

Plankton Assemblage Variability in a River-Dominated Temperate Estuary During Late Spring (High-flow) and Late Summer (Low-flow) Periods

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Abstract Seasonally variable freshwater flows are known to influence estuarine plankton assemblages. There has been little recent study of the plankton dynamics of the Columbia River Estuary (CRE), a large, river-dominated estuary that has experienced great modification to its hydrological cycle. Zooplankton (>75 µm) were collected during four late spring (high-flow) cruises and three late summer (low-flow) cruises in 2005 and 2006. Surface-water microplankton (5–200 µm) were collected during cruises in 2005. Zooplankton and phytoplankton assemblage composition varied along an axial salinity gradient and between flow periods. Estuarine zooplankton were strongly seasonal and dominated by the calanoid copepod *Eurytemora affinis* in the late spring, high-flow period and by the invasive calanoid *Pseudodiaptomus forbesi* in the late summer, low-flow period. The phytoplankton assemblage was dominated by freshwater diatoms, primarily *Aulacoseira* spp. The ciliate *Mesodinium rubrum* (= *Myrionecta rubra*) reached high densities during the low-flow period, but otherwise, distinct high-flow and low-flow

phytoplankton assemblages were not detected. Comparison to prior studies in the CRE suggests that the plankton assemblage composition during the low-flow period has undergone considerable change, which may in turn have important trophic implications.

Keywords Zooplankton · Microplankton · Columbia River Estuary · Freshwater flow · Non-indigenous species · Copepods · *Mesodinium* · *Pseudodiaptomus*

Introduction

Estuaries are physically complex environments that support an abundance of organisms. Lower trophic levels are often living at physiological extremes, but the few taxa that are adapted to the estuarine environment thrive and can reach very high densities, supporting macrozooplankton, fish, and other higher level consumer populations. Estuarine zooplankton assemblages are commonly regulated by salinity and temperature and in many estuaries there is a predictable seasonal succession of dominant copepod taxa (Jeffries 1962; Wooldridge and Melville-Smith 1979). Phytoplankton assemblages may likewise vary with salinity and temperature and also with level of turbulence, turbidity, light, and nutrients (Margalef 1978; Muylaert et al. 2000; Cloern and Dufford 2005; Rothenberger et al. 2009; Shen et al. 2011). The timing and magnitude of freshwater discharge, through its influence on salinity, temperature, mixing, nutrient delivery, and residence time (among other factors), may play an important role in determining species composition within estuaries.

As global climate continues to warm, patterns of precipitation are changing (Dore 2005). In the Pacific Northwest of the U.S., precipitation is increasingly falling as rain rather than snow (Wu et al. 2012). For rivers of the Pacific Northwest whose discharge is dominated by snow-melt, this is predicted

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to result in an increase in winter river discharge, a decrease in summer discharge, and maximum discharges occurring earlier in the year (Wu et al. 2012). Earlier peak discharges could affect the timing and/or magnitude of spring plankton blooms (Yin et al. 2005). Decreased summer discharges will increase water residence times in the estuaries of these rivers and increase the potential for local warming. To predict how plankton assemblages in the estuaries of snow-melt dominated rivers will respond to long term changes in temperature and the hydrological cycle, it is necessary to understand their current relationships with these variables as well as to a host of other potentially influential factors.

The Columbia River is the second largest river in the United States and its discharge influences the physical and biological environment of the northeast Pacific Ocean and neighboring estuaries (Roegner et al. 2002; Hickey and Banas 2003; Peterson and Peterson 2008). The hydrological cycle, morphology, and ecology of the Columbia River have already been substantially modified by human activity. The building of dams, bathymetric changes due to dredging and diking, and water removal have dampened variability in discharge and increased stratification and residence time in the estuary (Sherwood et al. 1990; Bottom et al. 2005). The creation of a series of impoundments along the river has promoted freshwater phytoplankton growth (Sullivan et al. 2001) and shipping activity has brought non-indigenous taxa to the river and estuary (Cordell et al. 2008). In the Columbia River Estuary (CRE), here defined as the saline reach of the river system, the results of these physical changes as modeled by Sherwood et al. 1990 have likely resulted in differential exploitation by planktonic taxa. Two known examples include an invasive Asian calanoid copepod (Orsi and Walter 1991), *Pseudodiaptomus forbesi*, that now dominates the zooplankton (>75 μm) assemblage present during the late summer period (Bollens et al. 2012). Second, and perhaps most obvious, are the extensive “red water” blooms of the coastal and estuarine mixotrophic ciliate, *Mesodinium rubrum* (= *Myrionecta rubra*), which for at least the past several decades has formed persistent late summer and autumn blooms in the estuary (Herfort et al. 2011). The most recent investigation of the plankton community was over 20 years ago (Simenstad et al. 1990); thus, it is unclear how the plankton community as a whole has changed since these two perturbations.

Seasonally variable freshwater flows are known to influence estuarine plankton abundance and assemblage via physical forcing (e.g., mixing, residence time) and delivery of nutrients, organic matter, and sediment (Schlacher and Wooldridge 1996; Livingston et al. 1997; Gillanders and Kingsford 2002; Kimmerer 2002; Vincent et al. 2002), although how estuarine assemblages differ with varying levels of freshwater discharge remains largely undescribed in many estuaries. The specific objectives of this study were to (1)

describe the zooplankton (>75 μm) and autotrophic microplankton (5–200 μm) assemblages present in the CRE and to (2) compare them between late spring (high river flow) and late summer (low river flow) periods, to (3) relate variation in assemblages to environmental variables, and to (4) compare that variation between zooplankton and autotrophic microplankton assemblages. Finally, we (5) address differences and similarities between sampled assemblages and those present approximately 40 years ago and discuss these differences in light of past changes in river flow and the introduction of new species.

Methods

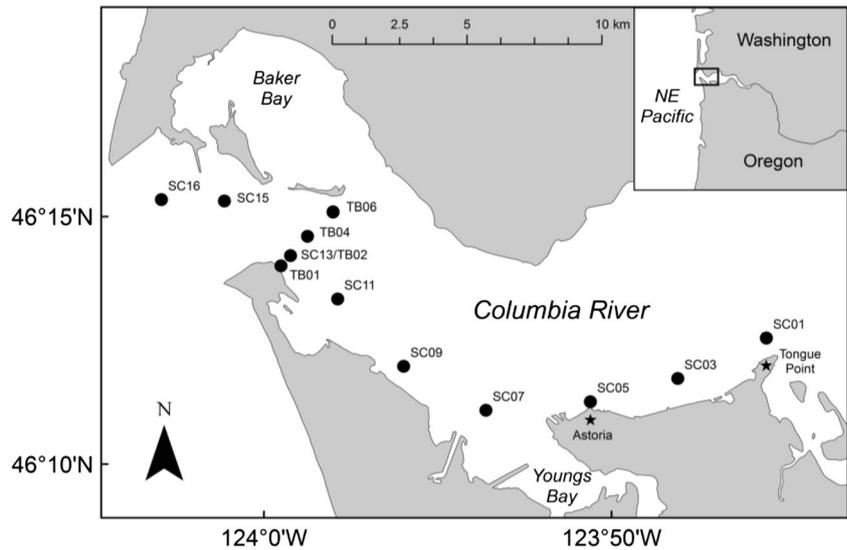
Sampling Location

The CRE is a river-dominated, mesotidal estuary that experiences mixed semi-diurnal tides (Chawla et al. 2008). Two seasonal peaks in discharge occur each year: a larger peak in April–June due to snowmelt, with flows generally exceeding $10,000 \text{ m}^3 \text{ s}^{-1}$, and a second peak in November–March due to winter rainfall (Hickey et al. 1998; Chawla et al. 2008). These flow patterns result in a partially-mixed water column. Increased salinity intrusion occurs during the low-flow period (July–October), where flows may drop below $2,000 \text{ m}^3 \text{ s}^{-1}$ (Chawla et al. 2008), and may extend 20–44 km from the mouth (<http://www.stccmop.org/>). Salinity stratification varies on a spring–neap cycle, with stratification and salinity incursion being greater on neap tides (Jay and Smith 1990). The estuary has two channels which separate 15 km from the mouth; the south channel is dredged and more highly influenced by freshwater discharge, whereas the north channel is more tidally influenced (Chawla et al. 2008). Residence time in the estuary has been estimated at 1–9 tidal cycles (Neal 1972).

Sampling

Zooplankton and microplankton were sampled during seven cruises aboard the M/V *Forerunner* timed to occur during late spring, high river flow or late summer, low river flow periods. Spring cruise dates — June 9, 2005, June 23, 2005, May 30, 2006, and June 22, 2006 — and summer cruise dates — August 10, 2005, August 25, 2005, and September 13, 2006 — are referred to herein as cruises S1–S4 and A1–A3, respectively. Samples were collected along the main (south) channel of the estuary between Tongue Point, OR (46.221 N, 123.755 W) and the estuary mouth (46.256 N, 124.054 W; Fig. 1). Samples were also collected along an across-channel (north–south) transect between Hammond, OR (46.200 N, 123.952 W) and Chinook, WA (46.273 N, 123.945 W; Fig. 1). During cruises in 2005, samples were collected on

Fig. 1 Along- and across-channel sample stations in the Columbia River Estuary. *Inset:* regional location of estuary



both downstream and upstream along-channel transects and across-channel transects; during 2006, only the downstream along-channel and the across-channel transects were sampled.

Zooplankton samples were collected via vertical net hauls from 0.5 m above bottom to surface using a 75- μm mesh, 0.5-m-diameter conical net equipped with a standard flowmeter (General Oceanics). Contents were immediately rinsed from the net and preserved in a 5–10 % formalin–seawater solution. Microplankton were sampled from the surface water via bucket and 200 ml were immediately preserved with a 5 % Lugol’s solution and stored in opaque bottles. In addition, vertical profiles of salinity, temperature, turbidity (NTU), and chlorophyll *a* fluorescence (mg m^{-3}) were collected at each station using a Sea-Bird 19 plus CTD with a Wet Labs WET Star fluorometer and OBSSCUFA. All samples were collected during daylight hours.

Our cruises occurred at varying times of the lunar cycle, but the three low-flow cruises all occurred near neap tides. Particularly during periods of low flow, neap tides in the CRE result in a greater salinity intrusion and more highly stratified water column compared to spring tides, which promote mixing (Jay and Smith 1990; Roegner et al. 2011). Results from a fourth low-flow cruise on August 22, 2006 that occurred on a spring tide are not presented as the data sheets necessary for abundance calculations were lost overboard. However, proportional abundance data from this cruise were compared to other summer cruises to ensure that zooplankton assemblages sampled during neap tides were representative of assemblages present during spring tides. A similar comparison was not possible for microplankton because data were available for 2005 only.

Zooplankton individuals were identified to the lowest taxonomic level possible and counted under a dissecting microscope at 25 \times . Abundances were calculated as concentration (individuals m^{-3}). For microplankton samples, 2.5 to 25 ml

was subsampled and settled in Utermöhl chambers. Diatoms, chlorophytes, ciliates, dinoflagellates, flagellates, and cyanobacteria were identified, sized and counted using a Nikon Eclipse TS100 inverted microscope at 200 \times . Diatoms that we were not identifiable to Order were abundant in our samples and divided into size classes based on cell volumes. Centric diatoms were divided into small (<4,000 μm^3), medium ($\geq 4,000$ to <40,000 μm^3), and large ($\geq 40,000$ μm^3) groups. Pennate diatoms were divided into small (<1,000 μm^3) and large ($\geq 1,000$ μm^3) groups. Abundances were calculated as cells l^{-1} .

Community Analyses

Hierarchical agglomerative cluster analysis was used to assess sample similarity and compare late spring, high-flow and late summer, low-flow plankton assemblages. Log-transformed ($x+1$) abundances were analyzed with a Sørensen (Bray–Curtis) distance measure and a flexible beta (–0.25) linkage. Indicator species analysis (ISA; Dufrêne and Legendre 1997) identified representative taxa for each cluster. Due to the high number of potential indicator taxa investigated, Bonferroni-corrected alpha levels of 0.0007 and 0.0005 were used in significance tests for zooplankton and phytoplankton taxa, respectively.

Variation within zooplankton and microplankton samples was described in separate nonmetric multidimensional scaling (NMDS) ordinations. Log-transformed ($\log x+1$) taxon abundances were ordinated using the Sørensen (Bray–Curtis) distance measure. Rare taxa (present in fewer than 5 % of samples), eggs, and nauplii (copepod and barnacle) were removed from the analysis. In some cases, rather than removing a rare species, it was lumped with other unidentified members of the same genus (e.g., *Chaetoceros pendulum* was added to *Chaetoceros* spp.). All multivariate analyses

were conducted using PC-Ord v. 5.10 (McCune and Mefford 2006).

For each cruise, we measured a suite of environmental variables, which was used to interpret water column variability, and for correlation to NMDS ordination axes. Measured local water column variables were surface and water column average temperature and salinity. Temperature and salinity stratification were calculated as the difference between surface and bottom measurements. Several biological variables were also included: Species richness and diversity (Shannon's index) as calculated for each zooplankton and microplankton sample, and surface and water column average chlorophyll *a* fluorescence.

We also included several variables to describe the condition of the estuary on each cruise date. Average river discharge from the previous month, week, and day of the cruise were calculated from measurements recorded at the Beaver army terminal in Oregon (http://waterdata.usgs.gov/usa/nwis/uv?site_no=14246900). Four-day cumulative mean daily wind stress (CWS) was calculated from hourly wind vector data collected near the Columbia River bar (Station 46029; 46.12°N, 124.51°W) and retrieved from <http://ndbc.noaa.gov>. Four-day CWS is a reliable indicator of upwelling with negative values of CWS correlating with increased maximum daily salinity in the CRE (Roegner et al. 2011). Three temporal variables were also included: (1) Julian date; (2) a seasonal index contrasting high- and low-flow periods, calculated as $\sin(360/365(\text{Day of Year}))$ with January 1 set as day 0, April 1 as 1, and September 31 as -1; and (3) the number of days elapsed since the spring transition, which signals the initiation of the upwelling season (Huyer et al. 1979). To facilitate interpretation and discussion of temporal and spatial variation, NMDS plots were rotated to maximize the correlation to the seasonal index on one axis and the correlation to river km on the second axis. An arbitrary cut-off of $r=0.5$ was used to identify the environmental variables which most strongly correlated to assemblage variation.

Results

Environmental Conditions

River discharge varied greatly between 2005 and 2006, with 2005 experiencing lower than average discharge, and 2006 much higher than average discharge, during the spring and early summer (Fig. 2). Conditions during our late summer cruises were more similar, though river discharge was lowest during cruise A3. During our spring cruises, salinity was largely homogeneous vertically over most of the sampled area of the estuary, with strong stratification occurring near the mouth on most cruises (the exception being cruise S3, when high flows advected the salt wedge from the estuary). During

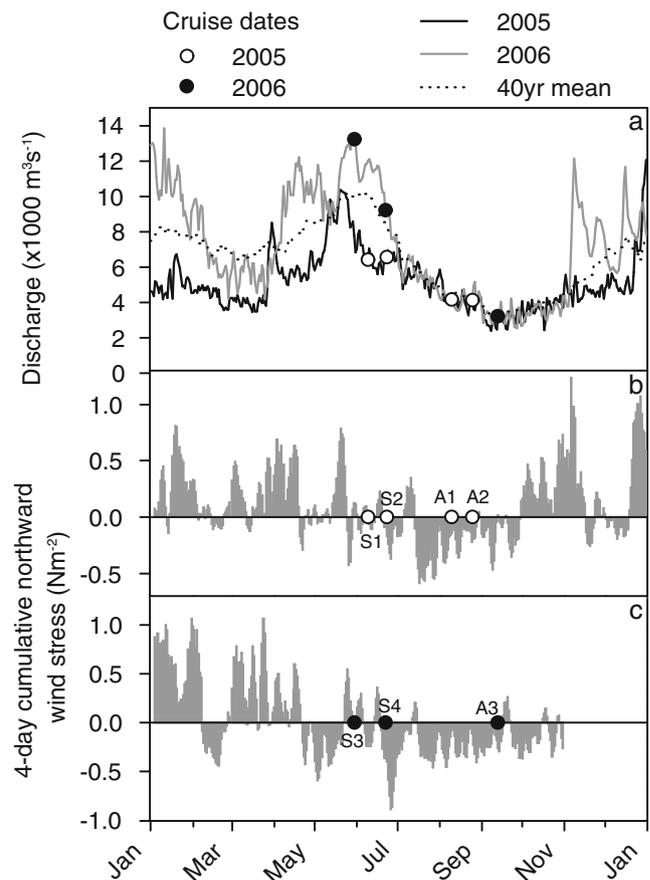


Fig. 2 Distribution of cruises with respect to **a** Columbia River flow for 2005 and 2006 as well as the average flow of the previous 40 years as measured at the Beaver army terminal, 87 km upstream of the estuary mouth, and 4-day cumulative wind stress for **b** 2005 and **c** 2006, as a proxy for upwelling. Open circles and filled circles indicate 2005 and 2006 cruise dates, respectively

the late summer cruises, the water column was stratified with the salinity intrusion extending beyond our most inland station.

Salinity and salinity stratification generally increased toward the mouth of the estuary during all cruises. Temperature profiles mirrored those of salinity, with warmer surface water entering from the river. In general, the chlorophyll *a* gradient reversed between the seasons, increasing landward in the spring and towards the mouth of the estuary during the summer (data not shown). Chlorophyll *a* values were generally depressed in the top meter of the water column. A more detailed description of the hydrographic conditions and chlorophyll *a* fluorescence patterns of the estuary during our cruises is included in the work of Roegner et al. (2011).

Dominant Taxa

During high-flow periods, the zooplankton assemblage was dominated by the copepods *Eurytemora affinis*, *Coullana*

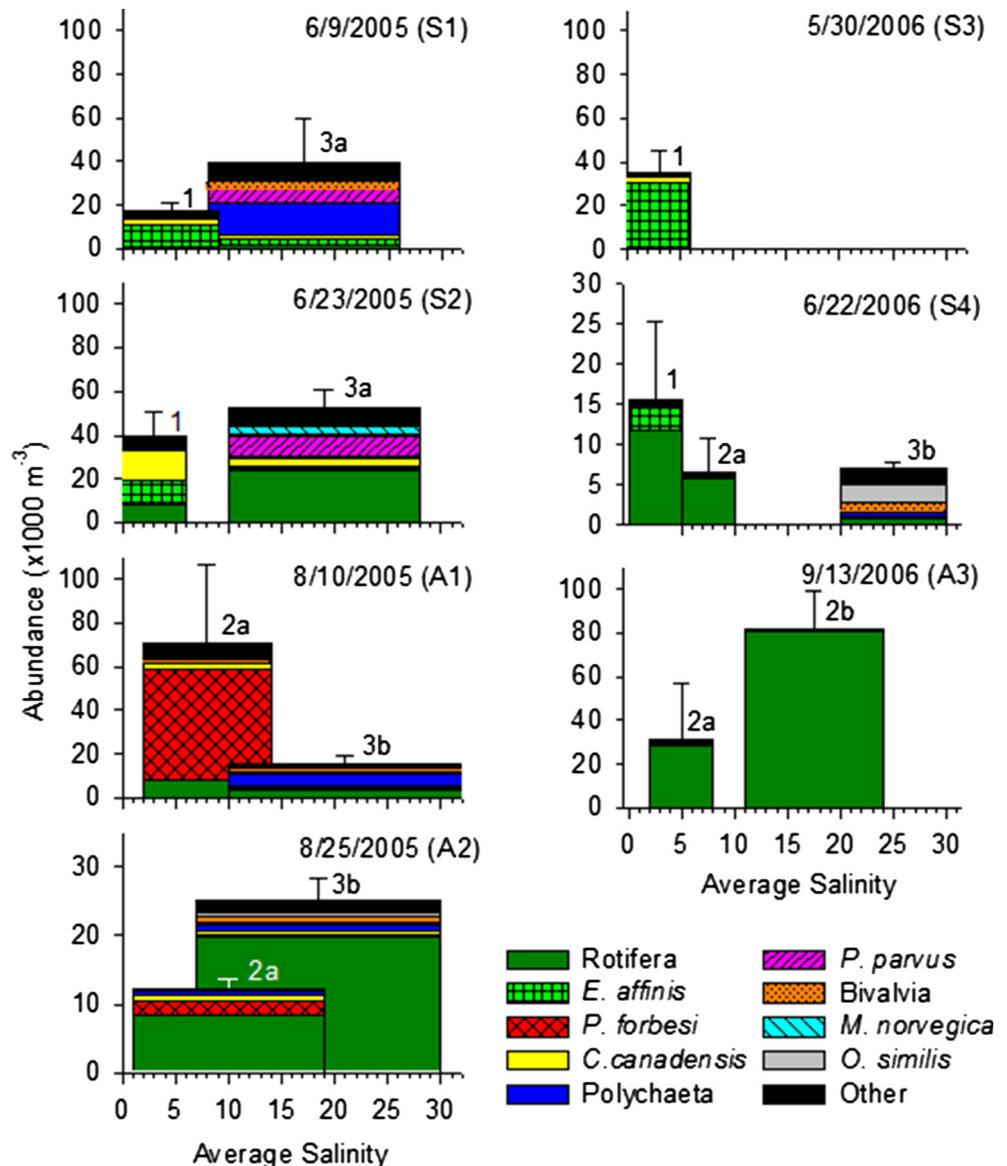
canadensis, and *Paracalanus parvus*, and by rotifers and polychaete larvae (Fig. 3). During low-flow periods, rotifers, *P. forbesi*, and polychaete larvae were the most abundant taxa.

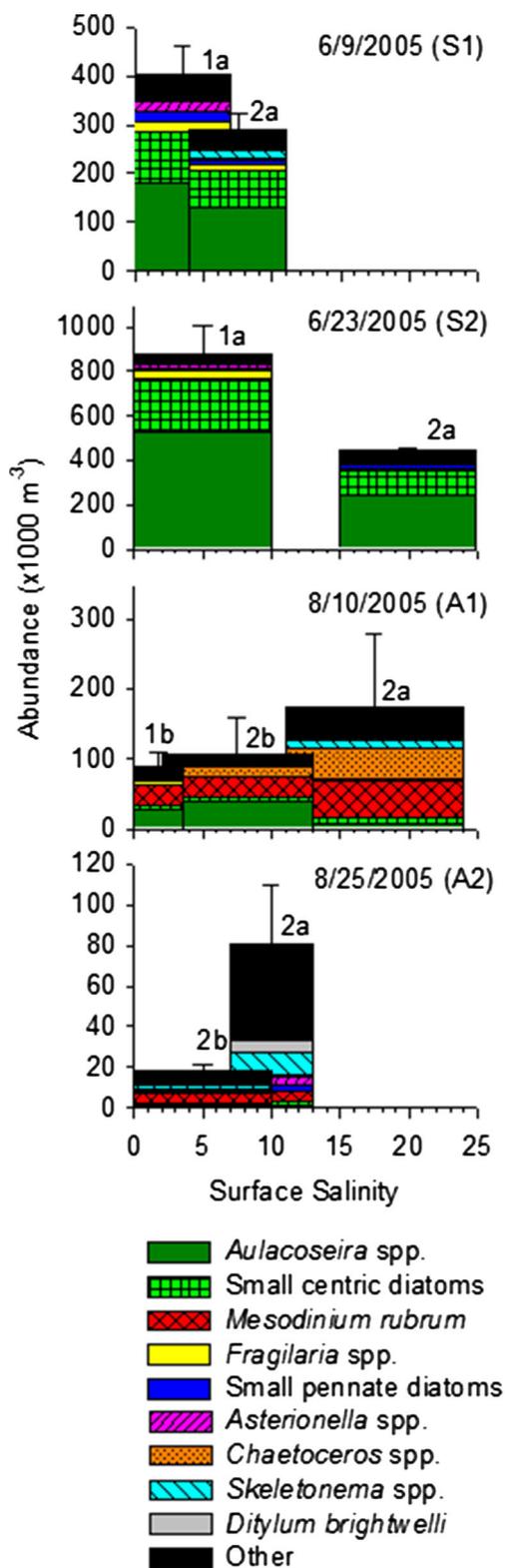
The microplankton were overwhelmingly dominated by autotrophic/mixotrophic protists, therefore we refer to them hereafter as “phytoplankton.” Phytoplankton were most abundant in spring, particularly during cruise S2, and the assemblage was dominated by diatoms, particularly *Aulacoseira* spp., and other small (<4,000 μm³) centric diatoms (Fig. 4). During high-flow cruises, phytoplankton were more abundant at the mouth of the estuary, in more saline waters, and the assemblage was dominated by the mixotrophic ciliate, *M. rubrum*. Phytoplankton assemblage composition varied along-channel with the occurrence of more marine species towards the mouth of the estuary (Fig. 4).

Plankton Community Analyses

The first division of the cluster analysis of zooplankton samples from 2005 and 2006 separated upstream samples collected during the spring (cluster 1) from those collected nearer the estuary mouth and during low-flow cruises (Online Resource 1). During cruise S3, this cluster extended to the estuary mouth. The second division separated downstream samples (clusters 3a and 3b) from those collected upstream during August cruises and throughout the estuary during cruise A3 (clusters 2a and 2b). The subsequent two divisions resulted in five clusters, referred to here as 1, 2a, 2b, 3a, and 3b. Cluster 1 was dominated by *E. affinis* and was indicated by the presence of *Diacyclops thomasi*, oligochaetes, and the rotifer, *Asplanchna* spp. (Online Resource 2).

Fig. 3 Zooplankton (>75 μm) assemblages present during each cruise. Stacked bars represent abundances (individuals × 1,000 m⁻³) of dominant taxa averaged within a cluster. Bar width reflects the range of water column average salinities over which the cluster was collected. Cluster labels are located next to the error bars. Error bars represent 1 standard error of the mean total abundance. Where stacked bars overlap, the salinity range of the clusters overlapped during that cruise. Please note that the x-axis for the cruise S4 panel begins at 5 as we have no salinity data for cluster 1 samples during this cruise. These samples were collected from our four most upstream stations. Also note different y-axis scales





Clusters 2a and 2b were assemblages dominated by rotifers and *P. forbesi*. Cluster 2a (primarily August samples) had a high abundance of *P. forbesi* and was indicated by the presence of *Limnoithona tetraspina*,

◀ **Fig. 4** Microplankton (5–200 μm) assemblages present during each cruise. Stacked bars represent abundances (individuals $\times 1,000 \text{ cells l}^{-1}$) of dominant taxa averaged within a cluster. Bar width represents the range of surface water salinities over which the cluster was collected. Cluster labels are located next to the error bars. Error bars represent 1 standard error of the mean total abundance. Where stacked bars overlap, the salinity range of the clusters overlapped during that cruise. Please note different y-axis scales

and the cladocerans *Moina* sp. and *Diaphanosoma* sp. Cluster 2b differed from cluster 2a by having a greater abundance of rotifers and low abundances of most other taxa. It was indicated by the presence of the harpacticoid copepod *Ectinosoma* spp. Nearer the mouth of the estuary, clusters 3a and 3b were dominated by rotifers and polychaete larvae, and marine taxa, including *P. parvus* and *Oithona similis*, were abundant. The two designations of cluster 3, a and b, indicate the influence of the marine taxa associated with warm- and cold-water coastal currents, respectively. Cluster 3a occurred toward the mouth of the estuary during spring 2005 and was indicated by the presence of *Acartia tonsa*, *Corycaeus anglicus*, and *Leimia vaga* (Online Resource 2). Cluster 3b occurred toward the mouth during August 2005 and cruise S4 and was indicated by *Acartia longiremus*, *Centropages abdominalis*, *Tortanus* sp., and *Calanus* sp.

Upon the first division of the microplankton cluster analysis (Online Resource 1), samples collected upstream during cruises S1, S2, and A1 clustered together, apart from samples from cruise A2 and from stations near the estuary mouth. The spring cluster (1a) was present during cruise S1 and S2 and was dominated by *Aulacoseira* spp. and unidentified small centric diatoms. Cluster 1a was indicated by the presence of *Melosira varians*, *Asterionella* spp., and unidentified large centric diatoms (Online Resource 3). The phytoplankton assemblage sampled during cruise A1 (cluster 1b) was more similar to that present in the spring than it was to the assemblage present during cruise A2 in late August (cluster 2b), despite the dominance of *M. rubrum* on both dates. This was due, in part, to the relatively high contribution of *Aulacoseira* spp. and the relatively low contribution of *Skeletonema* spp. to total abundance during cruise A1, compared to that during cruise A2 (Fig. 4). Cluster 1b was indicated by the presence of the freshwater green alga, *Dictyosphaerium* spp. Cluster 2b was dominated by *M. rubrum*, and by *Aulacoseira* spp. where the cluster occurred in early August, but lacked any strong indicators. A marine cluster (2a), present during all cruises at stations near the estuary mouth, was dominated by the seasonal taxa present upstream (i.e., *Aulacoseira* spp. in the spring and *M. rubrum* in the late summer) but was indicated by many marine taxa, including *Asterionellopsis glacialis*, *Ceraulalina* spp., *Chaetoceros curvisetus*, and *Ditylum brightwelli* (Online Resource 3).

Associations Between Plankton and Environmental Conditions

The NMDS ordination of 107 zooplankton samples with abundance data from 67 taxa represented 89 % of the between-sample variation on two axes with a stress of 13.7 (Fig. 5). The primary axis, explaining 47 % of the variation, roughly separated upstream and downstream samples and was strongly correlated with salinity ($r=-0.92$; Online Resource 4). This axis represented the opposing gradients of marine and freshwater taxa abundances. For instance, the neritic cyclopoid copepod *O. similis* and the freshwater cladoceran *Bosmina longirostris* were among the species whose abundances varied most strongly along this axis ($r=-0.85$ and $r=0.63$, respectively; Online Resource 5). The second axis explained 42 % of the variation and primarily represented temporal fluctuation in the abundances of estuarine taxa. Samples sorted roughly in order of increasing river discharge along this axis. Days from spring transition, season, wind stress, and temperature stratification (Online Resource 4) and *E. affinis* and *Pseudobryda* sp. abundances were most strongly correlated with this axis ($r=0.82$ and $r=0.75$, respectively).

The NMDS ordination of 79 microplankton samples with abundance data from 92 taxa explained 86 % of the variation between samples on three axes with a stress of 13.9 (Fig. 6). The strongest axis, Axis 3, was related to 49 % of between-

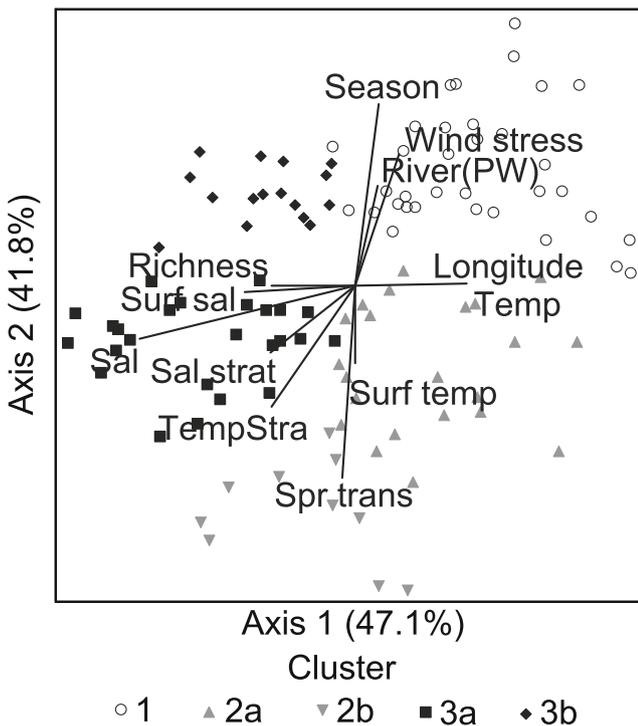


Fig. 5 NMS of 2005–2006 mesozooplankton samples with cluster overlay. Joint plot cut-off is $r^2=0.3$. *Sal* salinity, *strat* stratification, *temp* temperature, *surf* surface, *Spr. trans* spring transition, *TempStra* Temperature stratification, *river (PW)* river discharge from the previous week. Stress=13.7

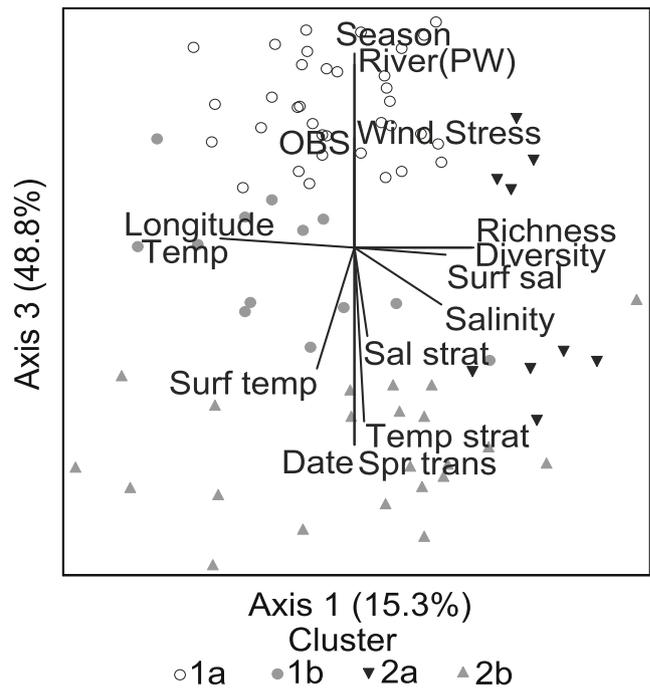


Fig. 6 NMS plot of microplankton samples with cluster overlay. Axis 2 is not shown. Joint plot cutoff $r^2=0.3$. *OBS* turbidity (NTU), *Sal* salinity, *strat* stratification, *temp* temperature, *surf* surface, *Spr. trans* spring transition, *river (PW)* river discharge from the previous week. Stress 13.9

sample variation and was largely temporal, with the phytoplankton assemblage varying along a seasonal gradient of decreasing stratification, surface water temperature, and julian date with increasing river discharge (Online Resource 4). Many marine and freshwater taxa varied along this axis (Online Resource 6). A secondary axis represented 15 % of between-sample variation and was largely spatial, describing a gradient of decreasing water column average temperature and increasing average salinity and surface salinity approaching the mouth of the estuary. Several marine genera correlated with this axis, including *Ceraulalina* spp. and *Dactyliosolen* spp. A third axis, representing 22 % of variation, correlated strongly to *Dictyosphaerium* spp., *Ankistrodesmus* spp., and filamentous bacteria abundances, but was not correlated to any of our measured environmental variables.

Discussion

Spatial and Temporal Variation in Plankton

The composition of CRE zooplankton and, to a lesser extent, phytoplankton assemblages differed between high-flow and low-flow periods. Notably, zooplankton dominance switched from *E. affinis* to *P. forbesi* (Fig. 3), and *M. rubrum* (Fig. 4) became the dominant phytoplankter in late summer. Distinct high- and low-flow plankton assemblages are often recorded

in estuaries, such as the Pearl River Estuary, China (Tan et al. 2004), Darwin Harbour, Australia (Duggan et al. 2008), and the San Francisco Estuary (SFE), USA (Bollens et al. 2011). River flow and the seasonal patterns of abundance of most estuarine zooplankton taxa largely explained variation in the zooplankton assemblage of the CRE between flow periods (Fig. 5; Online Resources 4 and 5).

We did not observe distinct high- and low-flow assemblages for the surface-water phytoplankton of the CRE. The phytoplankton assemblage present during the first low-flow cruise was more similar to the assemblage present during high flows than it was to that present during our second low-flow cruise (Online Resource 1a). The abundance of freshwater phytoplankton appeared to peak throughout the estuary in the late spring. As freshwater phytoplankton decreased over the low-flow period, the marine contribution to the assemblage became prominent, particularly toward the mouth of the estuary. In agreement with observed patterns in chlorophyll *a* (Roegner et al. 2011), spatial trends in both phytoplankton abundances and assemblage composition indicate a shift from riverine to marine-derived phytoplankton between high- and low-flow cruises as a function of decreasing river flow and the initiation of upwelling-favorable winds. Previous studies have shown that variability in estuarine phytoplankton production is climate-driven and related to variables influenced by freshwater discharge (Cloern 1991; Lehman 2004). It is possible that greater differences could have been detected between high- and low-flow phytoplankton assemblages had we compared depth integrated phytoplankton samples. However, it also seems plausible that, as the phytoplankton assemblage was largely dominated by freshwater taxa (as opposed to estuarine resident taxa in the case of the zooplankton), their composition was less influenced by conditions within the estuary.

Zooplankton and, to a lesser extent, phytoplankton assemblages of the CRE also varied spatially along a salinity gradient, in agreement with previous studies in other estuaries (Miller 1983). Assemblages at the mouth of the estuary generally differed from those upstream and spatial variation was driven largely by the changing abundances of coastal and freshwater taxa along the axis of the estuary (Online Resource 5). Coastal zooplankton taxa differed between cruises and reflected the direction of coastal currents at the time of sampling. The spring coastal current transition and onset of upwelling were delayed by 2–3 months in 2005 (Fig. 2; Schwing et al. 2006), and warm water taxa off of the central Oregon coast were anomalously abundant (Mackas et al. 2006). This resulted in differing zooplankton assemblages (3a and 3b) at the mouth of the CRE during spring 2005 and spring 2006, as revealed by the NMDS ordination and cluster analysis. We do not have phytoplankton data for 2006; however, as upwelling-fuelled phytoplankton are advected into the estuary (Roegner et al. 2011), the marine

contribution to the estuarine assemblage in spring 2005 may have been reduced compared to years with more typically timed upwelling.

Spring High-flow and Summer Low-flow Assemblages

During the high-flow period, the plankton assemblage of the CRE was dominated by *Aulacoseira* spp., small centric diatoms, and the copepod *E. affinis*. *E. affinis* reached a maximum estimated abundance of 79,760 individuals m^{-3} during cruise S3. Previous studies of CRE zooplankton have noted the springtime dominance of *E. affinis* (Haertel and Osterberg 1967; Jones et al. 1990), a cryptic estuarine calanoid that is abundant in many Northern Hemisphere estuaries (Lee 1999).

High-flow assemblages were present at flows which ranged from 6,300 to 13,100 $\text{m}^3 \text{s}^{-1}$ and total zooplankton abundance was not reduced during the higher flows. The estimated abundances of many individual taxa were, however, much lower in 2006 (which had higher flows) than in 2005, with the notable exceptions of our rotifer group and *E. affinis*. Kimmerer (2002) and Kimmel and Roman (2004) have previously noted the positive influence of increased freshwater discharge on the *E. affinis* populations in the SFE, and in Chesapeake Bay, USA, respectively. *E. affinis* is a tidal vertical migrator (Morgan et al. 1997), which may have enabled it to maintain position during high flows. This is in contrast to *C. canadensis*, which does not employ vertical migration for maintenance of position (Morgan et al. 1997) and whose abundances appeared depleted in spring 2006 compared to 2005 (Fig. 3).

During our 2005 low-flow cruises, river discharge was approximately 4,300 $\text{m}^3 \text{s}^{-1}$ and the ciliate *M. rubrum* and the copepod *P. forbesi* dominated the phyto- and zooplankton, respectively. During our 2006 low-flow cruise, river discharge was approximately 3,500 $\text{m}^3 \text{s}^{-1}$, and except for our most inland station, rotifers dominated the zooplankton assemblage in the estuary, accounting for greater than 75 % of the total zooplankton abundance. Possible explanations for the low abundances of *P. forbesi* during our lowest flow cruise include lower temperatures in the estuary and high flows during the previous spring which may have flushed overwintering stages out of the estuary into the coastal ocean.

Historically, among the phytoplankton, abundances of the diatoms *Fragilaria* spp. and *Aulacoseira granulata* peaked during the low-flow period (Haertel et al. 1969). No mention of *M. rubrum* is found in Haertel and Osterberg (1967) or Haertel et al. (1969) though they sampled during late summer when red water blooms are now commonly observed. We speculate that reduced vertical mixing and increased residence time that have occurred since large-scale regulation of the flow cycle began in the late 1960s (Sherwood et al. 1990) may now favor motile phytoplankton species over diatoms during periods of low flow. In the SFE, *M. rubrum* blooms

occur during neap tides and periods of high water column stability and stratification (Cloern et al. 1994). The ability of *M. rubrum* to vertically migrate (Villarino et al. 1995) combined with dampened Columbia River flow variability (Sherwood et al. 1990) may have allowed this species to take advantage of a niche novel to the CRE.

Within the zooplankton, *P. forbesi*, once exceeding 223,440 individuals m^{-3} , often comprised greater than 50 % of the sampled assemblage during late summer in the CRE. Kimmerer and Orsi (1996) have suggested that, in the SFE, *E. affinis* may have suppressed *P. forbesi* populations until *E. affinis* populations declined due to predation by the introduced clam, *Potamocorbula amurensis*. *E. affinis* may limit the temporal range of *P. forbesi* in the CRE as peak *P. forbesi* abundances occur during late summer, a period of historically low *E. affinis* abundance (Haertel and Osterberg 1967; Jones et al. 1990). *P. forbesi* may also be limited by lower springtime water temperatures.

The non-indigenous copepods present in the CRE (Bollens et al. 2012) are a subset of those found to the south in the highly invaded SFE (Orsi et al. 1983; Orsi and Walter 1991; Orsi and Ohtsuka 1999), a known source of “high risk” ballast water (Cordell et al. 2008). Absent from the sampled zooplankton assemblage at the time of this study were the calanoid copepods *Acartiella sinensis*, *Tortanus dextrilobatus*, and *Pseudodiaptomus marinus* and the oithonid cyclopoid copepod *Oithona davisae*. Based on the temperature–salinity space occupied by these taxa in the SFE (Hooff and Bollens 2004; Bollens et al. 2011; Bollens unpublished data), *A. sinensis* and *T. dextrilobatus* would be able to colonize the CRE. In addition to a smaller total complement of non-indigenous copepod species, two of the non-indigenous copepods that are present in the CRE, *L. tetraspina* and *S. doerrii*, are present at much lower densities than are commonly seen in the SFE (Kimmerer et al. 1998; Bollens et al. 2011). These invasions in the CRE are considered more recent than those of the SFE (Cordell et al. 2008), and it is possible that these populations may still be increasing. Alternatively, there may be some aspects of the CRE, such as its high flows and short residence time, or reduced inoculation rate, which make it a more difficult environment for these species to colonize. Conversely, *P. forbesi* is as abundant (or perhaps more abundant) in the CRE than in the SFE, despite being a more recent invasion (Cordell et al. 2008). *P. forbesi* and *E. affinis* both carry their eggs, whereas *T. dextrilobatus*, *A. sinensis*, and *S. doerrii* are broadcast spawners. Brooding versus broadcast spawning in relation to flushing time may play a role in copepod invasion success, in addition to its potential influence on predation rates (e.g., Bollens and Frost 1991).

We identified the plankton assemblages present during high- and low-flow periods in the CRE, and noted how these assemblages have changed over time. In the CRE, these alterations have unknown implications for material

transformations and trophic linkages. In the SFE, changing zooplankton taxonomic composition has been linked to pelagic fish declines (Winder and Jassby 2011); however, the diets of age-0 striped bass, and larval and juvenile delta and longfin smelts have shifted to include *P. forbesi* (Hobbs et al. 2006; Bryant and Arnold 2007; Whitley and Bollens 2013). Conversely, *L. tetraspina*, which is known to feed on small *M. rubrum* cells (Bouley and Kimmerer 2006), has been implicated in the decline of some fishes (Gould and Kimmerer 2010). Further research is needed to assess the ecological ramifications of changes in copepod species dominance and of massive blooms of mixotrophic ciliates that generate autochthonous estuarine production that likely did not historically exist. Finally, this research was conducted over a relatively short time scale during a period of continued regional environmental change, and cannot be considered an endpoint. Research and monitoring must continue to document the continued evolution of the CRE ecosystem to predict whether and how the seasonality of plankton assemblages will change under conditions of climate change.

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