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Sink or swim? Copepod population maintenance in the Columbia River estuarine turbidity-maxima region

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Abstract Maintenance of estuarine zooplankton populations in large river-dominated estuaries with short residence times has been an intriguing subject of investigation. During three different hydrological seasons, autumn 1990, summer 1991, and spring 1992, we intensively sampled zooplankton populations in the estuarine turbidity maxima (ETM) region of the Columbia River estuary of Oregon and Washington, USA. One of the principal objectives was to investigate retention mechanisms of the predominant zooplankton species, the harpacticoid copepod *Coullana canadensis* and the epibenthic calanoid copepod *Eurytemora affinis*. In the ETM, *C. canadensis* densities mirrored those of turbidity gradients and were almost always greater at the river bed, while *E. affinis* densities were greater higher in the water column during the flood and lower in the water column during the ebb. Cross-correlation and time-series analyses determined that *C. canadensis* densities were highly positively correlated with turbidity and that most of the variability was explained by the lunisolar diurnal (K_1) and principal lunar (M_2) tidal components occurring once every 23.93 h and once every 12.42 h, respectively. This indicates that *C. canadensis* populations are most probably maintained in the estuary through the same near-bottom circulation features that trap and concentrate particles in the ETM. In contrast, densities of the more motile species *E. affinis* were highly correlated with negative velocities, or ebb tide, and most of the variability in population densities could be explained by the principal lunar tidal component; therefore, we hypothesize that this species is probably vertically migrating on a tidal cycle into different flow layers to avoid population losses out of the estuary.

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Introduction

Maintenance of planktonic populations in estuaries is very complex because of the periodically strong freshwater and tidal flows (Miller 1983). Mechanisms often cited for the maintenance of estuarine zooplankton populations include: (1) a high reproductive rate relative to loss due to flushing (Ketchum 1954; Gupta et al. 1994); (2) passive amassment in the zone of particle entrapment or estuarine turbidity maxima (ETM) (Castel and Veiga 1990); and (3) behavioral responses to physicochemical cues, such as vertical migration to make use of stratified flows (Trinast 1975; Cronin and Forward 1979; Woolridge and Erasmus 1980; Cronin 1982; Hough and Naylor 1991 1992) or lateral movement to areas of decreased flushing such as channel margins (Cronin et al. 1962).

The harpacticoid *Coullana canadensis* (Willey, 1923)[1] and the calanoid *Eurytemora affinis* (Poppe, 1880) are the two most predominant copepods in the Columbia River estuary, where they are found from River Kilometer (RKm) 5 to RKm 45, but are most abundant from RKm 20 to RKm 25 (Haertel and Osterberg 1967; Simenstad and Cordell 1985; Jones et al. 1990; Simenstad et al. 1990; Cordell et al. 1992). Simenstad et al. (1990) suggested that ≃65% of the secondary production in the Columbia River estuary may be attributed to suspension feeders in the mid-estuary channel (ETM) region of the estuary, where *C. canadensis* and *E. affinis* predominate. In addition, increased turbidity in the ETM may offer protection from known visual predators such as starry flounder (*Platichthys stellatus*) and Pacific tomcod (*Microgadus proximus*) (Haertel and Osterberg 1967). These copepods comprised 61 to 75% of the zooplankton

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[1] formerly *Scottolana canadensis* (Por, 1984)

in the ETM during studies in 1990 to 1992 (Morgan 1993; Simenstad et al. 1994b). ETM detritus and associated microbes are probably an important source of energy for estuarine copepods (Heinle and Flemer 1975; Heinle et al. 1977). High concentrations of particle-attached bacteria occur in the Columbia River ETM (Baross et al. 1994), and studies by Simenstad et al. (1994a) suggest that *C. canadensis* and *E. affinis* are effective grazers of these particles. Thus, the ability of these zooplankters to maintain large populations in this food-rich region may be very important to food-web structure and energy transfer in this ecosystem.

Materials and methods

Sampling design

Sampling was conducted in the tidally-influenced region of the Columbia River estuary (Fig. 1) in autumn (21 September to 10 October) 1990, summer (4 July to 2 August) 1991, and spring (15 May to 21 June) 1992. Sampling was carried out from two research vessels simultaneously. The 38 m R.V. "Robert Gordon Sproul" was anchored, and either the 20 m M.V. "Snow Goose" (1990 and 1992) or the 20 m R.V. "Clifford Barnes" (1991) moved throughout the study area. All near-bed physical measurements and total-water-column chemical and biological samples were taken in a Eulerian mode from the stationary vessel, as the ETM moved beneath the vessel with the tidal cycles. Samples taken from the roving vessel were in part in a Lagrangian mode (i.e. sampling following the ETM as it moved up and down the estuary). Along- and across-channel physical processes were measured from the roving vessel. Although a number of sample series were conducted between RKm 0 and 90, we herein focus only on those from the ETM region in the South Channel at Buoy 37 (RKm 22), the Buoy 39 intensive ETM sampling station (RKm 24), and the East Mooring Basin (RKm 25) (Fig. 1).

Sampling series were either 14 or 30 h in duration. In 1990, 30 h series were conducted; these were designed to encompass one full tide cycle to determine differences between the flood and ebb-associated ETM events. In 1991, both 14 and 30 h series were conducted. The 14 h series encompassed transition from ebb to flood (or vice versa) and were designed to distinguish physicochemical and biological structure in the ETM water column. Both types of series were conducted during strong and weak neap and spring-tide cycles to examine differences in zooplankton composition and distribution between these tidal regimes. In 1992, we conducted one 112 h series, (four consecutive 30 h series) to examine the transition between spring and neap tides. Although sampling was conducted during both spring and neap tides, only results from spring and the long spring–neap transition series are presented; neap ETM events are of low magnitude (Reed and Donovan 1994), and it is during spring tidal series that most of the advection of water and sediments occurs (Jay and Smith 1990; Jay and Musiak 1994).

Zooplankton samples and physical data

Zooplankton were sampled from the anchored vessel using a vertical pump-profiling system with a Hydromatic SP50A1 pump modified for deployment to depths exceeding 15 m (Miller and Judkins 1981). The pump was attached to the frame housing the conductivity, temperature, and depth (Seabird SBE 9/11 CTD) and optical backscatter (D&A Instruments OBS) sensors (Simenstad et al. 1994b). A 30.5 m length of 5.1 cm diam, rigid reinforced PVC hose linked the pump to the deck of the vessel and was clipped to the CTD cable; the pump delivered $\simeq$11 liters min^{-1} at the deck. In 1990, the CTD frame was lowered to within 0.5 m of the bottom, and CTD and OBS measurements were recorded continuously during its descent. After flushing the system for $\simeq$30 s, water from the main flow was pumped to the vessel deck. Water was filtered directly through an 80 µm screen for 2 min, for a total sample volume of 22 liters. The CTD–pump-profiling system was then raised to the level of the strongest salinity gradient, or to mid-depth if the water column was well mixed, and sampling was repeated. A final sample was taken at 0.5 m below the surface. This procedure was repeated every 2 h through each 30 h series. The 1991 procedures were similar, except that instead of directly filtering samples,

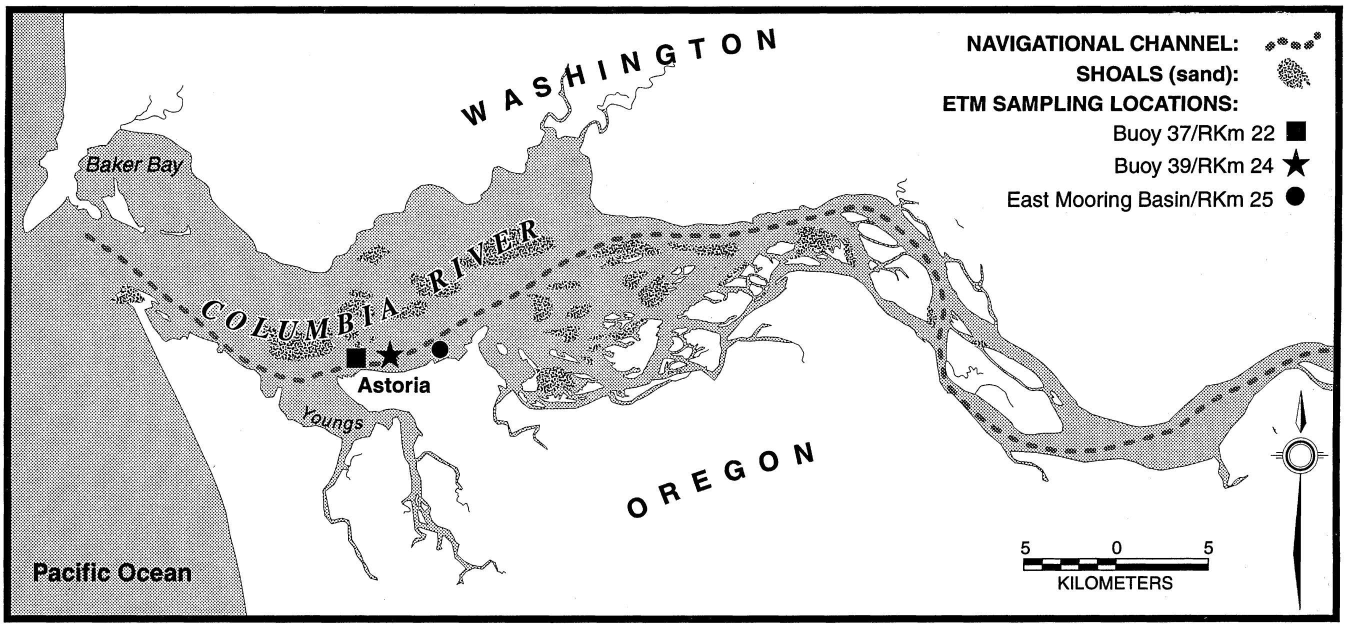

Fig. 1 Columbia River ETM (estuarine turbidity maxima) sampling sites at Buoy 37 (River Kilometer 22), Buoy 39 (River Kilometer 24), and East Mooring Basin (River Kilometer 25)

20 liters of water were first collected in a plastic carboy. This was done to control for the possibility of variable flow from the pump system when using a timed sample. The contents of the carboy were thoroughly mixed and the entire measured volume was filtered through an 80 μm screen. The sample volume was 10 liters for the 14 h series, and these were collected every hour. These collections also began at 0.5 m off the bottom, but were followed by samples at depths of 1 m off the bottom and thereafter in 1m increments up into the water column. A total of six depths were sampled, so that the upper sample was 5 m off the river bed.

Water-velocity data in autumn 1990 were generated by harmonic prediction programs (Foreman 1978) using data collected in 1980 (Jay and Smith 1990), and in summer 1991 and spring 1992 velocity data were collected with an 1.2 MHz RD Instruments Acoustic Doppler Current Profiler (ADCP) and a 4 m high, seven-instrument strata boundary-layer frame (BLF) (Geyer 1988). The BLF was equipped with Smith triplet current meters, SeaBird CT cells and D&A Instrument OBS sensors and deployed from the anchored vessel to obtain detailed profiles of tidal and turbulent fluxes near the bed. On the roving vessel, we used an ADCP to provide three-dimensional coverage of the remainder of the velocity field. The smoothed ADCP profiles used 3 to 4 min averages of data. A velocity-profile model in conjunction with CTD data was used to extend ADCP velocity-profiles to the bed. The model was calibrated using the boundary-layer frame measurements (Simenstad et al. 1994b). In years when harmonic program predictions and ADCP data could be compared, tidal height differences were <2 cm (J. Musiak personal communication).

In all years, filtered samples were washed into a container and fixed with 5% buffered formaldehyde. In the laboratory, zooplankton samples were filtered through a 153 μm screen that retained all calanoid copepodites and all but a few early-stage harpacticoid copepodites. These samples were scanned to determine if sub-sampling was necessary. Sub-samples were taken until the count for the most numerous species exceeded 100. All copepods were divided by species and into the following life-history categories: copepodids, adult males, adult females, and ovigerous females. *Eurytemora affinis* copepodids were also further divided into life-history stages. Raw numbers were standardized to numbers m^{-3}.

Data analysis

Tidal state and depth analysis

Preliminary analyses, by means of Student's *t*-test, Mann–Whitney rank sum, one-way ANOVA or Kruskal–Wallis one-way ANOVA on ranks, indicated that both tidal state and depth were important factors influencing ETM copepod densities and distribution (Morgan 1993; Simenstad et al. 1994a). Therefore, after examination for autocorrelation within the data, each time series was categorized into three tide stages (transition, flood, and ebb) using all available physical data (Morgan 1993). Transition was considered to be occurring any time the velocity at that depth was <15 cm s^{-1}; flood when the velocity was greater than that in a landward direction, and ebb when it was greater in a seaward direction. Densities at each tidal state and depth were analyzed for significant differences by means of a one-way ANOVA or a Kruskal–Wallis one-way ANOVA on ranks.

Time-series analysis

To better understand the fluctuations of copepod densities in the ETM region in relation to longer term physical processes, we analyzed our data with two types of time series analysis: cross-correlation (CCA) and harmonic analyses. Because we found no significant differences in the distribution of the densities of each copepod species between spring-tide series for each species (Morgan 1993), spring tide data within each year were pooled for each species. This allowed us to examine relationships between physical variables and copepod near-bottom densities. We used CCA to determine strength of concurrent correlations between the physical variables and copepod densities and the existence of consistent lags in correlation between these variables. On a longer time scale, CCA was used to determine correlations between physical variables and copepod densities indicative of periodicity or cycles in the data.

We used harmonic analysis to assess periodicities in copepod densities that corresponded to known periodicities in physical and biological cycles. Different physical variables have different periodicities. For example, the light–dark frequency occurs once every 24 h, and diurnal tidal fluctuation occurs once every 12.4 h (Gagnon and Lacroix 1981; Cronin 1982). We assessed only for periodicities corresponding to major tidal components and fitted a descriptive harmonic-constituent-based model to the original data (Foreman 1977). This analysis indicated the percent of variability in the data that can be attributed to each of the tidal frequencies examined. Because this harmonic analysis program was designed for physical data, it does not work as well on highly variable biological variables (Foreman 1977). To improve the fit of the model, copepod densities were square-root transformed to dampen this variation. The overall fit of the model was tested for significance using the *F*-statistic ($\alpha = 0.05$). This cannot prove a causal relationship, but is intended to support or refute visual and other statistical analyses.

Results

Physical patterns

In the Columbia River estuary, turbidity maxima usually occur twice during a tidal cycle (Reed and Donovan 1994). ETM with higher turbidities and longer duration occurred at the beginning of the flood accompanied by increasing salinities and landward (positive) velocities. Shorter, less turbid ETM occur at the end of the ebb, concurrent with decreasing salinities and seaward (negative) velocities (Fig. 2). Reed and Donovan (1994) provide a more detailed description of the particle character and composition of the ETM.

Coullana canadensis distribution

Maximum near-bottom densities of *Coullana canadensis* were coincident with both flood and ebb ETM. Not only did the timing of peaks in copepod densities and turbidity correspond well, but the magnitude of the density peaks also followed the same general pattern of OBS turbidity levels. Total densities were usually highest during flood tides regardless of depth and were almost always more abundant near the bottom than at the surface (present Fig. 3, and Morgan 1993). Data from samples taken at finer depth resolution, during the 14 h series in 1991, showed that a density gradient extended from the bottom up into the water column (Fig. 2). This trend of highest densities in the bottom 1 m was consistently maintained.

Results from cross-correlation analyses clearly indicated concurrent cyclic trends between some of the physical variables and *Coullana canadensis* densities (Fig. 4). Cycles of densities were significantly positively correlated with turbidity cycles in all three years at the

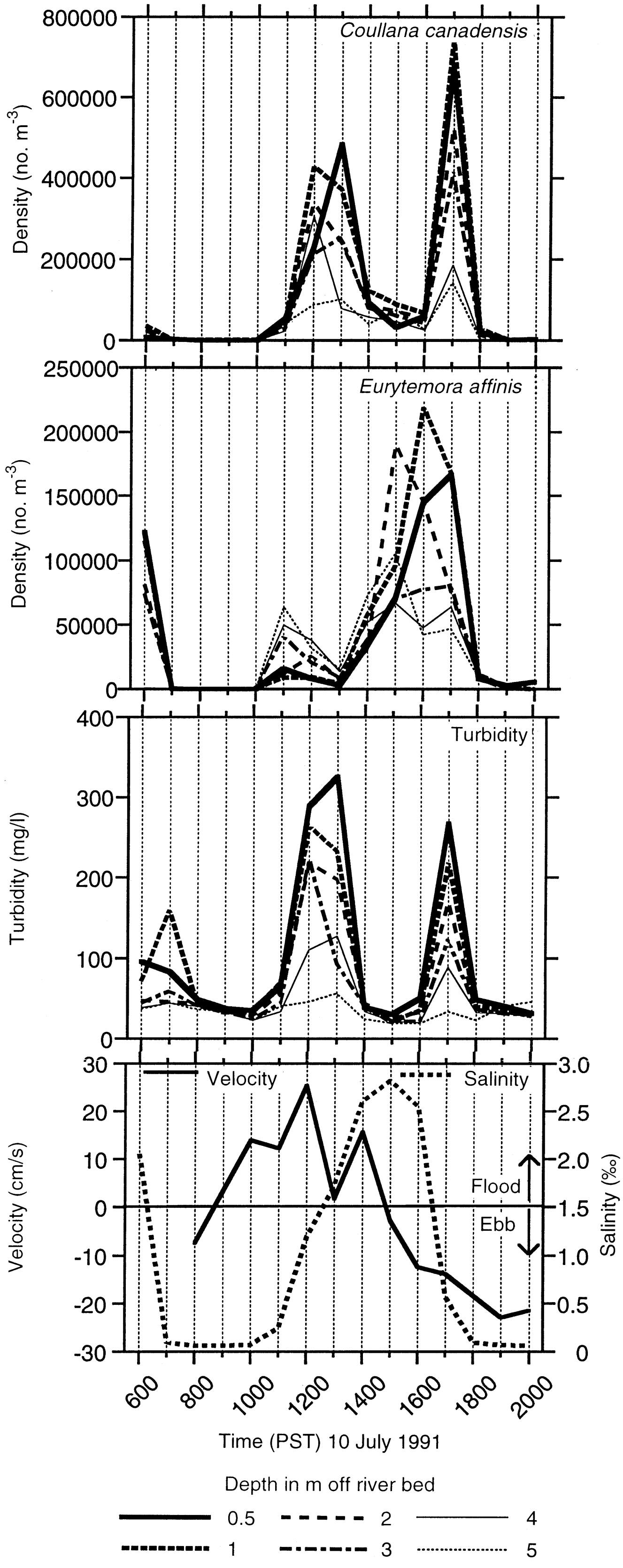

Fig. 2 *Coullana canadensis* and *Eurytemora affinis*. Density distribution at six depths off river bed in Columbia River estuary during 14 h series at the East Mooring Basin (River Kilometer 25) in summer 1991 (*PST* Pacific Standard Time in hrs)

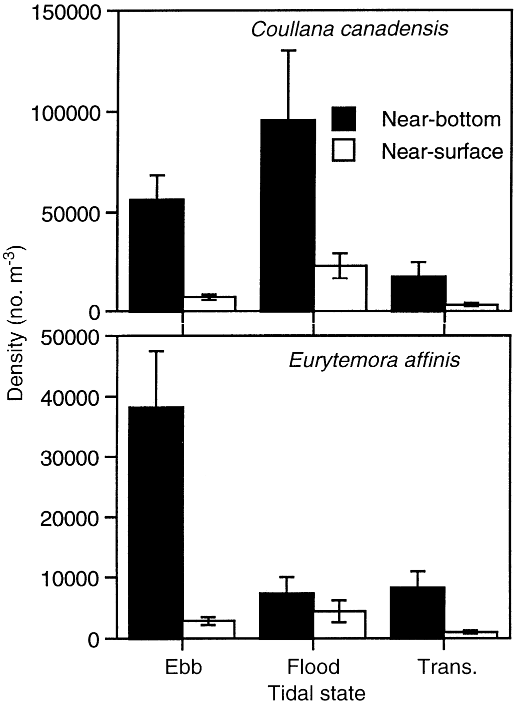

Fig. 3 *Coullana canadensis* and *Eurytemora affinis*. Density distribution as a function of tidal state and depth for three 30 h series at Buoy 39 (River Kilometer 24) in Columbia River estuary in autumn 1990 (*Trans.* transition)

0 h lag ($p \le 0.01$) and in 1990 at the 12 h lag ($p \le 0.05$). In 1992, greater time lags could be examined due to the length of the time series, and a significant correlation was also evident at the 26 h lag ($p \le 0.05$). A general negative correlation with salinity was seen, but no relationship trends between densities and velocity were apparent across years for this species.

Harmonic-analysis model predictions visually provided a close fit to the *Coullana canadensis* density-data (Fig. 5). The results of the overall goodness-of-fit test (Table 1) indicated that the model explained a statistically significant proportion of the variability ($p = 0.01$). Most of the variability in densities was explained by the K_1 (37.8%) and M_2 (26.6%) tidal components, which represent frequencies of once every 23.93 and once every 12.42 h, respectively (Table 2). In addition, the M_4 (once every 6.2 h) and $2MK_5$ once every 4.93 h, an interaction between the M_2 with itself and the K_1 components) were also important.

Eurytemora affinis distribution

Densities of *Eurytemora affinis* were generally highest near-bottom at or around the time of peak ebb velocities. These peaks did not seem to have any regular coincidence with the light/dark cycle, as peaks occurred at near-bottom and near-surface regardless of time of day (present Fig. 2, and Morgan 1993). Also, unlike *Coul-*

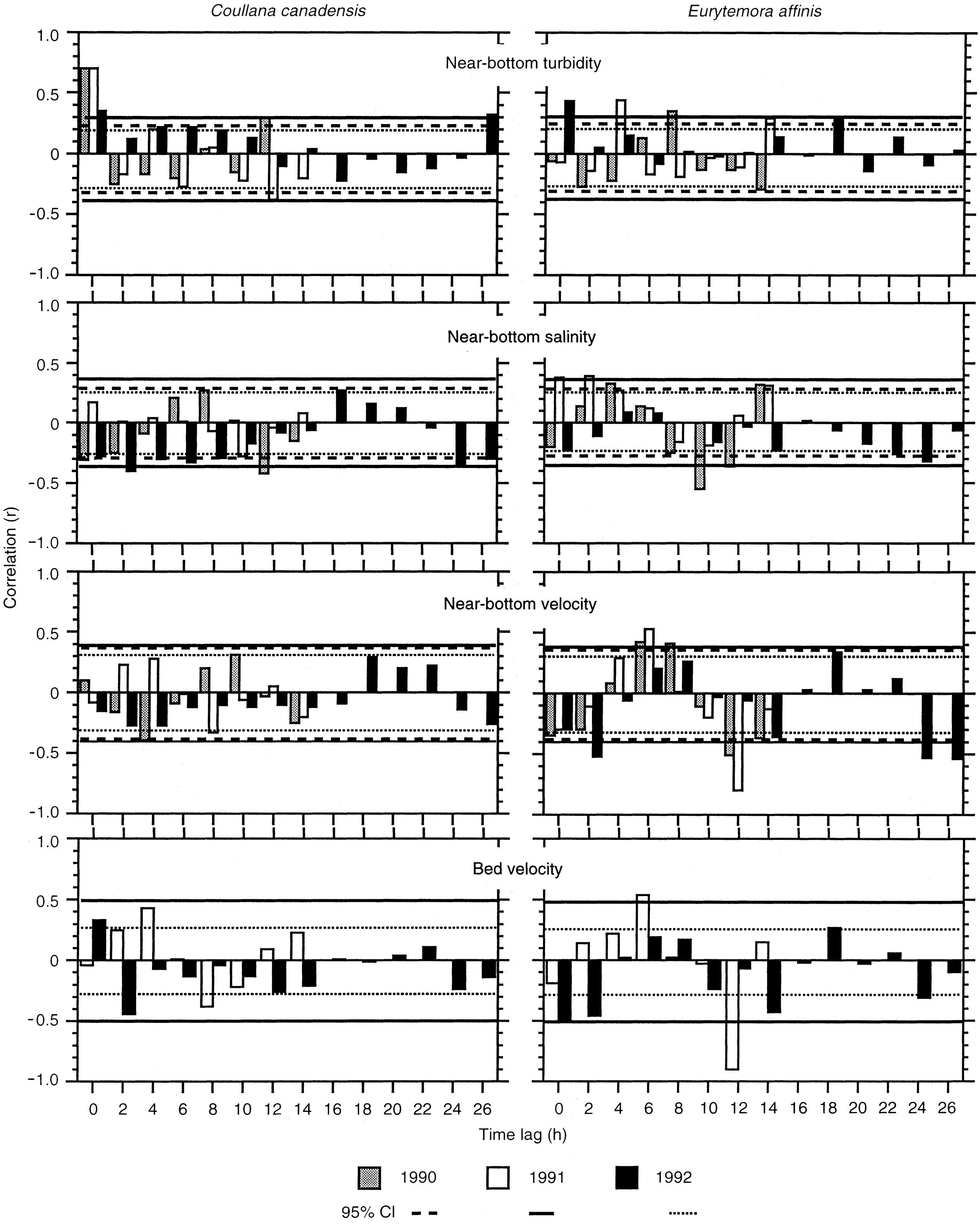

Fig. 4 *Coullana canadensis* and *Eurytemora affinis*. Cross-correlation analysis of near-bottom densities with physical variables in Columbia River estuarine turbidity-maxima region for 1990, 1991, and 1992 [Confidence interval (*CI*) = ± 2 ÷ square root (*n*)]

lana canadensis, *E. affinis* was usually more abundant during ebb events than during flood or transition events (Fig. 3). During the 14 h series, a density gradient extended from 0.5 to 5 m off the bed during ebb events (negative or seaward velocities). An opposite trend was evident during flood events (positive or landward ve-

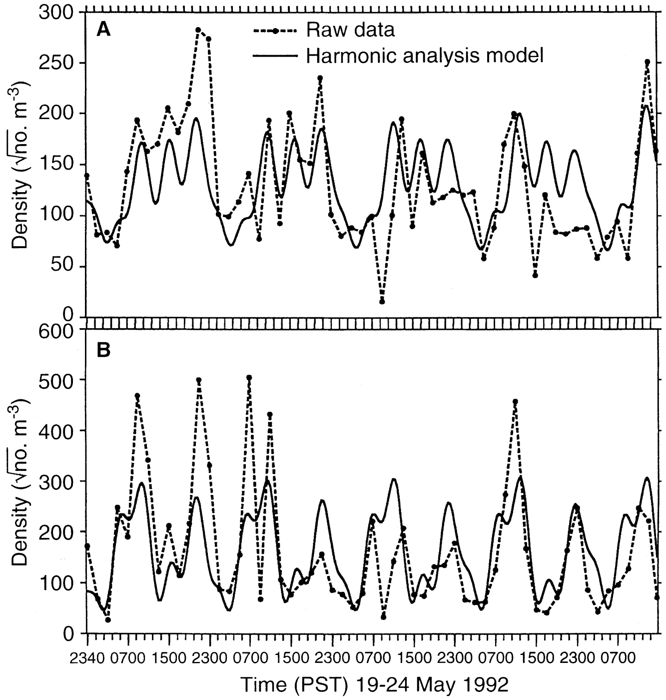

Fig. 5 *Coullana canadensis* (**A**) and *Eurytemora affinis* (**B**). Near-bottom square-root-transformed densities and their harmonic-analysis model predictions for 112 h series at Buoy 37 (River Kilometer 22) in Columbia River estuary in spring 1992 (*PST* Pacific Standard Time in hrs)

locities), where the 5 m (off-bottom) samples had highest densities and densities decreased as the sample depth approached 0.5 and 1 m from the bottom (Fig. 2). This pattern was typical during most spring sampling series (Morgan 1993).

Cross-correlation analysis indicated that densities had high negative correlations with velocity at time periods in the 0 to 2 h, the 12 to 14 h, and the 24 to 26 h ranges ($p \leq 0.05$). There were no distinct trends between densities and either turbidity or salinity (Fig. 4).

Harmonic-analysis model predictions also provided a good fit to the *Eurytemora affinis* density data ($p = 0.005$) (Fig. 5, Table 1). Most of the variability in the model (48%) was explained by the M_2 tidal component, but the $2MK_5$ was also an important frequency of variation in abundance for this species (Table 2).

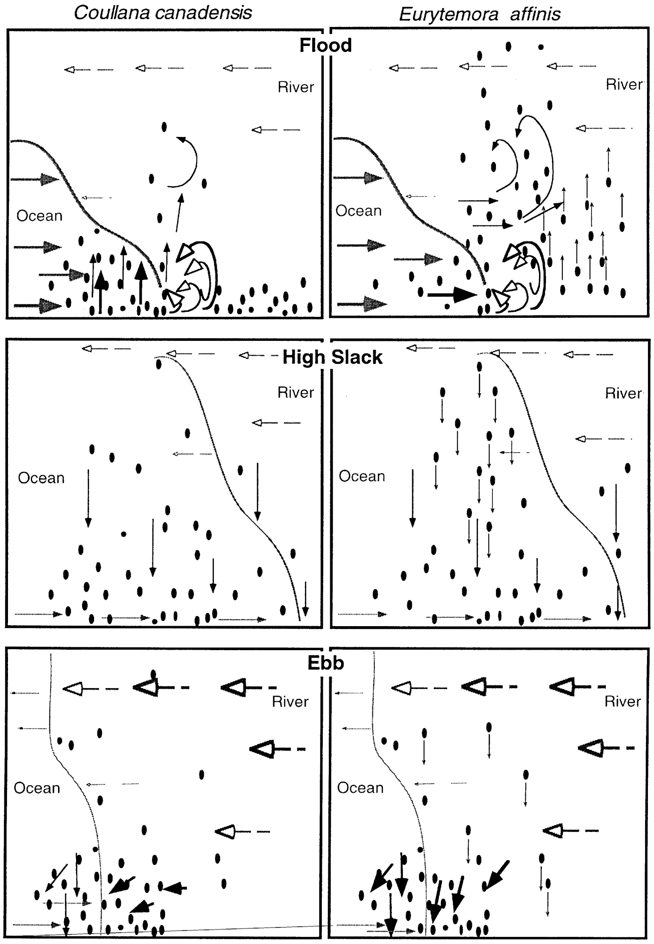

Fig. 6 *Coullana canadensis* and *Eurytemora affinis*. Model population-retention strategies in Columbia River estuarine turbidity-maxima region at different phases of tide (*Black ovals* copepods; *black arrows* copepod movement; *open arrows* and *continuous lines* resuspension; *gray arrows* and *gray curves* ocean water; *open arrows* and *dashed lines* river water; *arrow size* represents magnitude of relevant event)

Discussion

Mechanisms by which estuarine zooplankton are able to sustain viable populations under net outflow conditions have been hypothesized to involve both physical trapping and behavioral strategies. Larvae of a variety of crab species have been found to maintain

Table 1 *Coullana canadensis* and *Eurytemora affinis*. Analysis of variance results for fit of harmonic-analysis model to square-root-transformed near-bottom densities during 112 h time series in spring 1992

Source of variation	Sum of squares	(*df*)	Mean sum of squares	*F*-statistic	*p*
Coullana canadensis					
Total	190902.414	(56)			
Regression	71203.414	(10)	7120.341	2.74	0.0099
Residual	119699.000	(46)	2602.152		
Eurytemora affinis					
Total	822609.375	(56)			
Regression	329701.375	(10)	32970.138	3.08	0.0045
Residual	492908.000	(46)	10715.391		

Table 2 *Coullana canadensis* and *Eurytemora affinis*. Tidal components used in harmonic analysis of 112 h series in May 1992, and percent variability of near-bottom densities explained by each frequency in the model

Tidal component	Symbol	Period (solar hr)	*Coullana canadensis*	*Eurytemora affinis*
Diurnal components				
Lunisolar diurnal	K_1	23.93	37.75%	17.39%
Semi-diurnal components				
Principal lunar	M_2	12.42	26.58%	48.05%
	M_3	8.28	0.97%	5.29%
Quarter lunar	M_4	6.21	17.61%	9.61%
	$2MK_5$	4.93	17.08%	19.67%

populations or even effect net upstream transport by means of migration into stratified flows (Cronin 1982; Tankersley and Forward 1994). Studies on behavioral migration in copepods for population maintenance are rare, and findings have been mixed. Castel and Veiga (1990) stated that *Eurytemora affinis* populations in the Gironde River estuary of France are maintained through the same hydrological processes that trap and concentrate suspended particles. Hough and Naylor (1991, 1992), however, found that in the Conwy River estuary in Wales, *E. affinis* maintained itself through vertical migration into stratified flow layers. The integrated collection of physical variables and zooplankton samples during our study provides insight into the complex interactions between physical and biological processes at a spatial and temporal resolution not common in prior studies. The results illustrate that two predominant copepods in the Columbia River estuary, the harpacticoid *Coullana canadensis* and the calanoid *E. affinis*, most probably utilize two different means of population maintenance in this river-dominated estuary, where estuarine turbidity maxima provide strong particle-trapping and increased residence times.

Particle trapping

Patterns of turbidity density and distribution created by the circulation features of the estuary can be used as a model for the behavior of a passive particle in this system. During periods of ebb (seaward) tide, ETM particles are advected down river, with the highest export rates occurring at the surface. After ebb tide, higher densities of sediment and particles occur on the bottom because of settling during slack water. As the flood tide moves in, it resuspends such sediments and initiates landward advection of the already concentrated particles. Many of these particles also become trapped in less dense water above the density gradient (Jay and Musiak 1995). The closer a particle is to the bed, the more bed stress is required to lift it into the water column. Bed stress is highest in the higher velocity seaward of the salt intrusion. Thus, particles very near the bed are not lifted as high into the water column and are not transported as far as those slightly off the bottom. In other words, a cycle of advection, settling, and resuspension facilitates retention of passive particles in the estuary (Fig. 6: *Coullana canadensis*).

Coullana canadensis distribution

Abundances of *Coullana canadensis* were usually greater near the bottom than at the surface, which agrees with the Haertel and Osterberg's (1967) classification of this species as a benthic invertebrate. The density distribution mirrors that of suspended particulate matter, with concentrations near the bottom greater than higher in the water column (Simenstad et al. 1994a; Jay and Musiak 1995). Because this species' temporal and spatial patterns of abundance and distribution had a high correlation with that of turbidity, it is very likely that it was being retained in the same manner as sediment and organic particles that are trapped and concentrated in the ETM (Fig. 6). This is further confirmed by the lack of *C. canadensis* specimens in samples taken at both the upriver and downriver ends of the estuary (Cordell et al. 1992; Simenstad et al. 1994a), although extreme ebb tidal velocities prevented sampling during peak export phases (e.g. spring ebb during high freshwater discharge). This evidence, substantiated by the harmonic analysis, indicates that daily and twice daily tidal frequencies are both important in shaping the abundance and distribution patterns of *C. canadensis*. Although the densities of this species are often extremely high, they are not the cause of the high turbidity measurements. Particulate organic carbon measurements (POC) from the estuary were never higher than 6% by weight of the total suspended particulate matter (SPM) (Prahl et al. 1997). If copepods constituted the bulk of the SPM, POC would be 35 to 40% by weight.

A passive population-maintenance strategy by *Coullana canadensis* does not preclude other mechanisms such as reproductive cycle adaptations. For populations of *C. canadensis* in the Saco River estuary in Maine, USA, Gupta et al. (1994) have suggested life-history adaptations to the hydrology of the system. They propose that the high river flows in spring and early summer delay peaks of population recruitment until lower river flows during late summer. This late peak in the population provides a source of adult individuals that overwinter and reproduce during the next season (Lonsdale et al. 1993). Saco River estuary hydroperiod and seasonal peaks in *C. canadensis* densities are similar to those in the Columbia River estuary, suggesting the possibility of similar life-history strategies for this system.

Eurytemora affinis distribution

Results from our Columbia River ETM study indicated that, although dispersal of *Eurytemora affinis* into the upper water column occurs during flood tides, the highest population densities are 0.5 to 2 m above the bed during the ebb tide, in a zone of net residual landward flow (Fig. 2). Patterns of abundance and distribution did not match those of turbidity, suggesting that physical trapping is not the method that this copepod uses to maintain populations in the Columbia River estuary. *E. affinis* has been considered epi- or hyperbenthic by some authors (Haertel and Osterberg 1967; Sibert 1981), although in some systems it occurs in the water column and vertically migrates on a diel schedule to avoid predation and to increase fecundity (Vuorinen 1986, 1987; Ban and Minoda 1989). In the Columbia River ETM, *E. affinis* was regularly found throughout the water column, and harmonic analysis revealed patterns of *E. affinis* movement that occurred on a diurnal tidal rather than a diel cycle.

As with *Coullana canadensis*, seaward advection of individuals near the surface would occur during the ebb tide. This suggests that the greater the proportion of the population lower in the water column, the lower the advective losses. Settling or swimming to a position lower in the water column or into bottom detritus and sediments could occur prior to the ebb in order to avoid major advective losses. Castel and Veiga (1990) measured sinking rates of 0.193 cm s^{-1} for non-ovigerous and 0.340 cm s^{-1} for ovigerous individual *Eurytemora affinis* in the laboratory. Thus, it is possible that an individual may sink from 2.3 to 4.1 m during a 20 min slack-tide period, typical in the Columbia River ETM region. During a slack tide most of the population could sink to depths sufficient to avoid peak ebb velocities on the surface. The density gradient reversed during flood tide, with dispersal up into the water column. If populations of *E. affinis* are able to undergo short-range vertical migration, they could be more easily transported up river with counter-gradient flow near the bed during flood tides. Jay and Musiak (1995) consider the net flow in the bottom 5 m of the estuary's dominant channels to be landward. Harmonic analysis confirmed high near-bottom densities of *E. affinis* once every 12.4 h, which is coincident with ebb events.

Castel and Veiga (1990) concluded that because *Eurytemora affinis* could not maintain itself in experimental chambers at simulated in situ velocities, maintenance in an estuary could not be explained by behavioral mechanisms. However, Hough and Naylor (1991, 1992) observed tide-related vertical migrations for *E. affinis* in the mid-estuary region of the Conwy River estuary in Wales. Further laboratory investigations found that the swimming activity of *E. affinis* collected from mid-estuary was highest during the flood tide and lowest during the ebb tide (Hough and Naylor 1992). This corresponds to our findings that *E. affinis* densities were greater higher in the water column during the flood and lower in the water column during the ebb. In addition, Hough and Naylor observed differences in swimming activity level related to position along the estuary and semilunar cycle (increasing or decreasing spring and neap tides). They further speculated that these circatidal swimming rhythms would be a very effective mechanism of population retention in an estuary experiencing two-layer flow. The results of our study in the Columbia River estuary suggest that active, behaviorally-induced movements could play an integral role in the population-retention mechanisms of this species. *E. affinis* may use a cycle of landward and vertical movements into the water column during the flood, settling during slack-tide periods, and vertical sinking accompanied by seaward advection during the ebb tides (Fig. 6), which could be very effective in retaining populations on the scale of the entire estuary.

Anthropogenic changes in the Columbia River watershed have influenced almost every major component of this watershed. Changes in water and sediment flow and temperature are pervasive and culminate in altered estuarine processes (Simenstad et al. 1992). The present study, in combination with previous work in the estuary, has demonstrated that there is an intricate link between the physical and biological processes in the estuary. The integration of techniques, such as harmonic analysis, commonly used to investigate physical properties of the system, is a natural progression for biological investigations. Our study has shown that integrated, interdisciplinary investigation of overlapping complex physical and biological processes, can lead to a more mechanistic understanding of the controls on and alterations to estuarine production.

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