Estuaries and Coasts (2011) 34:1255–1261
DOI 10.1007/s12237-011-9405-7

Vertical Distribution and Migration of Decapod Larvae in Relation to Light and Tides in Willapa Bay, Washington

Joanne K. Breckenridge · Stephen M. Bollens

Received: 24 November 2010 / Revised: 18 March 2011 / Accepted: 11 April 2011 / Published online: 3 May 2011

Abstract We investigated the occurrence of behaviors that maximize predator avoidance and seaward transport in estuarine decapod zoeae by collecting larvae from discrete depths in a partially mixed estuary, Willapa Bay, Washington, USA, and relating their abundance and vertical distribution to a suite of environmental variables. Abundances of first zoeae of *Neotrypaea californiensis* and Pinnotheridae were associated with tidal phase, diel phase, and water height. Both taxa were most abundant during ebb tides, and abundances increased with water height, suggesting behaviors that enhanced seaward transport. Additionally, *N. californiensis* were both shallower and more abundant at night, indicative of behaviors to avoid visual predators. Our results suggest that both tidal transport and predator avoidance are important and sometimes interactive selective forces shaping larval decapod behavior.

Keywords Decapod vertical distribution · Diel vertical migration · Selective tidal-stream transport · Decapod behavior · Predator avoidance

Introduction

The vertical distribution and migration of planktonic organisms can have population level consequences in terms of food acquisition, predation levels, metabolism, and reproduction (Bollens and Frost 1991; Hays 2003). Because current speed and direction may vary with depth, the vertical distribution of planktonic organisms also largely influences its horizontal distribution and is of particular importance to species with a benthic adult stage (Thorson 1950).

Planktonic larvae of many benthic estuarine species develop in coastal waters, returning to estuaries as postlarvae for settlement (Bilton et al. 2002; Roegner et al. 2007). In addition to increasing genetic exchange and dispersal potential, development in coastal waters is considered favorable because estuaries are thought to have both a higher concentration of predators and to be more physiologically stressful environments than coastal waters, as they experience large and rapid variation in temperature and salinity (Morgan 1995; Bilton et al. 2002).

Lower-estuarine invertebrates often possess behaviors that maximize the proportion of larvae reaching coastal waters (Bilton et al. 2002; Paula et al. 2004). Tides are a predictably variable component of the physical environment (Hill 1991) that can be exploited to enhance seaward transport, either by releasing larvae at high water (Provenzano et al. 1983; Morgan and Christy 1995) or through synchronizing vertical migrations to coincide with specific tides, a behavioral mechanism called selective tidal-stream transport (STST; Forward and Tankersley 2001). By altering vertical position with respect to the benthic boundary layer, where water velocity is lower, organisms can enhance unidirectional transport. Many examples of tidally timed vertical migrations have been found among the larvae of decapod crustaceans (Queiroga and Blanton 2005). Swimming and orientation in decapod larvae may be subject to both endogenous rhythms (Zeng and Naylor 1996; López-Duarte and Tankersley 2007) and exogenous stimuli. Vertical distribution and migratory

J. K. Breckenridge (✉) · S. M. Bollens
School of Biological Sciences, Washington State University,
14204 NE Salmon Creek Ave,
Vancouver, WA 98686, USA
e-mail: jbreckenridge@vancouver.wsu.edu

S. M. Bollens
School of Earth and Environmental Sciences,
Washington State University,
14204 NE Salmon Creek Ave,
Vancouver, WA 98686, USA

behavior can therefore be influenced by various water column properties, including pressure (Forward and Wellins 1989; Tankersley et al. 1995), temperature (Sulkin et al. 1980), salinity (Sulkin 1984), and by interactions between these stimuli (Sulkin et al. 1980).

Decapods are also sensitive to the diel light cycle (Forward et al. 1984), and within estuaries, larval release and upward vertical migration occur most frequently on nocturnal high tides (Cronin and Forward 1982; Morgan and Christy 1995; Paula et al. 2004). These behaviors occur in a wide range of planktonic animals and are considered to be driven in large part by predation (Bollens and Frost 1989, 1991; Cohen and Forward 2009).

Willapa Bay is a strongly tidal, shallow estuary with a predominantly mixed water column during summer months. Vertical mixing may hinder an organisms' ability to vertically migrate as well as dampen cues given by environmental variables (Lochman et al. 1995). The larval ghost shrimp, *Neotrypaea californiensis* (Thalassinidae: Callianassidae) and pea crabs, Pinnotheridae, are dominant decapod members of the mesozooplankton in Willapa Bay, Washington, during summer months (Graham and Bollens 2010). As adults, *N. californiensis* reside in burrows in the estuary sediments (Dumbauld et al. 1996). Pinnotheridae are commensal within these burrows or within bivalves (Schmitt et al. 1973).

We hypothesized that *N. californiensis* and Pinnotheridae zoeae would possess (1) behaviors promoting export from the estuary and (2) predator avoidance, and investigated the presence of STST and diel vertical migration (DVM) behaviors. We predicted that larvae would have a shallower distribution and/or a higher abundance on ebb tides to enhance seaward export and a deeper distribution and/or reduced abundances during daylight to avoid visual predators. We further asked whether vertical distributions and abundances could be predicted by various environmental variables, namely, salinity, temperature, degree of stratification, and water height.

Materials and Methods

Study Site

Willapa Bay, Washington, is characterized as a partially mixed estuary with a strong tidal influence, mixed semidiurnal tides with a mean tidal range of 2.7 m (Banas et al. 2004), and an approximate area of 260 km^2 (Dumbauld et al. 1996). We conducted our study from a single site located approximately 12 km from the mouth of the estuary, on the southern side of Willapa Channel, across from Toke Point, WA (Fig. 1). Total water column depth varied between 6 and 10 m during our study.

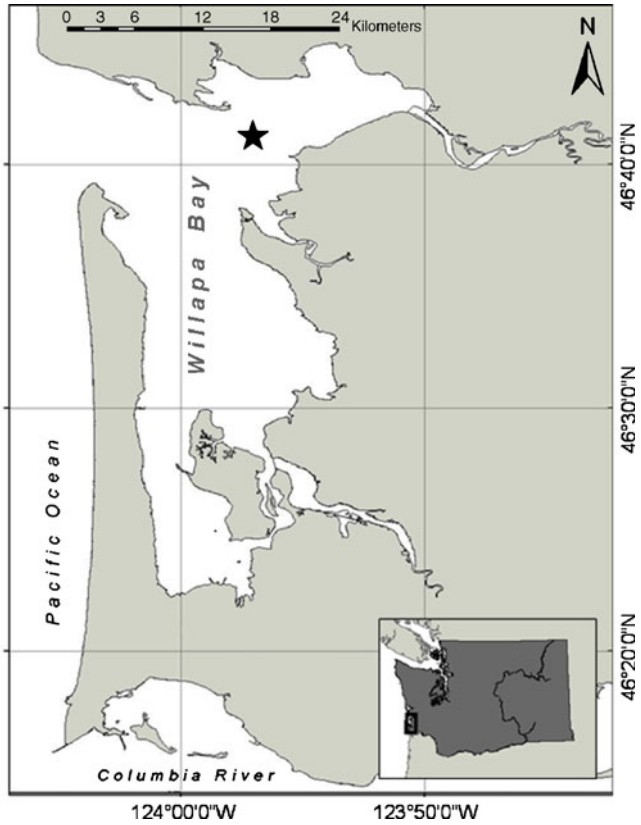

Fig. 1 Willapa Bay, Washington, USA. Location of fixed station (46° 40′57.56″, −123°58′9.77″) where all samples were collected is indicated by the *star* symbol

Field Sampling

From an anchored boat, we collected replicate plankton samples from discrete depths within the water column every 3 h over a tidal cycle during three sampling periods. Samples were collected using a 6.5 hp deck-mounted pump connected to a 6 cm diameter hose. The pump was run for approximately 5 min, drawing an average volume of 860 L which was passed through a 500-μm mesh net suspended in water. Plankton samples were preserved in 10% buffered formalin. Water column profiles for salinity and temperature were taken by CTD (Seabird SBE 25) cast at the beginning and end of each depth series (approximately every 1.5 h). Degree of stratification and water height were used as proxy measures of vertical mixing and hydrostatic pressure, respectively. Sampling occurred on spring tides during 16–18 May 2006, 9–10 October 2006, and 15–16 May 2007 over 26-, 23-, and 20-h periods, respectively. May and October sampling dates were chosen to coincide with spawning and recruitment periods, respectively, of *N. californiensis*. In May 2006 and October 2006, replicate samples were taken from three depths: 1 m above bottom, mid-water column (halfway between surface and bottom), and 1 m below surface. In May 2007, a fourth sample at 0.5 m above

bottom was added. A total of 157 samples were collected. Decapod zoeae in the samples were counted and identified to the lowest possible taxonomic level based on Puls (2001).

Data Analysis

We calculated relative weighted mean depths (WMD) of larvae after Frost and Bollens (1992) as normalized for depth by Queiroga (1998):

$$\text{Relative WMD} = \frac{\sum n_i \times d_i}{\sum n_i} \times \frac{1}{D_t}$$

Where n was the untransformed abundance (number per cubic meter) of larvae at depth, d, and D was the total depth of the water column. Dividing WMD by D controlled for variability in total water depth caused by tides and gave us a relative depth, where a value of 1 is the bottom and 0 is the surface (Queiroga 1998). Because the larval abundances from which relative WMD values were calculated varied widely, a separate weighting variable was calculated as the square root of total abundance. This weighting variable was used in all statistical analyses of WMD and caused WMD values resulting from higher abundances to have a stronger influence on the result.

To determine how the measured environmental variables were related to the vertical distribution and abundance of zoeae, the relative WMD and abundance were analyzed in separate multiple linear regressions with water height, index of stratification (calculated by subtracting the salinity at the surface of the water column from that at the bottom), and depth specific values of salinity and temperature as predictors. Sampling date was included as a dummy variable. Where the data did not meet the assumptions of regression, Spearman's ranked correlations were calculated. All regression analyses were performed using SAS v. 9.1 and a Šidák-Bonferroni corrected alpha of 0.0253.

To investigate the presence of STST and DVM behaviors, the relationships of the vertical distribution of zoeae to tidal phase and diel phase were investigated in two-way analyses of variance (ANOVAs) with sampling date used as a nesting factor. Log (x+1) transformed abundances were analyzed in a similar manner with depth included as a third factor. Significant relationships of abundance and WMD with continuous environmental variables (e.g., water height) could confound comparisons between categorical variables (e.g., tidal phase) where, for instance, the water height was on average higher during the sampling of one tide than the other. Where this situation arose, WMD and abundances were regressed upon the continuous variables and residuals used in the ANOVAs. Data which had unequal variances were rank-transformed, which equalized variances on all occasions. Mean ranks were analyzed in the original ANOVA models with interaction terms following the method proposed by Conover and Iman (1981). P values generated from the rank-transform approach were more conservative than those from the initial ANOVAs. All ANOVAs were calculated using SPSS v.16 and a Šidák-Bonferroni corrected alpha of 0.0253.

Results

Of the decapod zoeae collected, the first zoeae of *N. californiensis* and of Pinnotheridae were found in sufficient numbers for statistical analysis. The Pinnotheridae that we collected were not described in the literature and were therefore lumped for statistical analysis. Eight pinnotherid species with undescribed larval stages occur in the Northeast Pacific and have estuarine host species: *Pinnixa eburna*, *Pinnixa faba*, *Pinnixa littoralis*, *Pinnixa occidentalis*, *Pinnixa schmitti*, *Pinnixa tubicola*, *Pinnotheres pugettensis*, and *Scleroplax granulata* (Puls 2001, 2002). Mid- and late-stage Pinnotheridae zoeae also were collected in very low abundance and were not included in any analyses. No later-stage *N. californiensis* zoeae were found. *N. californiensis* collected in October 2006 were excluded from analyses due to low numbers of specimens.

Average salinities were lower during the May samplings (27.5 for 2006 and 28.7 for 2007) than during the October sampling (31.7). The widest range of values of salinity and temperature occurred in May 2007, clearly showing a tidal influence as well as some stratification. During the October 2006 sampling, temperature and salinity were homogenous over both depth and time.

Vertical Distribution

While vertical distributions of both taxa were highly variable (Figs. 2 and 3), we did detect relationships between relative WMD and water height, tidal phase, and diel phase. The vertical distribution of *N. californiensis*, as calculated by relative WMD, became shallower as water height increased ($F_{(3,15)}$=22.10; r^2=0.829; P<0.001) and at night (General linear model (GLM) on residuals, $F_{(1,14)}$=7.39, P=0.017; Figs. 3b and 4a).

The vertical distribution of Pinnotheridae was not predicted by any of the variables included in the regression model. When analyzed in a two-way nested ANOVA with tidal and diel phase as main effects and sampling date as a nesting factor, Pinnotheridae mean relative WMD did not vary between main effects (Fig. 4b).

Abundance

Abundances showed strong tidal and diel patterns during our sampled periods, increasing on ebb tides for both taxa,

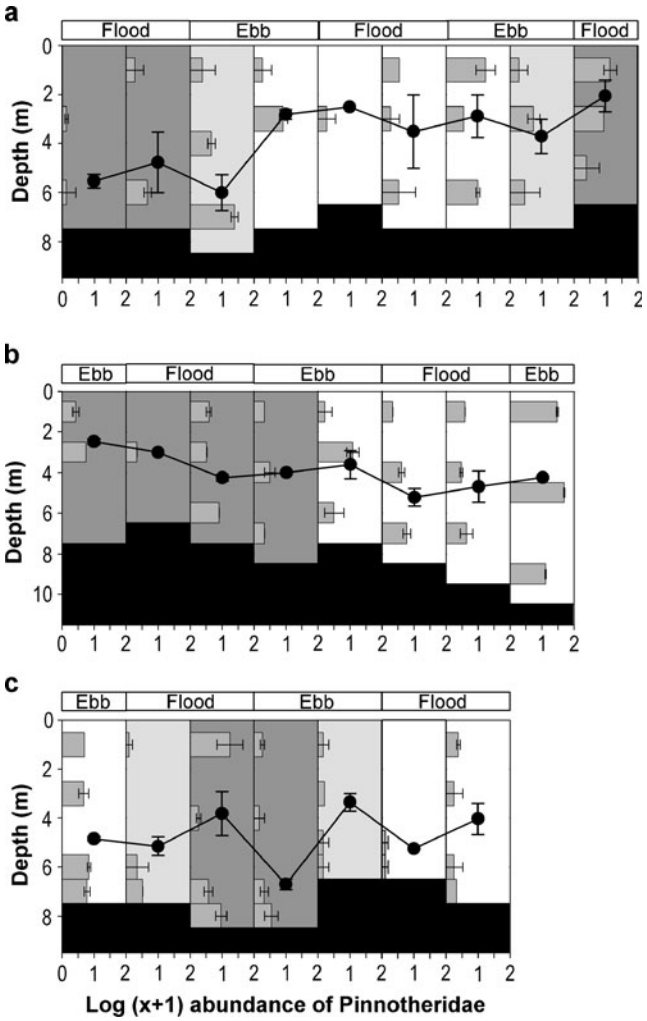

Fig. 2 Log (x+1) abundance at sampled depths (*bars*) and WMD (*line*) of Pinnotheridae first zoeae over time during three samplings; 16–18 May 2006 (**a**), 9–10 October 2006 (**b**), and 15–16 May 2007 (**c**). The width of each panel is log 2. *Shaded areas* represent night with paler shading indicating periods of twilight. Tidal phase is indicated *above* the figure. Total water column height varied over the sampled periods, as represented by the *blackened areas* at the *base* of the figures. *Error bars*=±1 SE

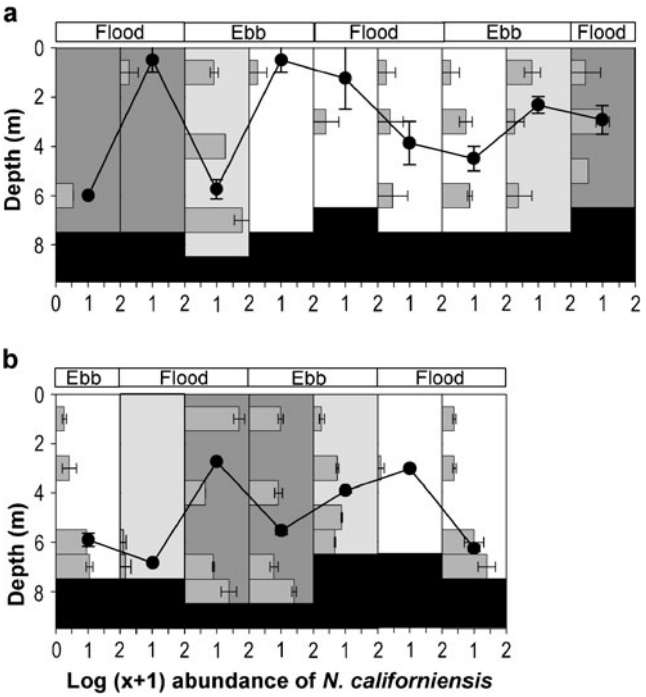

Fig. 3 Log (x+1) abundance at sampled depths (*bars*) and WMD (*line*) of *N. californiensis* first zoeae over time during two samplings; 16–18 May 2006 (**a**) and 15–16 May 2007 (**b**). The width of each panel is log 2. *Shaded areas* represent night with paler shading indicating periods of twilight. Tidal phase is indicated *above* the figure. Total water column height varied over the sampled periods, as represented by the *blackened areas* at the *base* of the figures. *Error bars*=±1 SE

at night for *N. californiensis* and during the day for Pinnotheridae (Fig. 5). The degree of vertical salinity stratification was not related to the total water column abundance of either Pinnotheridae or *N. californiensis* zoeae (P=0.149 and 0.388, respectively).

The abundance of *N. californiensis* increased with water height (r^2=0.145, df=95, F=7.865, P<0.001). *N. californiensis* zoeae were most abundant on nocturnal ebb tides (tide×diel phase, GLM on residuals, $F_{(1,92)}$=6.80, P=0.011; Fig. 5a).

Pinnotheridae abundance increased with water height (Spearman's r^2=0.370, df=156, P<0.001) and salinity (Spearman's r^2=0.281, df=156, P<0.001). Pinnotheridae zoeae were most abundant on daytime ebb tides (tide×diel phase, GLM on ranks, $F_{(1,33)}$=9.28, P=0.003; Fig. 5b).

Discussion

For both *N. californiensis* and Pinnotheridae zoeae, our sampling revealed clear patterns in abundance associated with tidal phase, diel phase, and water height. Variation in mean depth was less consistent, though where distributions did differ between tidal and diel phases, it was in the predicted manner (shallower at night and during ebb tides). Increased abundances during ebb tides paired with increased abundances (and in the case of *N. californiensis* shallower distributions) at higher water levels suggest that these taxa possess behaviors that promote export out of the estuary. In the case of *N. californiensis*, higher abundances and shallower distributions at night suggest the presence of DVM behaviors that reduce susceptibility to visual predators.

As is commonly observed for decapod larvae (Queiroga and Blanton 2005), *N. californiensis* were more abundant at night. This has been observed previously in *N. californien-*

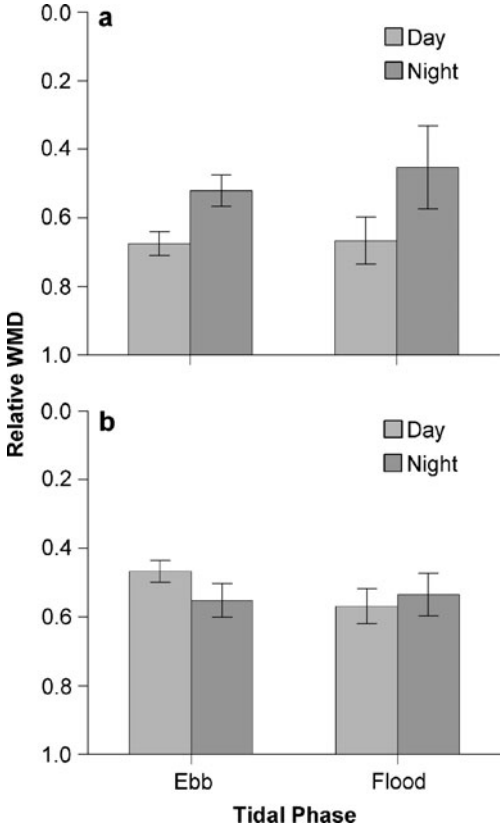

Fig. 4 Relative WMD by tidal and diel phase of *N. californiensis* (**a**) and Pinnotheridae (**b**) zoeae. *Error bars*=±1 SE

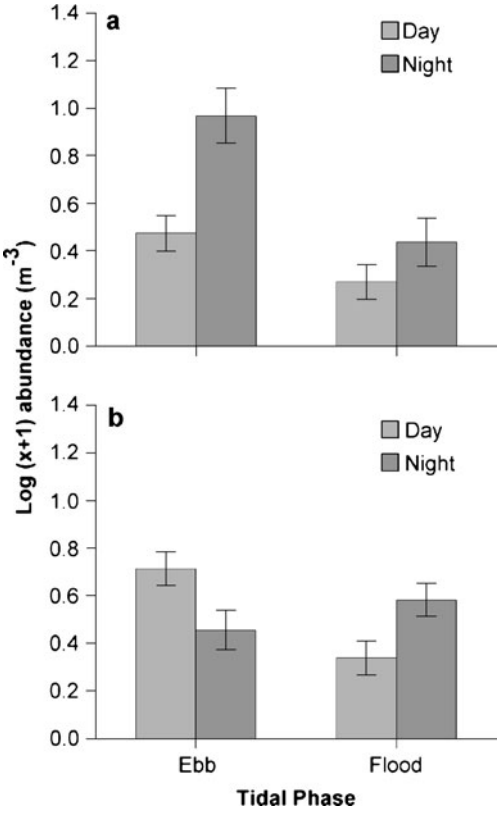

Fig. 5 Mean log (*x*+1) abundances by tidal and diel phase of *N. californiensis* (**a**)and Pinnotheridae (**b**) zoeae. *Error bars*=±1 SE

sis in South Slough, Oregon, where peak densities were reached specifically on night ebbs (Pimentel 1983; Puls 2002). In laboratory investigations, *N. californiensis* exhibited upward nocturnal vertical migration (Breckenridge and Bollens 2010). Higher nocturnal abundances and DVM are generally considered to be predator avoidance mechanisms (e.g., Bollens and Frost 1989, 1991).

Unlike *N. californiensis*, Pinnotheridae abundances did not differ between diel phases. Pinnotheridae first zoeae are typically less than 1 mm in diameter whereas *N. californiensis* first zoeae are approximately 2 mm in length. The absence of reduced abundances during daylight may reflect the decreased susceptibility of smaller zooplankters to vertebrate predators (Brooks and Dodson 1965; Frost and Bollens 1992). However, because we were only able to identify Pinnotheridae zoeae to family, our observations may reflect a range of species-specific behaviors, both within and across sampling dates. Indeed, in a nearby study that lumped Pinnotheridae, Puls (2002) had results supporting the presence of contradicting behaviors with respect to seaward export.

Though the WMD of *N. californiensis* was correlated to water height, indicating a shallower distribution at high water, it did not vary between tidal phases. Puls (2002) found that first zoeae of *N. californiensis* were more abundant in surface than in bottom waters during nocturnal ebb tides in the South Slough estuary, Oregon, whereas Pimentel (1983) found that they were uniformly distributed across depths over both tidal phases. Other Callianassids have been found to perform tidal migrations, e.g., *Nihonotrypaea harmandi* on the inner shelf of western Kyushu, Japan (Tamaki et al. 2010).

The results of a 24-h sampling series conducted in Yaquina Bay, Oregon, by McCrow (1972) showed increased densities of first zoeae of *N. californiensis* occurring on the night ebb tide and peaking during the period immediately prior to highest high water. Estuarine brachyurans are known to release their larvae at high water (reviewed by Forward 1987; Morgan and Christy 1995), and peak abundances of first zoeae commonly occur at this time (Forward and Tankersley 2001). McCrow (1972) suggested that *N. californiensis* larval release is synchronized to ebb tides but, to our knowledge, this hypothesis has never been tested. While tidally synchronized larval release would be adaptive, particularly in a mixed estuary, changes in abundance may also be explained by advection and vertical migration, and we cannot discount the possibility of vertical migration occurring over a scale that we did not sample. For instance, DiBacco et al. (2001) demonstrated that first zoeae of *Pachygrapsus crassipes* in

San Diego Bay, California, exploited the sediment–water interface during flood tides to maximize unidirectional transport. Puls (2002) also suggested that *N. californiensis* might be residing on the bottom during flood tides. Be it by STST or synchronized larval release, the highly tidal pattern of abundance we observed suggests the presence of behaviors promoting seaward export in *N. californiensis* and, to a lesser degree, Pinnotheridae zoeae.

Water height was consistently a significant predictor of zoeal abundances. Both *N. californiensis* and Pinnotheridae zoeae were more abundant with increased water height. Moreover, *N. californiensis* became shallower with increasing water height. Change in water height has been used as a proxy for change in pressure, a highly conservative indicator of tidal phase (Queiroga 1998). In shallow temperate estuaries, relative change in hydrostatic pressure would be large, depending on tidal amplitude. The larvae of many decapod taxa alter their swimming speed in response to changes in pressure, orienting themselves via gravity or light (Sulkin 1984; Queiroga and Blanton 2005). Laboratory studies by Forward and colleagues (Forward and Wellins 1989; Forward et al. 1989) have shown that zoeae of the estuarine brachyuran species *Rhithropanopeus harrisii* and *Neopanope sayi* are able to perceive relatively small changes in absolute hydrostatic pressure and respond to rates of pressure change with behaviors indicative of active depth regulation. However, these changes would not necessarily be detected in a natural environment (Tankersley et al. 1995). Rather than resulting from a direct response to change in pressure, changing abundance and vertical distribution with water height may be the result of endogenous circatidal rhythms, which have been found in the zoeae of several brachyuran taxa (Zeng and Naylor 1996; López-Duarte and Tankersley 2007).

Though we found evidence of behaviors promoting seaward export, we did not find any evidence for tidally timed vertical migration in *N. californiensis*. In *Callinectes sapidus*, larval export was hastened through seaward migration on the part of ovigerous females prior to larval release on a high tide (Tankersley et al. 1998). The range of adult *N. californiensis* is generally restricted to areas near the estuary mouth (McCrow 1972; Johnson and Gonor 1982), and this coupled with tidally timed larval release may be sufficient, particularly in a highly tidal estuary, to rapidly flush first zoeae out of the estuary.

In summary, our results suggest that *N. californiensis* possesses behaviors to reduce susceptibility to visual predators. Our results also provide evidence that both *N. californiensis* and Pinnotheridae possess behaviors promoting seaward transport of the first zoeal stage and that these are most strongly linked to water height. These results, when combined with those from previous studies of different taxa and other estuaries, suggest that both tidal transport and predator avoidance are important and sometimes interactive selective forces shaping larval decapod behavior.

Acknowledgments We are grateful to I. McComas, R. Hooff, E. Graham, A. Helms and K. Olsen for support in the field and to B. Tissot and G. Rollwagen-Bollens for manuscript review. This work was partially supported by ONR grant N000140610200 to S.M. Bollens.

References

Banas, N.S., B.M. Hickey, and P. MacCready. 2004. Dynamics of Willapa Bay, Washington: a highly unsteady, partially-mixed estuary. *Journal of Physical Oceanography* 34: 2413–2427.

Bilton, D.T., J. Paula, and J.D.D. Bishop. 2002. Dispersal, genetic differentiation and speciation in estuarine organisms. *Estuarine, Coastal and Shelf Science* 55: 937–952.

Bollens, S.M., and B.W. Frost. 1989. Predator-induced diel vertical migration in a planktonic copepod. *Journal of Plankton Research* 11: 1047–1065.

Bollens, S.M., and B.W. Frost. 1991. Diel vertical migration in zooplankton: rapid individual response to predators. *Journal of Plankton Research* 13(6): 1359–1365.

Breckenridge, J.K., and S.M. Bollens. 2010. Biological thin layer formation: interactions between the larval decapod *Neotrypaea californiensis*, haloclines, and light. *Journal of Plankton Research* 32(7): 1097–1102.

Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150(3692): 28–35.

Cohen, J.H., and R.B. Forward Jr. 2009. Zooplankton diel vertical migration—a review of proximate control. *Oceanography and Marine Biology. Annual Review* 47: 77–110.

Conover, W.J., and R.L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* 35(3): 124–129.

Cronin, T.W., and R.B. Forward. 1982. Tidally timed behavior: effects on larval distributions in estuaries. In *Estuarine comparisons*, ed. V. Kennedy, 505–520. New York: Academic Press.

Dibacco, C., D. Sutton, and L. McConnico. 2001. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay–ocean exchange. *Marine Ecology Progress Series* 217: 191–206.

Dumbauld, B.R., D.A. Armstrong, and F.L. Feldman. 1996. Life-history characteristics of two sympatric Thalassinidean shrimps, *Neotrypaea californiensis* and *Upogebia pugettensis*, with implications for oyster culture. *Journal of Crustacean Biology* 16(4): 689–708.

Forward, R.B. 1987. Larval release rhythms of decapod crustaceans: an overview. *Bulletin of Marine Science* 41: 165–176.

Forward, R.B., and R.A. Tankersley. 2001. Selective tidal-stream transport of marine animals. *Oceanography and Marine Biology. Annual Review* 39: 305–353.

Forward, R.B., and C.A. Wellins. 1989. Behavioral responses of a larval crustacean to hydrostatic pressure: *Rhithropanopeus harrisii* (Brachyura: Xanthidae). *Marine Biology* 101: 159–179.

Forward, R.B., T.W. Cronin, and D.E. Stearns. 1984. Control of diel vertical migration: photoresponses of a larval crustacean. *Limnology and Oceanography* 29(1): 146–154.

Forward, R.B., C.A. Wellins, and C.U. Buswell. 1989. Behavioral responses of larvae of the crab *Neopanope sayi* to hydrostatic pressure. *Marine Ecology Progress Series* 57: 267–277.

Frost, B.W., and S.M. Bollens. 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1137–1141.

Graham, E.S., and S.M. Bollens. 2010. Macrozooplankton community in relation to environmental variables in Willapa Bay, Washington, USA. *Estuaries and Coasts* 33(1): 182–194.

Hays, G.C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503: 163–170.

Hill, A.E. 1991. Vertical migration in tidal currents. *Marine Ecology Progress Series* 75: 39–54.

Johnson, G.E., and J.J. Gonor. 1982. The tidal exchange of *Callianassa californiensis* (Crustacea, Decapoda) larvae between the ocean and the Salmon River Estuary, Oregon. *Estuarine, Coastal and Shelf Science* 14: 501–516.

Lochman, S.E., R.M. Darnell, and J.D. McEachran. 1995. Temporal and vertical distribution of crab larvae in a tidal pass. *Estuaries* 18: 255–263.

López-Duarte, P.C., and R.A. Tankersley. 2007. Circatidal swimming behavior of brachyuran crab larvae: implications for ebb-tide transport. *Marine Biology* 151: 2037–2051.

McCrow, L.T. 1972. The ghost shrimp *Callianassa californiensis* Dana, 1854, in Yaquina Bay, Oregon. MS thesis, Oregon State University, Corvallis, OR, 56 pp.

Morgan, S.G. 1995. Life and death in the plankton: larval mortality and adaptation. In *Ecology of Marine Invertebrate Larvae*, ed. L. R. McEdward, 157–191. Boca Raton: CRC Press.

Morgan, S.G., and J.H. Christy. 1995. Adaptive significance of the timing of larval release by crabs. *The American Naturalist* 145(3): 457–479.

Paula, J., C. Bartilotti, T. Dray, A. Marcia, and H. Queiroga. 2004. Patterns of temporal occurrence of brachyuran crab larvae at Saco mangrove creek, Inhaca Island (South Mozambique): implications for flux and recruitment. *Journal of Plankton Research* 26(10): 1163–1164.

Pimentel, G.E. 1983. Recruitment of larvae of the ghost shrimp, *Callianassa californiensis* (Crustacea, Decapoda), in the south slough estuary, Oregon. MS Thesis, University of Oregon, Eugene, OR.

Provenzano Jr., A.J., J.R. McConaugha, K.B. Philips, D.F. Johnson, and J. Clark. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. *Estuarine, Coastal and Shelf Science* 16(5): 489–499.

Puls, A.L. 2001. Arthropoda: Decapoda. In *An identification guide to the larval marine invertebrates of the Pacific Northwest*, ed. A.L. Shanks, 181–252. Corvallis: Oregon State University Press.

Puls, A.L. 2002. Transport of zooplankton in South Slough, Oregon. MS Thesis, University of Oregon, Eugene, OR, 95pp.

Queiroga, H. 1998. Vertical migration and selective tidal stream transport in the megalopa of the crab *Carcinus meanas*. *Hydrobiologia* 375/376: 137–149.

Queiroga, H., and J.O. Blanton. 2005. Interaction between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Advances in Marine Biology* 47: 107–214.

Roegner, G.C., D.A. Armstrong, and A.L. Shanks. 2007. Wind and tidal influences on crab recruitment to an Oregon estuary. *Marine Ecology Progress Series* 351: 177–188.

Schmitt, W.L., J.C. McCain, and E.S. Davidson. 1973. Decapoda I Brachyura I Fam. Pinnotheridae. In *Crustaceorum catalogus 3*, ed. H.-E. Gruner and L.B. Holthuis, 160. The Netherlands: Den Haag. Dr. W. Junk NV.

Sulkin, S.D. 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Marine Ecology Progress Series* 15: 181–205.

Sulkin, S.D., W. Van Heukelem, P. Kelly, and L. Van Heukelem. 1980. The behavioral basis of larval recruitment in the crab *Callinectes sapidus* Rathbun: a laboratory investigation of ontogenetic changes in geotaxis and barokinesis. *The Biological Bulletin* 159: 402–417.

Tamaki, A., S. Mandal, Y. Agata, I. Aoki, T. Suzuki, H. Kanehara, T. Aoshima, Y. Fukuda, H. Tsukamoto, and T. Yanagi. 2010. Complex vertical migration of larvae of the ghost shrimp, *Nihonotrypaea harmandi*, in inner shelf waters of western Kyushu, Japan. *Estuarine, Coastal and Shelf Science* 86: 125–136.

Tankersley, R.A., L.M. McKelvey, and R.B. Forward Jr. 1995. Responses of estuarine crab megalopae to pressure, salinity and light: implications for flood-tide transport. *Marine Biology* 122: 391–400.

Tankersley, R.A., M.G. Wieber, M.A. Sigala, and K. Kachurak. 1998. Migratory movements of ovigerous blue crabs, *Callinectes sapidus*: evidence for selective tidal-stream transport. *The Biological Bulletin* 195: 168–173.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review* 25: 1–45.

Zeng, C., and E. Naylor. 1996. Endogenous rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus meanas*: implications for ebb-tide offshore dispersal. *Marine Ecology Progress Series* 132: 71–82.