species collected, and was the primary species associated with summer upwelling conditions, but it showed significant interannual and seasonal fluctuations in abundance and occurrence. Other abundant taxa included sanddabs (*Citharichthys* spp.), English sole (*Parophrys vetulus*), and blacksmelts (Bathylagidae). Two-way cluster analysis revealed strong species associations based primarily on season (before or after the spring transition date). Ichthyoplankton abundances were compared to biological and environmental data, and egg and larvae abundances were found to be most correlated with sea surface temperature. The Pacific Decadal Oscillation changed sign (from negative to positive) in late 2002 and indicated overall warmer conditions in the North Pacific Ocean. Climate change is expected to alter ocean upwelling, temperatures, and Columbia River flows, and consequently fish eggs and larvae distributions and survival. Long-term research is needed to identify how ichthyoplankton and fish recruitment are affected by regional and large-scale oceanographic processes.

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The Columbia River and its plume form a biologically rich environment. It is the largest river flowing into the Pacific Ocean in North America (Sherwood et al., 1990), has relatively large salmon runs, a healthy white sturgeon (*Acipenser transmontanus*) population, and probably the largest American shad (*Alosa sapidissima*) run in the world. The Columbia River estuary is also one of the largest estuaries on the west coast (Emmett et al., 2000) and supports abundant piscivorous marine mammal and bird populations (NMFS, 1997; Collis et al., 2002). Important marine fisheries located in the Columbia River plume include those for the following species: Dungeness crab (*Cancer magister*), salmon (*Oncorhynchus* spp.), and Pacific sardine (*Sardinops sagax)* (Emmett et al., 2005, 2006).

River plumes and their associated fronts are important habitats for fishes during their larval stages (Grimes and Funucane, 1991; Govoni and Grimes, 1992; Govoni, 1997). Large freshwater discharges from the Columbia River create abrupt oceanographic fronts that may be important for salmon (Schabetsburger et al., 2003; DeRobertis et al., 2005) and other fish species, and they concentrate some species of zooplankton (Morgan et al., 2005). The Columbia River plume has also been shown to be an important spawning and rearing habitat for some fishes (Richardson, 1981; Doyle et al., 1993, 2002; Doyle, 1995; Emmett et al., 1997), particularly for the northern stock of northern anchovy (*Engraulis mordax*) (Richardson, 1981). This region also has regular upwelling, which is a dominant feature of the California Current system and in the Columbia River plume region, and it ultimately determines the amount of primary, and probably secondary, production within this system (Hickey and Banas, 2003).

Ichthyoplankton surveys have been conducted to augment available abundance data on many commercially important fish species and are often used to determine spawning biomass (Lasker, 1985; Hunter and Lo, 1993) as well as to understand recruitment processes (Bailey, 1981; Cowan and Shaw, 2002). Data sets generated by such ichthyoplankton investigations provide an opportunity to determine the role that oceanographic processes and climate change play in recruitment variability of commercially valuable species.

There have been relatively few ichthyoplankton surveys conducted off the Pacific Northwest. In previous ichthyoplankton surveys conducted off Oregon, Richardson and Pearcy (1977), Brodeur et al. (1985), and Auth and Brodeur (2006) identified the ichthyofaunal community, but these surveys were relatively short in duration and the area near the Columbia River was not sampled. Other coastal ichthyoplankton surveys

have been conducted off the Columbia River, but have been limited to one year (Waldron, 1972) and thus it was not possible to identify any relationship between fluctuations in ocean conditions and changes in the ichthyofaunal community. However, Doyle (1995) did extensive sampling during spring (April–May), and some during other months from 1980–85 and 1987, and found distinct changes in the Northwest ichthyoplankton community resulting from the 1983 El Niño. Later, Doyle et al. (2002) examined ichthyoplankton in the Northeast Pacific, including the Pacific Northwest and the Columbia River plume, and identified regional, onshore, and offshore differences in the ichthyoplankton communities. Northern anchovy was a dominant species off the Pacific Northwest during all these ichthyoplankton surveys. Northern anchovy eggs and larvae have been found to be abundant around the Columbia River plume (Richardson, 1981; Emmett et al., 1997). However, detailed information on the temporal and annual variability of the dominant ichthyoplankton components is lacking. This is noteworthy, given the importance of larval and postlarval fishes in the diets of salmon in the plume region (Schabetsberger et al., 2003; DeRobertis et al., 2005) and the important role that forage fishes, particular northern anchovy, Pacific herring (*Clupea pallasi*), and smelt, play in the diet of piscivorous fishes, mammals, and birds in this region. Our study was initiated to provide data to address this need, and to further elucidate the early life histories of fish species that use the Columbia River plume under a variety of environmental conditions.

Repeated plankton sampling at two stations just south of the mouth of the Columbia River over a 6-year period provided us an opportunity to study interannual and seasonal changes in the diversity and species assemblages in the nearshore ichthyoplankton community of this region. We also identified the effects of fluctuating river flows and nearshore oceanic environmental conditions on the ichthyofaunal community. We were provided this opportunity because of the fortuitous overlap of our research with the regime change in the Pacific Decadal Oscillation (Mantua et al., 1997) in late 2002 (Goericke et al., 2005).

Materials and methods

Study site

The Columbia River has a diverse drainage basin that covers approximately 670,000 km^2 and has average flows of approximately 10,000 m^3/s the latter of which create a surface lens, or plume, of low-salinity water in the adjacent ocean that can extend up to 400 km offshore (Barnes et al., 1972). During summer, the plume flows outward and southward, but during winter it is confined to a narrow band along the Washington coast (Anderson, 1972; Hickey and Banas, 2003). In summer months the plume is characterized by lower salinities (<32 psu), higher turbidities, and higher temperatures than the corresponding variables for surrounding waters and is an important habitat for many species of invertebrates and fishes (DeRobertis et al., 2005; Morgan et al., 2005; Emmett et al., 2006).

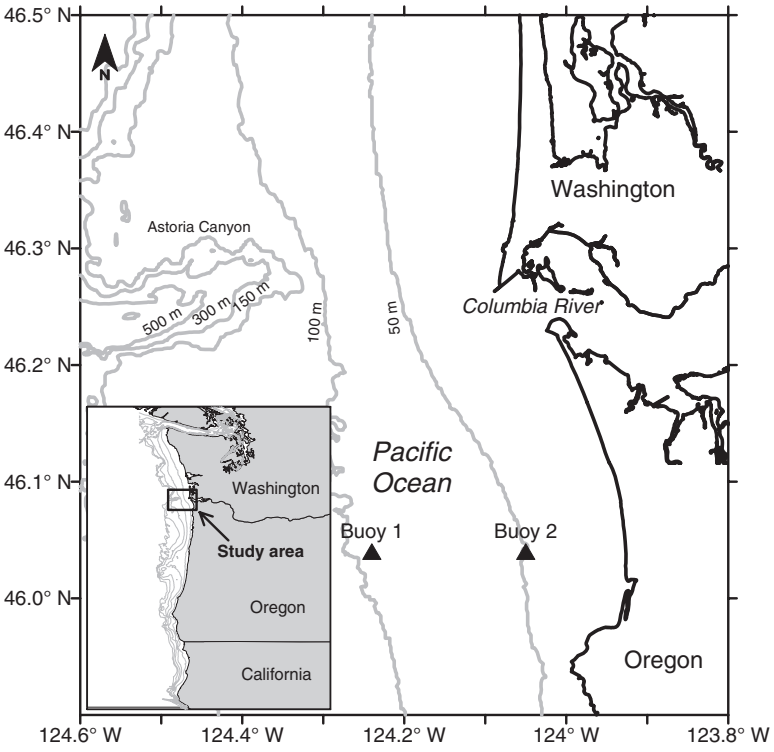

Figure 1

Map of the study area showing locations of two buoys off the Columbia River, Oregon, where ichthyoplankton was collected during survey cruises of the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 1999–2004. Also shown are depth contours (50–500 m) and the location of Astoria Canyon.

Data collection

Plankton samples were collected at two stations approximately every two weeks during the spring and summer, as well as occasionally during fall and winter in 1999–2004 (Table 1). The first station, buoy 1, is located 30 km from the mouth of the river and has a bottom depth of 98 m. The second station, buoy 2, is located 20 km from the mouth of the river and has a bottom depth of 47 m (Fig. 1). Oblique plankton tows to a depth of approximately 40 m were conducted with a 1-m diameter net with 335-μm mesh and a centrally mounted flow meter. The net was washed with seawater after each tow, and the contents were preserved in a 10% buffered formalin in seawater solution. Any large scyphomedusas captured in the net were rinsed and removed from the sample. A Niskin

Table 1

Total number (by year and month) of ichthyoplankton samples collected off the Columbia River, Oregon, during survey cruises conducted by the National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

	1999	2000	2001	2002	2003	2004	Total
January	2	0	0	0	0	0	2
February	0	0	1	0	0	0	1
March	2	2	0	0	0	0	4
April	3	1	0	2	2	2	10
May	4	3	4	1	6	6	24
June	2	2	6	3	6	4	23
July	2	2	5	2	4	4	19
August	0	0	0	0	0	0	0
September	1	0	0	0	0	0	1
October	0	0	0	0	0	0	0
November	0	0	0	0	0	0	0
December	1	0	0	0	0	0	1
Total	17	10	16	8	18	16	85

bottle was used to collect a water sample for chlorophyll analysis at the 3-m depth at each station. A conductivity-temperature-depth (CTD) cast was also conducted to within 5 m of the bottom at each station.

Before they were sorted, ichthyoplankton samples were rinsed in fresh water with a 332-μm mesh sieve. The samples were then poured into a large Pyrex dish on a light box. All fish larvae and eggs were removed from the samples. Identifications were made to the lowest possible taxa by using a dissecting microscope and taxonomic information, primarily from Matarese et al. (1989) and Moser (1996). Zooplankton volume was determined by allowing the sample to settle in a graduated cylinder overnight. Zooplankton volumes and ichthyoplankton densities were standardized by adjusting these numbers by the volume of water filtered by the net.

Data analysis

Species diversity was calculated with the Shannon-Weaver index of diversity, H' (Shannon and Weaver, 1949; Krebs, 1989), where higher values denote greater species diversity. Species evenness was calculated with Simpson's index of evenness, λ, which ranges between 0 and 1, and where a value of 1 indicates that all taxa have the same density within a sample (Krebs, 1989).

To eliminate the effect of rare and uncommon taxa, data from each station were filtered to remove those taxa that occurred in less than 5% of the samples, thus leaving 12 egg taxa and 12 larval taxa for further analysis of the community structure. Agglomerative hierarchical two-way cluster analyses were conducted to identify taxa and sample assemblages. For this analysis, densities were averaged from both stations from a single collection date. Samples with no ichthyoplankton were excluded. Catch distributions were highly skewed and thus were $\log_{10}(catch/1000\ m^3+1)$ transformed to de-emphasize the few high catches. We constructed separate two-way clusters for eggs and larvae data with the Bray-Curtis distance measure and a flexible beta (β=−0.25) clustering algorithm, using PC-ORD software (vers. 5, MJM Software Design, Gleneden Beach, OR).

A nonparametric multiresponse permutation procedure (MRPP) (Kruskal, 1964; Mather, 1976) was used to test the hypothesis of no difference between two or more groups. Factors tested were station (buoy 1 and 2), year (1999, 2000, 2001, 2002, 2003, 2004), and season (downwelling and upwelling), before and after the spring transition date as defined by Logerwell et al. (2003). The date of the spring transition is the day when the ocean conditions switch from downwelling to upwelling, as identified by analyzing Bakun upwelling indices and sea level conditions along the Pacific Northwest (Logerwell et al., 2003). Identification of the primary taxa associated with each grouping was done by using an indicator species analysis (ISA). The ISA measures the fidelity of a taxon within a particular group in relation to its abundance in all groups and assigns an indicator value for that taxon per group. A statistical significance was then calculated by a Monte Carlo resampling method with 1000 runs. These tests were also run with PC-ORD V5 software. Relationships between environmental conditions and the ichthyoplankton community were investigated by using the BVSTEP procedure in the PRIMER software package (vers. 5, PRIMER-E Ltd, Lutton Ivybridge, UK). This analysis is analogous to forward stepwise multiple regression and compares nonparametrically paired species and environmental similarity matrices. Species similarity matrices were calculated by using Bray-Curtis similarities on fourth-root transformed data. Environmental matrices

were calculated by using the normalized Euclidean distance on fourth-root transformed data. Environmental variables in the analysis included sea surface temperature, salinity, chlorophyll *a* at 3 m, the settled volume of zooplankton, and Columbia River flow (measured by U.S. Geological Survey at Beaver, OR).

A paired *t*-test was used to determine if environmental conditions and zooplankton volumes at the two stations were significantly different. To account for interannual and seasonal variations in sampling, only those samples collected within a similar season were considered. All statistical tests were considered significant at the $\alpha < 0.05$ level.

Results

In total, 85 samples were collected during this study, comprising a total of 155,302 fish eggs and 3565 fish larvae, representing 34 taxa and 17 families. However, a majority (n=78) of these samples were taken from April to August and formed the primary data set that was analyzed (Table 2). The family Pleuronectidae had the greatest number of taxa (9), followed by the family Cottidae (6). The actual number of fish species collected was probably higher than the number we report because some eggs and larvae could be identified only to genus or family, namely eggs and and larvae of Osmeridae, Bathylagidae, *Citharichthys* spp., *Sebastes* spp., and *Sebastolobus* spp. Nine taxa were found only once during our sampling.

The most abundant fish eggs were those of northern anchovy, sanddab (*Citharichthys* spp.), blacksmelt (*Bathylagus* spp.), jack mackerel (*Trachurus symmetricus*), and Pleuronectidae, in descending order of abundance (Fig. 2A). The most abundant larvae, in descending order, were northern anchovy, English sole (*Parophrys vetulus*), sand sole (*Psettichthys melanostictus*), rex sole (*Glyptocephalus zachirus*), and Pacific tomcod (*Microgadus proximus*) (Fig. 2B). The unidentified Pleuronectidae eggs were of four species (butter sole [*Isopsetta isolepis*], English sole, starry flounder [*Platichthys stellatus*], and sand sole) which cannot be identified to species at early egg stages. Unusual egg occurrences included those of Pacific viperfish (*Chauliodus macouni*), opah (*Lampris guttatus*), and jack mackerel. These species are considered either offshore (viperfish and opah) or southern, warm-water spawners (jack mackerel). Jack mackerel eggs were observed in 1999–2002, but not in 2003 or 2004 (Fig. 2A). Peak jack mackerel spawning occurred in July 1999 and June 2000–2002, although some eggs were also found from May to September during most years.

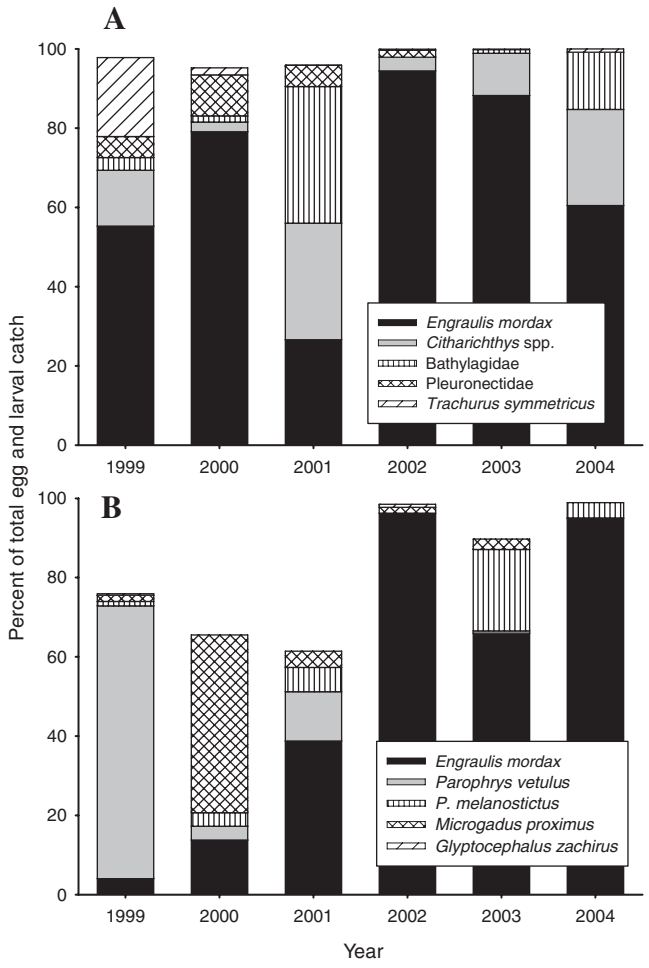

Figure 2

The top five egg (**A**) and larval (**B**) taxa collected at two stations off the mouth of the Columbia River, Oregon, as a percentage of total catch for each year from 1999 through 2004.

Northern anchovy accounted for 76% of all eggs collected, and were found from May through July (Fig. 3). Overall, northern anchovy were present in 53 of the total 85 samples collected. Peak northern anchovy egg abundance varied interannually, occurring in June of 1999, 2001, and 2002; July of 2000; and in May of 2003. The highest annual density of northern anchovy eggs was observed in 2003, when eggs were almost four times as abundant as those observed in 2002 (Fig. 3). Northern anchovy eggs dominated the catch in all years except 2001, when blacksmelt and sanddab contributed about equally to the catch (Fig. 2).

Northern anchovy larvae were the most abundant fish larvae, and represented 68% of all larvae collected. In 1999, 2001, and 2002, peak numbers of these larvae occurred in June, whereas in 2000, northern anchovy larval numbers peaked in July. In 2003 and 2004, northern anchovy larval numbers peaked in May and represented the majority of the larval fish catch (Fig. 2B).

Nine samples contained only one egg or larval fish species (and therefore a diversity and evenness of zero), and three samples contained no ichthyoplankton. Overall sample diversity ranged

Table 2

Taxonomic and stage composition of ichthyoplankton collected during survey cruises conducted by the National Oceanic and Atmospheric Administration, National Marine Fisheries Service approximately every two weeks from late April to August 1999–2004 from two stations located off the Columbia River, Oregon. Occurrence is the number of samples in which the life stage of a taxon was found.

Species	Common name	Occurrence (n=78)	Density (no. /1000 m^3)	Number captured	Stage collected
Clupeidae					
Sardinops sagax	Pacific sardine	4	0.00899	86	Eggs
Engraulidae					
Engraulis mordax	Northern anchovy	52	7.09502	118,089	Eggs
		23	0.18015	2435	Larvae
Bathylagidae	Blacksmelts	18	0.81678	11,027	Eggs
Chauliodontidae					
Chauliodus macouni	Pacific viperfish	2	0.00012	2	Eggs
Gadidae					
Microgadus proximus	Pacific tomcod	13	0.00278	32	Larvae
Lampridae					
Lampris guttatus	Opah	1	0.00011	1	Eggs
Gasterosteidae	Stickleback	1	0.0001	1	Larvae
Scorpaenidae					
Sebastes spp.	Rockfish	2	0.00021	2	Larvae
Sebastolobus spp.	Thornyheads	5	0.0004	6	Eggs
Hexagrammidae					
Ophiodon elongatus	Lingcod	2	0.00186	2	Larvae
Cottidae					
Artedius spp.[1]		1	0.00007	1	Larvae
Artedius harringtoni	Scalyhead sculpin	2	0.00031	5	Larvae
Clinocottus acuticeps	Sharpnose sculpin	1	0.00012	1	Larvae
Leptocottus armatus	Staghorn sculpin	1	0.00026	2	Larvae
Ruscarius meanyi	Puget Sound sculpin	1	0.00008	1	Larvae
Liparidae					
Liparis spp.	Unid. snailfish	2	0.00018	3	Larvae
Liparis fucensis	Slipskin snailfish	1	0.00008	1	Larvae
Liparis pulchellus	Showy snailfish	2	0.00025	3	Larvae
Carangidae					
Trachurus symmetricus	Jack mackerel	15	0.19986	2178	Eggs
Bathymasteridae					
Ronquilis jordani	Northern ronquil	1	0.00095	12	Larvae
Pholidae					
Pholis spp.	Unid. gunnel	1	0.00004	1	Larvae
Icosteidae					
Icosteus aenigmaticus	Ragfish	2	0.00034	4	Eggs
Ammodytidae					
Ammodytes hexapterus	Pacific sandlance	2	0.00187	2	Larvae
Paralichthyidae					
Citharichthys spp.	Sanddab	50	1.66568	22,186	Eggs
		1	0.00008	1	Larvae
Pleuronectidae	Unid. flounder	20	0.04348	673	Eggs
		2	0.00029	3	Larvae
Glyptocephalus zachirus	Rex sole	6	0.00667	34	Eggs
		3	0.00546	5	Larvae
Isopsetta isolepis	Butter sole	6	0.00072	9	Larvae
Lepidopsetta bilineata	Southern rock sole	1	0.00029	4	Larvae

continued

Table 2 (continued)

Species	Common name	Occurrence (n=78)	Density (no. /1000 m^3)	Number captured	Stage collected
Pleuronectidae (cont.)					
Lyopsetta exilis	Slender sole	4	0.00082	9	Eggs
		2	0.00016	2	Larvae
Microstomus pacificus	Dover sole	8	0.00566	65	Eggs
		4	0.00123	24	Larvae
Parophrys vetulus	English sole	6	0.00101	11	Larvae
Platichthys stellatus	Starry flounder	1	0.00016	2	Larvae
Pleuronichthys decurrens	Curlfin sole	4	0.00504	5	Eggs
		1	0.00015	2	Larvae
Psetticthys melanostictus	Sand sole	7	0.00920	112	Eggs
		17	0.01202	164	Larvae

[1] Either *Artedius corallinus* or *A. notospilotus*.

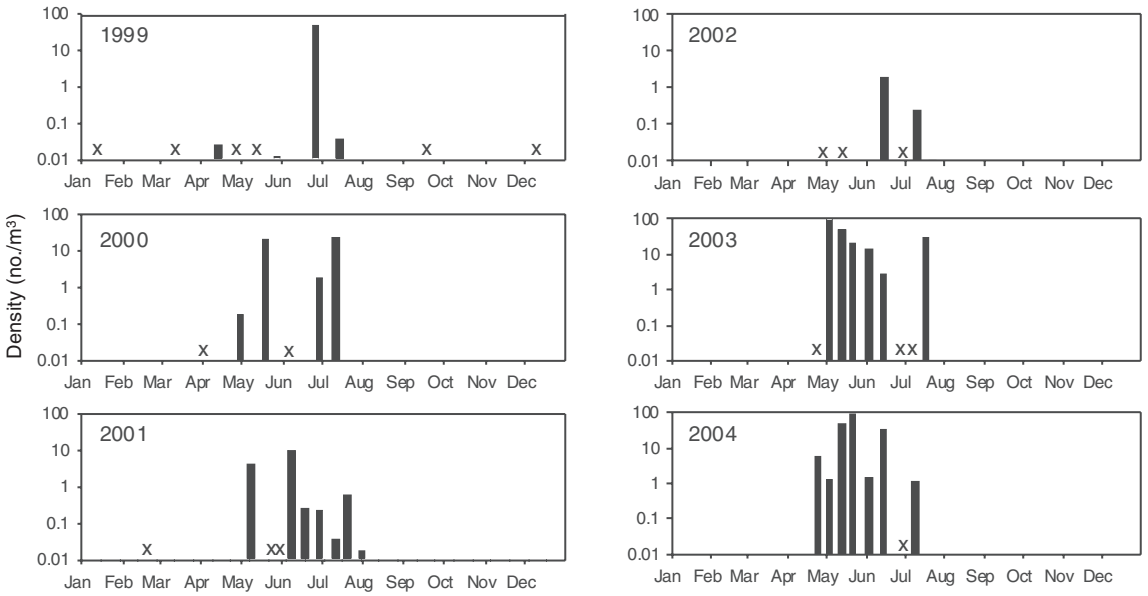

Figure 3

Densities of northern anchovy (*Engraulis mordax)* eggs sampled off the mouth of the Columbia River, Oregon, in relation to sampling date for 1999 through 2004 (note log scale on *y*-axis). An X represents dates when sampling occurred but no northern anchovy eggs were collected.

from 0 to 1.7 and evenness from 0 to 1. Over all years, diversity was highest in April for eggs at both stations and for larvae at buoy 1, whereas at buoy 2, peak diversity for larvae occurred in March. Lowest diversities occurred in late fall and especially in December. Evenness was highest in April and lowest in December.

More than half of all species included in the egg-stage cluster analysis were flatfish from the families Pleuronectidae and Paralichthyidae (Fig. 4) . The most closely grouped species were the northern anchovy and sanddab. Other taxa with a similar abundance pattern included the blacksmelt (Bathylagidae) and Pleuronectidae. Three sampling groups emerged in the egg cluster analysis (Fig. 4). The first group or cluster (A) consisted mainly of samples collected in winter–spring (December–early May), before the spring transition, and was dominated by rex sole and other flatfishes. Cluster B was composed of mainly late spring (April–June) samples and was dominated by jack mackerel and sanddab eggs. In contrast, Cluster C was predomi-

nately a spring–summer (May–July) group dominated by northern anchovy, sanddab, and blacksmelt (Fig. 4).

Among the larvae, Pacific sandlance (*Ammodytes hexapterus*), rex sole, and curlfin sole (*Pleuronichthys decurrens)* were tightly clustered, as were northern anchovy and thornyheads (*Sebastolobus* spp.) (Fig. 5). The remaining larger clusters consisted of mainly flatfishes and Pacific tomcod. Sampling clusters were less defined for larval fish than for eggs (Fig. 5). Cluster A consisted of samples collected from multiple years and months, and most were collected before the spring transition. No species dominated these collections. In contrast, Cluster B was dominated by Pacific tomcod and Dover sole (*Microstomus pacificus*). Cluster C occurred entirely during May and June and was distinguished by the high abundance of northern anchovy (Fig. 5).

There were very limited differences in the biological or physical oceanographic conditions between the two sampling stations. Only salinity was significantly different between the two stations (t-test, $P<0.05$). Temperature, chlorophyll a, zooplankton densities, and densities of the five most abundant ichthyoplankton species were not significantly different between stations. However, there were significant annual differences in temperatures (ANOVA, $P<0.05$), but not salinities or chlorophyll a at these stations during the study period (Table 3). There were also large annual differences in the date of the spring transition (Table 3). The BVSTEP analysis revealed that temperature explained most of the interannual variation in the ichthyoplankton community (Spearman $\rho=0.345$), (ρ ranges from –1 to 1, where values farthest from zero indicated a stronger correlation) followed by salinity ($\rho=0.194$) and Columbia River flow ($\rho=0.145$). Chlorophyll a and overall ichthyoplankton densities did not provide any explanatory power and did not relate to variations in ichthyoplankton species composition.

The egg and larval fish data showed very few differences when these data were grouped and compared by year, season, and station. MRPP analysis revealed few significant differences between groups (Table 4). The taxonomic composition of the dominant egg or

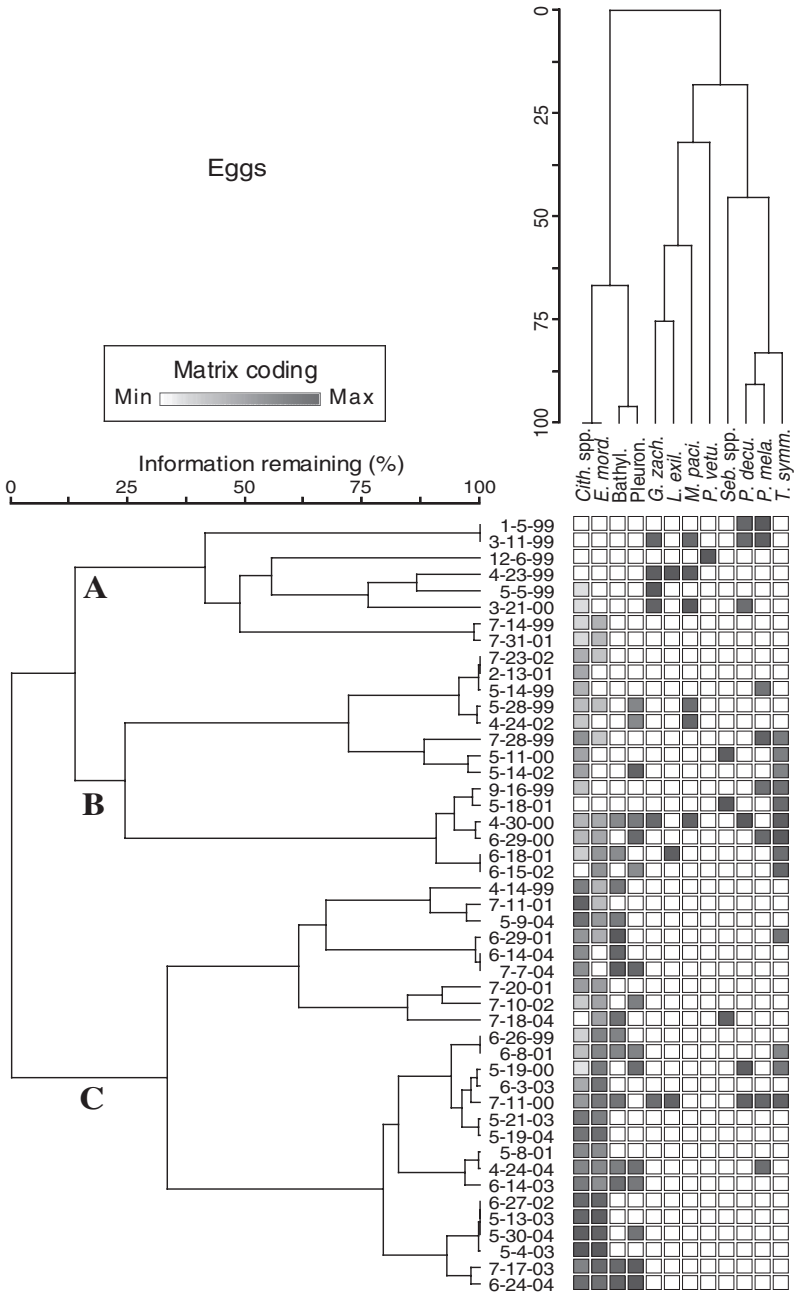

Figure 4

Two-way cluster analysis of egg densities by sampling date. The taxa clusters are oriented vertically at the top of the figure and sampling date clusters are oriented horizontally at the left side of the figure. The color of the boxes denotes relative abundance of each taxon during each sampling period as shown in the matrix coding legend. The taxa names are abbreviated as: *Cith.* spp. (*Citharichthys* spp.), *E. mord.* (*Engraulis mordax*), Bathyl (Bathylagidae), Pleuron. (*Pleuronectidae), G. zach. (Glyptocephalus zachirus), L. exil. (Lyopsetta exilis), M. paci. (Microstomus pacificus),* P. vetu. (*Parophrys vetulus*), *Seb.* spp. (*Sebastolobus* spp.), *P. decu.* (*Pleuronichthys decurrens*), *P. mela.* (*Psetticthys melanostictus*), and *T. symm.* (*Trachurus symmetricus*). "Information remaining" is a scaled measure of the amount of information that is left after stations are grouped.

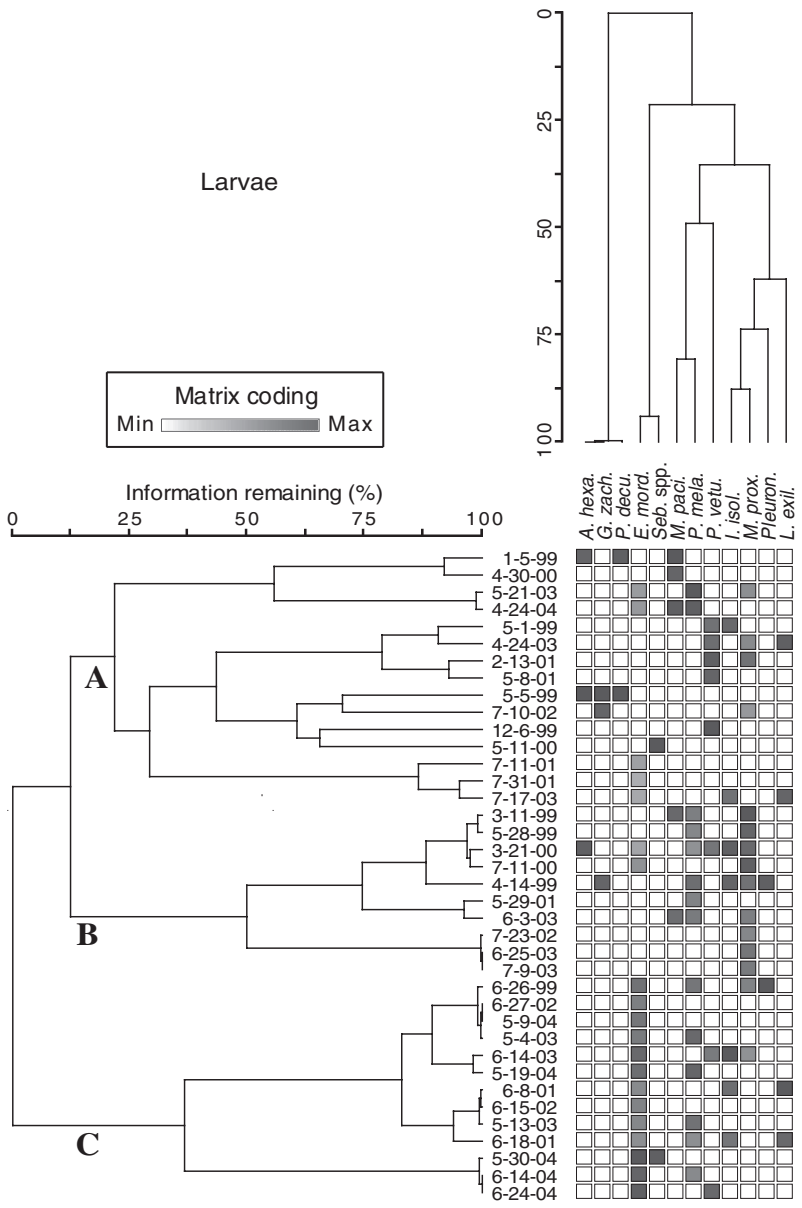

Figure 5

Two-way cluster analysis of larval densities by sampling date. The taxa clusters are oriented vertically at the top of the figure and sampling dates are oriented horizontally at the left side of the figure. The color of the boxes denotes relative abundance of each taxon during each sampling period as shown in the matrix coding legend. The taxa names are abbreviated as: *A. hexa.* (*Ammodytes hexapterus*), *G. zach.* (*Glyptocephalus zachirus*), *P. decu.* (*Pleuronichthys decurrens*), *E. mord.* (*Engraulis mordax*), *Seb.* spp. (*Sebastes* spp.), *M. paci.* (*Microstomus pacificus*), *P. mela.* (*Psetticthys melanostictus*), *P. vetu.* (*Parophrys vetulus*), *I. isol.* (*Isopsetta isolepis*), *M. prox.* (*Microgadus proximus*), Pleuron. (Pleuronectidae), and *L. exil.* (*Lyopsetta exilis*). "Information remaining" is a scaled measure of the amount of information that is left after stations are grouped."

larval taxa did not differ between the two stations, and no indicator species were identified for either station. Year of sampling was a significant factor for eggs; 2003 and 2004 showed a different composition from most other years. However, eggs of only 3 of the 12 species (curlfin sole and jack mackerel for 2000; northern anchovy for 2003) were determined to be useful indicator species. Season was not a significant factor overall for eggs, or for the two taxa considered indicators of downwelling and upwelling conditions. For larvae, year was a marginally insignificant factor overall, although there were pairs of years that were significantly different. Season was a significant factor for larvae: Dover sole and English sole larvae were indicative of winter downwelling, and northern anchovy were indicative of summer upwelling seasons. Station was not a significant factor for eggs or larvae.

Discussion

The timing of upwelling (spring transition), and its associated ocean temperatures, appears to be very important in determining the structure of the ichthyofaunal community off the Columbia River and probably within the California Current. Upwelling is what brings nitrates into the Columbia River plume (Lohan and Bruland, 2006) and the California Current and ultimately determines primary and probably secondary production (Hickey and Banas, 2003). As such, it is not surprising that fishes within this region have evolved life histories adapted to its presence (Bowen and Grant, 1997; Ware and Thomson, 1991). However, although upwelling drives the nutrient enrichment processes it also can disrupt the abilities of larval coastal fishes to successfully recruit if they are unable to take advantage of transport and retention processes (Bakun, 1996).

Several factors account for the high abundance of northern anchovy eggs and larvae captured during our study. The Columbia River plume is an important spawning habitat for northern anchovy (Richardson, 1981; Emmett et al., 1997) and most samples were collected during the typical northern anchovy spawning season (May–August). Fur-

Table 3

Average annual 3-m salinity, temperature, and chlorophyll *a* values at two stations off the Columbia River, Oregon. Also shown is average spring (April–June) Columbia River flows and day of the spring transition. The day of the spring transition (when upwelling begins) was identified with the methods of Loggerwell et al., 2003. Only temperature and Columbia River flows were found to have significant annual differences (ANOVA, $P<0.05$).

Year	Salinity	Temperature (°C)	Chlorophyll *a* (μg/L)	Columbia River flows (m^3/s)	Day of spring transition
1999	28.53	11.51	4.81	9999	1 Apr
2000	29.92	12.61	2.34	8132	12 Mar
2001	29.19	13.28	2.66	4506	2 Mar
2002	27.93	12.61	6.12	8640	21 Mar
2003	26.68	12.93	5.61	8316	22 Apr
2004	27.50	14.09	5.07	6777	19 Apr

Table 4

Results of the multi-response permutation procedure (MRPP) and indicator species analysis (ISA) for annual, seasonal (before and after the spring transition [Logerwell et al., 2003]), and station differences in composition of the dominant egg and larval ichthyoplankton taxa. Shown are the MRPP *A*-statistic, overall significance value, and significant pair-wise comparisons that emerged. The significant indicator species are listed with the year or season with which each species is associated in parentheses.

Stage	Variable	MRPP *A*-statistic	*P* value	Significant differences between levels	Significant indicator species
Eggs	Year	0.1253	<0.001	2003 ≠ all years but 2004 2004 ≠ all years but 2002, 2003	*Pleuronichthys decurrens, Trachurus symmetricus* (2000), *Engraulis mordax* (2003)
	Season	0.0231	0.087	None	*Psetticthys melanostictus, Microstomus pacificus* (downwelling), *E. mordax, Citharichthys* spp. (upwelling)
	Station	0.0019	0.631	None	None
Larvae	Year	0.1027	0.068	2003 ≠ 1999 and 2004 2002 ≠ 2004	*E. mordax* (2004)
	Season	0.0787	0.018	downwelling ≠ upwelling	*Parophrys vetulus, M. pacificus* (downwelling) *E. mordax* (upwelling)
	Station	0.0003	0.412	None	None

thermore, northern anchovy eggs are positively buoyant and appear to concentrate in plume fronts (Morgan et al., 2005), which often occurred in our sampling region. The observed annual increase in northern anchovy egg densities appear to be strongly linked to the increase in the abundance of adult northern anchovy population in the study area (Emmett et al., 2006). Anchovy egg densities also may have been influenced by Columbia River spring flows. For example, densities of northern anchovy egg and larvae were lower in 2001, a drought year during which Columbia River flows were very low and the plume area was relatively small (Brodeur et al., 2005). However, numbers of northern anchovy eggs were also down in 2002, which was not a drought year, but was the year that the Pacific Decadal Oscillation (PDO) changed from negative to positive (Goericke et al., 2005).

Richardson (1981) found that the peak of northern anchovy spawning in 1975 and 1976 occurred in July, whereas we found that the peak of spawning occurred in May during five of the six study years. However, this difference could have been due to Richardson (1981) not sampling in May and June. Brodeur et al. (1985) found northern anchovy spawning during April 1983, but 1983 was a strong El Niño year and therefore there were unusually warm ocean conditions. Jones et al. (1990) found northern anchovy eggs and larvae in the Columbia River estuary from April to September 1980,

with a peak in June. We are not certain whether the timing of northern anchovy spawning has shifted to earlier months, whether this early spawning was missed by previous surveys, or whether we have two different age-groups spawning at different times. Nevertheless, our results indicate that timing of northern anchovy egg surveys is an important parameter to consider during surveys to estimate spawning biomass (Emmett et al., 1997) and feeding success relative to plankton production cycles (Bollens et al., 1992).

Jack mackerel, which generally spawn off southern California (MacCall and Stauffer, 1983), are not commonly collected as juveniles very far north in the California Current. Because jack mackerel eggs hatch in 4.3 days at 12°C (Farris, 1961) and because we observed jack mackerel larvae, it appeared that jack mackerel spawned in the general vicinity of our study area. Jack mackerel spawning has been reported off Washington State and southern Oregon (Ahlstrom, 1956), but not for many years. Ahlstrom (1956) noted that there is a northward progression of the spawning season in areas north of Point Conception, California. During our study period, it was possible that adult jack mackerel moved north and into cooler waters inshore to feed and spawn. The recent capture of age-0 jack mackerel during pelagic fish surveys off Oregon and Washington (Brodeur et al., 2006) indicates that jack mackerel have recently spawned and recruited successfully off the Pacific Northwest coast.

The occurrence of rare taxa, such as opah, can be attributed to the long incubation time (up to 3 weeks) exhibited by most lampriform fish eggs (Olney, 1984). In this time, an egg spawned in the open ocean, the normal habitat of this species, could drift inshore to our sampling area. Similarly, Pacific viperfish eggs, released in the open ocean, can drift inshore. Little is known about their egg incubation period.

The occurrence of several offshore ichthyoplankton species in our study area may be related to the local topography. The Astoria Canyon lies directly seaward from the mouth of the Columbia River. During the upwelling season, the canyon causes currents to flow landward (Hickey, 1997), thus carrying normally offshore organisms closer to shore. Bosley et al. (2004) concluded that currents over the Astoria Canyon concentrate oceanic organisms and transport them shoreward and these actions may explain the occurrences of opah, Pacific viperfish, and jack mackerel eggs, and other offshore species (Richardson and Pearcy, 1977) in our coastal sampling.

Egg and larval composition at the two sampling stations did not differ significantly, probably because they were relatively close and thus had similar environmental conditions. Out of a total of five physical variables tested, only salinity was found to be significantly different between the two stations. Surface salinity is highly variable in this region because of the proximity of the Columbia River plume. While the plankton tow depths at each station were the same (40 m), we would have missed eggs and or larvae occurring below 40 m at the station farther offshore (buoy 1), which was in substantially deeper water. Boehlert et al. (1985) and Auth and Brodeur (2006) found fish larvae at depths greater than 40 m off the coast of Oregon, although the majority of fish larvae were in surface waters.

The cluster dendrograms were dominated by flatfish species because of the high number of pleuronectid species found along the Oregon coast, as well as the tendency of most of these species to have pelagic eggs. Overall patterns in the egg and larval clusters changed seasonally, and many of the samples collected during the downwelling or upwelling seasons were clustered together. MRPP analysis verified that season was an significant contributor to these cluster groups. The larval indicator species for downwelling conditions were English sole and Dover sole, which are typically winter spawners (although some spawning may occur all year). The indicator species for the upwelling season was northern anchovy, which spawns primarily in the spring and summer. In general, benthic and nearshore species spawn in winter, when larvae are less likely to be transported offshore. In 2003, the PDO shifted from a cool (negative) to a warm (positive) phase. This change resulted in southern or offshore taxa becoming more abundant in 2003–04. However, ichthyoplankton taxa in 2003 and 2004 were also significantly different mainly because of substantial increases in eggs and larvae of northern anchovy, a taxon that is not southern affiliated. The increase in northern anchovy eggs and larvae appeared linked to an increase in the abundance of the adult population.

Large-scale climate variability (as observed during our study period) can cause large changes in fish populations (Cushing, 1982; Beamish, 1993; Francis et al., 1998; Chavez et al., 2003). Pearcy (2002) and Brodeur et al. (2003, 2006) found that abnormal ocean conditions alter the ichthyofauna in the California Current region. Changing climate conditions can alter currents that advect fish eggs and larvae to or away from nursery areas, thus affecting recruitment. Altered currents may also lower the density and change the species composition of planktonic food organisms (Peterson and Schwing, 2003) and thus inhibit larval fish from finding adequate prey resources. In late 2002, the PDO (Mantua et al., 1997) became positive (with warm conditions) after four years of being negative (with cold conditions) (Goericke et al., 2005) and caused warmer ocean temperatures, increased diversity of warm-water copepods, and decreased cold-water copepods in the California Current (Hooff and Peterson, 2006). Changes in ocean temperatures can also cause shifts in the locations or timing of spawning and affect developmental durations through the early life stages of fishes (Sabatés et al., 2006; Phillips et al., 2007). Faster development through the egg and yolk-sac stages may help to minimize the time eggs are vulnerable to invertebrate predation (Bailey, 1981). In the California Current region, upwelling is the dominant feature that influences primary production, and therefore any climate-induced change that affects upwelling or Califor-

nia Current circulation patterns will alter zooplankton prey that larval fish feed on.

Climate-induced change in upwelling patterns, sea surface temperatures, and perhaps Columbia River flows will have large effects on the larval fish within our study area and in the broader California Current region. We examined interannual variation in the abundance of fish eggs and larvae in the Columbia River plume and have shown that the ichthyoplankton community changes in relation to the dynamic oceanographic processes of this region. However, research over a greater area and on a longer time scale is needed to determine the effects of these processes on the ichthyoplankton community, as well as to determine how recruitment of marine fish is being affected by regional and larger-scale variability in the marine environment.

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