

# Up and down or how to stay in the bay: retentive strategies of *Olympia* oyster larvae in a shallow estuary

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**ABSTRACT:** The decline of *Olympia* oysters along the US west coast has prompted interest in population recovery and therefore the larval biology of the species. *Olympia* oysters are estuarine dependent as adults. Larvae must be retained in or return to the estuary for successful recruitment. We examined larval abundance and tidally timed vertical migration for *Ostrea lurida* in Coos Bay, Oregon. Weekly zooplankton tows and CTD casts were conducted from June to October 2010 in alternating rising and falling tides. All larval stages were represented, confirming that larvae are retained in the estuary during their entire development. Possible mechanisms to increase retention are the timing of larval release and the behaviour of the larvae. No *Olympia* larvae were observed until mid-July, when water temperature rose over 16°C. Above this temperature, the probability of presence increased directly with temperature and indirectly with stratification (generalized additive model;  $R^2 = 0.89$ ); larvae were most abundant during the dry season (August to September), when low river inflow leads to long water residence times in the upper bay, where the water is warm (>16°C), salty (>25) and weakly stratified. Even in well-mixed conditions, *Olympia* oyster larvae performed tidally timed vertical migrations, moving deeper during falling tides (mean depth  $7.22 \pm 0.43$  and  $3.79 \pm 0.69$  m for falling and rising tides, respectively). High current speeds (>0.5 m s<sup>-1</sup>) overcame their swimming capability, preventing vertical migration and limiting the retentive effectiveness of this behaviour. Matching larval release with predictable hydrographical features (dry season) that favour larval retention in the bay may be the main factor determining population sustainability in Coos Bay.

**KEY WORDS:** *Olympia* oyster · Estuarine-dependent species · Tidal-timed migration · Phenology of reproduction · Larval dispersal · Meta-population connectivity · Self-recruitment

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## INTRODUCTION

The dynamics and structure of marine populations with complex life cycles are highly determined by larval dispersal patterns (Eckman 1996, Pineda et al. 2009). This is especially important for species with a sessile adult stage, since their dispersal is limited to the planktonic phase. Therefore, larval dispersal can determine not only the size of the local population but also the degree of connectivity between sub-populations (Cowen & Sponaugle 2009). A better under-

standing of these patterns is crucial information for restoration purposes, marine reserve network planning and management of exploited populations (Shanks et al. 2003, Palumbi 2004, North et al. 2010).

In addition, planktonic and sessile stages may have different physiological constraints; hence, both stages are not necessarily equally distributed. This is the case for many estuarine-dependent species in which adult-stage survival is linked to estuaries while larval development is not (Forward & Tankersley 2001); larvae must settle into an estuarine habitat

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to guarantee survival, constraining larval dispersal/migration patterns to either larval retention in the estuary during the entire planktonic phase or to larval export during an early stage and subsequent import to the embayment at a late larval stage (Epifanio 1988, Dame & Allen 1996, Gibson 2003). Both scenarios require larvae to move against the prevailing flow of the estuary at some point during their migration (Epifanio 1988, Dame & Allen 1996, Gibson 2003, Kunze et al. 2013). Since larval swimming speeds are between 1 and 3 orders of magnitude slower than horizontal currents in estuaries (Young 1995), larvae have often been considered passive particles (Caley et al. 1996). Nevertheless, increasing evidence demonstrates the capacity of many types of larvae to control their vertical position in the water column and thereby exploit vertical differences in current speed and direction to migrate into or remain within an estuary (Forward & Tankersley 2001, Metaxas 2001, Sponaugle et al. 2002, Queiroga & Blanton 2004, Shanks & Brink 2005, Morgan & Fisher 2010, Kunze et al. 2013, Morgan et al. 2014).

Vertical migrations between layers flowing in opposite directions have been reported as a mechanism that enables larvae to regulate their movement out of or into estuaries (Forward & Tankersley 2001, Kimmerer et al. 2014). Estuaries are frequently described as 2-layer circulation systems, with long-term subtidal transport seaward in the upper layer and landward near the bottom (Dyer 1997). In addition, circulation in estuaries is dominated by the oscillatory effect of tides. Bottom friction causes currents to slow near the substrate, leading to vertical asymmetry in current speeds, faster near the surface and slower near the bottom (Hill 1991). Many species have evolved behaviours, e.g. tidal-timed vertical migrations, that attempt to exploit the dynamic estuarine environment (Forward & Tankersley 2001). Because of the vertical asymmetry in estuary flow, larvae that reside near the bottom at a certain phase of the tide (falling tide for retention/landward movements and rising tide for seaward movements) and in the water column during the opposite tidal phase can effect their horizontal transport into or out of an estuary (Forward & Tankersley 2001).

Changes in the depth distribution of larvae have been related both to larval ontogeny and to responses to physical or hydrographic variables (Metaxas 2001, Kingsford et al. 2002). Ontogenetic changes in larval swimming activity have been interpreted as a response to adapt larval settlement locations to adult habitat requirements (Grosberg 1982, Dobretsov & Miron 2001, Baker & Mann 2003). Abiotic factors,

such as temperature, salinity or turbidity, have been suggested as environmental cues controlling larval vertical position (Metaxas 2001). Also, physical discontinuities can limit larval distributions to layers where conditions are more favourable to development or dispersal/migration (Tremblay & Sinclair 1990, Sameoto & Metaxas 2008, Daigle & Metaxas 2011, Lloyd et al. 2012) as well as enhanced food availability (Raby et al. 1994, Gallagher et al. 1996, Burdett-Coutts & Metaxas 2004, Sameoto & Metaxas 2008, Lloyd et al. 2012). The threshold responsible for triggering each of these cues and their relevance on larval depth distribution is species specific and mostly dependent on the species' particular life history (Forward & Tankersley 2001, Kingsford et al. 2002, Baker 2003, North et al. 2008, Sameoto & Metaxas 2008, Lloyd et al. 2012). However, even when evidence suggests that larval vertical distribution is influenced by tides, salinity gradients, current speed and turbulence (Carriker 1951, Nelson 1954, Wood & Hargis 1971, Hidu & Haskin 1978, Breckenridge & Bollens 2011, Fuchs et al. 2013, Wheeler et al. 2013, Morgan et al. 2014), controversy still exists on the relevance of this behaviour in comparison to physical transport in driving dispersal patterns (Andrews 1983, Deksheniesks et al. 1996, North et al. 2008, Kim et al. 2010, 2013, Narvaez et al. 2012). The importance of the behavioural component of larval transport is especially questioned in partially- and well-mixed environments, where increased turbulence associated with low stratification is assumed to overcome larval swimming capabilities (Andrews 1983, Tremblay & Sinclair 1990, Roegner 2000, Kim et al. 2010, Narvaez et al. 2012, Morgan et al. 2014).

Estuarine circulation is also greatly influenced by bay morphology, runoff and winds (Dyer 1997). Runoff and winds are markedly seasonal and can alter water column stratification, net transport direction and retentive characteristics of the embayment (Andrews 1983, Mann 1988, Largier et al. 1997, MacCready 1999, Ji et al. 2001, Kimbro et al. 2009). Hence, the timing of larval release into the plankton can optimize dispersal or retention of the larvae as well as larval survival (Cury & Roy 1989, Young et al. 1998, McCormick-Ray 2005, Byers & Pringle 2006, Ayata et al. 2010, Carson 2010, Carson et al. 2010, López-Duarte et al. 2012). The timing of larval release could be especially important for brooding species, which invest more resources in each offspring and have lower fecundity and, often, shorter pelagic larval duration (PLD; Buroker 1985).

The Olympia oyster is the only native oyster species on the US west coast. Following European settlement

of the west coast, over-exploitation of the Olympia oyster led to its decline and near extinction (Polson & Zacherl 2009). Recent restoration projects focused on rejuvenation of the species have had variable success (Groth & Rumrill 2009, Trimble et al. 2009). Our limited understanding of larval dispersal patterns in this species may contribute to the lack of success of some of these projects.

The Olympia oyster *Ostrea lurida* is a larviparous, estuarine-dependent species. Early larval development (6 to 18 d) occurs within the adult shell. After ~4 d of development in the brachial chamber, the straight-hinge veliger larva is already developed and continues to grow until release (165 to 189  $\mu\text{m}$ ) to the water column (Strathmann 1987). Shortly after release, the umbo becomes prominent and the larval shell becomes asymmetrical. Although veliger swimming capabilities are limited ( $\leq 0.1 \text{ cm s}^{-1}$ ; Chia et al. 1984), several studies support veliger capability to perform vertical migrations (Carriker 1951, Nelson 1954, Wood & Hargis 1971, Shanks & Brink 2005). Larvae attain competence to settle at 275 to 290  $\mu\text{m}$ , and competent larvae can be easily distinguished by an eyespot in the centre of their shell. PLD varies between 7 and 30 d (Strathmann 1987). The length of larval development varies mainly with temperature but also with salinity and food availability (Hori 1933, Loosanoff et al. 1966, Strathmann 1987). Water temperature has been suggested as the main trigger for Olympia oyster spawning (Hori 1933, Hopkins 1936), with a spawning threshold between 13 and 16°C (Hori 1933, Hopkins 1936, Oates 2013).

This study investigated the pattern of Olympia oyster larval dispersal in a partially mixed estuary (Coos Bay, Oregon) and related this to the hydrodynamics of the bay. We hypothesized that larvae are retained in the estuary during their entire development. The size frequency distribution of *O. lurida* larvae within the estuary was evaluated to determine if larvae were retained within the estuary or exported. If the larvae are retained, then all larval stages would be expected in the bay, whereas if the larvae are exported, only early and late stages would be present. If the larvae are retained in the bay, then the question arises as to how this is accomplished. The probability of retention could be enhanced if larvae were released when the residence time of water in the bay is high, or if lar-

vae have some kind of behaviour which increases retention even under dispersive conditions. We use the relationship between the presence/absence of the larvae and environmental variables as a proxy to identify possible environmental factors delimiting the presence of the larvae. In addition, larvae may make tidally timed vertical migrations, exploiting tidal currents to enhance retention. The capacity of the larvae to perform tidal-timed migrations was tested by comparing the vertical distribution of the larvae with the tidal phase and exploring the relationships between larvae vertical distribution and water column stratification, chlorophyll concentration and current speed and direction during a reproductive season.

## MATERIALS AND METHODS

Coos Bay is one of the larger estuaries on the Pacific coast of the United States (~50 km<sup>2</sup>). The estuary is classified as a drowned river valley (US Army Corps of Engineers 1994) and is formed by the junction of several sloughs (Fig. 1). A navigation channel with a minimum depth of 12 m and average width of 100 m is maintained by periodic dredging from the mouth of the bay to ~24 km up-estuary. Tides are mixed and semidiurnal, and mean tidal amplitude is around 2 m (Arneson 1976). Runoff is mainly from the Coos River

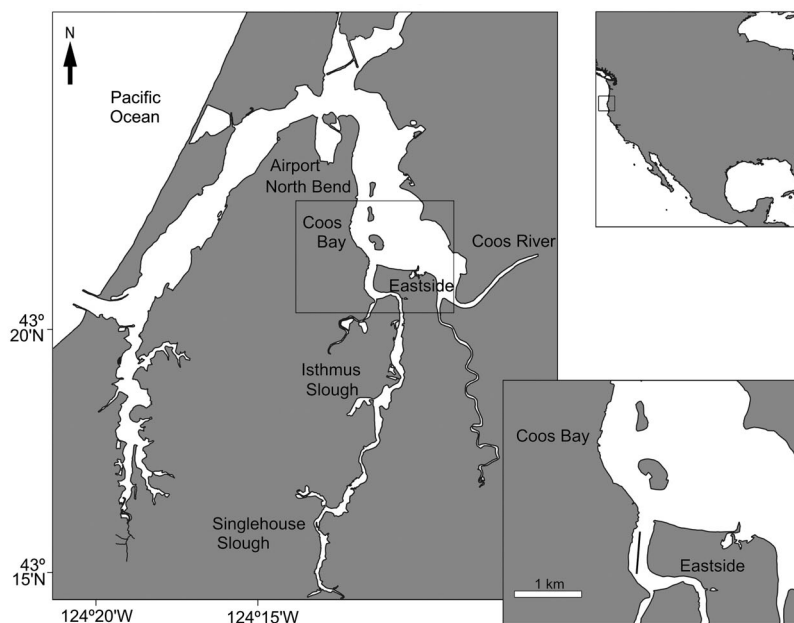


Fig. 1. Coos Bay (Oregon, USA) and close-up of the fixed sampling station (black line) where larval abundance and hydrographic variables were monitored from June 8 to October 6, 2010. Olympia oyster adult population is distributed from Shinglehouse Slough to the North Bend airport and is most abundant between East-side and Coos Bay

and is strongly related to a wet (late fall to early summer) and dry (mid-summer to early fall) season. This seasonality is also reflected in the salinity structure of the estuary, which is characteristically well mixed during the dry season and partially mixed in the wet season (Arneson 1976, US Army Corps of Engineers 1994). The Olympia oyster population in Coos Bay is distributed from Shinglehouse Slough to the North Bend airport, and is most abundant between Eastside and Coos Bay (Groth & Rumrill 2009; Fig. 1).

Larval abundance in the water column and hydrographic variables were monitored from June 8 to October 6, 2010, at 1 station where adult Olympia oysters are particularly abundant (Fig. 1). Weekly sampling was conducted during the day on alternating rising and falling tides according to NOAA tide height estimations for Coos Bay (except for 2 dates when boat availability forced sampling on consecutive rising tides [June 8 to 16 and September 22 to 29]). On each date, temperature, conductivity and chl *a* were measured through the water column with a Sea-Bird Model 19 CTD equipped with a WETStar fluorometer. In addition, 3 replicate depth-stratified plankton tows of 6 min duration were taken with a Tucker trawl (0.25 × 0.25 m) equipped with 2 nets (153 µm mesh). A trigger mechanism attached to the Tucker trawl activated by messengers from the surface allowed us to open and close the nets independently at different depths. Each net was equipped with a flow meter to determine volume filtered. The water column was divided into 2 depths for stratified plankton collection, from within 2 m off the bottom to mid-depth (lower) and from mid-depth to the surface (upper). Bottom depth was measured with a depth finder mounted on the hull of the boat. Average bottom depth during the sampling period at that section of the bay was ~12 m. Sample depth was estimated by wire angle and wire out. Zooplankton samples were preserved with buffered formalin.

In the laboratory, samples were inspected under an inverted compound microscope at a magnification of 40×. Olympia oyster larvae were counted, and the shell length of every individual was measured as the maximum length of the anteroposterior axis (lower; µm). Although Loosanoff et al. (1966) define the size of normal larvae of *Ostrea lurida* at the time of release as 185 µm, newly released veligers usually have shells 165 to 189 µm in length (Strathmann 1987). Only early and late umbonate stages were identified (the umbo starts to develop at ~190 µm length and becomes prominent at ~200 µm length; Hori 1933, Loosanoff et al. 1966, Strathmann 1987); earlier larval stages (165 to 190 µm) could not be

identified to species, but the duration of that stage (2 to 6 d for temperatures between 17 and 20°C; Hori 1933, Imai et al. 1954) is below the minimum water residence time estimated for the bay (6 d according to Arneson 1976). Larvae were identified morphologically using identification keys (Loosanoff et al. 1966, Shanks 2001) and a reference collection of larvae reared in the laboratory. Our ability to correctly identify larvae from morphology was tested by molecular techniques (16S rRNA gene amplification) on a set of samples preserved in ethanol (N = 5); there was a 100% match between the 2 techniques.

Estimations of current speed ( $Sp$ ;  $m\ s^{-1}$ ) at the mouth of the bay for the sampling time/dates were obtained from Nobeltec Tides & Currents 3.7 software. The reliability of those measures as representative of our sampling location was tested by cross-correlations between current speeds estimated by the software at the mouth of the bay and actual current speeds in our sampling section (11 drogoue deployments;  $r > 0.7$  at lag 0 for every deployment). Negative and positive values of current speed correspond to falling and rising tides, respectively. Temperature ( $T$ ; °C), Salinity ( $S$ ) and chl *a* ( $mg\ m^{-3}$ ) measurements were averaged by depth sampling intervals (lower and upper) for each sampling date. In addition, the level of stratification was estimated with the Brunt-Väisälä frequency ( $N$ ;  $rad\ s^{-1}$ ) using the standard formula (Emery 2004).

Generalized additive models (GAMs), as implemented in the mgcv library of R 2.15.2 (R Development Core Team 2012), were used to investigate the effects of the hydrographic parameters ( $Sp$ ,  $T$ ,  $S$ , chl *a*,  $N$ ), tide (rising or falling;  $R$  or  $F$ ) and depth (lower or upper) on the presence, abundance and vertical distribution of *O. lurida* in the water column. GAMs allow the exploration of non-linear functional relationships between dependent and explanatory variables, fitting predictor variables by smooth functions (Guisan et al. 2002). In the GAMs, continuous variables were considered as smoothed terms in the model and estimated with thin plate regression splines. Thin plate regression splines is the default smoothing technique for the mgcv library of R 2.15.2 (R Development Core Team 2012) because of its ability to minimize the mean squared error of any given basis dimension (Wood 2003, 2006). The effect of this set of variables was evaluated on Olympia oyster larvae presence/absence using a binomial distribution with a logit link. Larval abundance ( $A$ ;  $ind.\ m^{-3}$ ) was assessed conditionally on the presence of larvae using a Gaussian distribution on log-transformed larval abundance. The vertical distribution of the larvae

in the water column was evaluated using their weighted mean depth (WMD), calculated as:

$$\text{WMD} = \frac{\sum A_i z_i}{\sum A_i} \quad (1)$$

where  $A_i$  is the larval abundance in the  $i$ th depth interval, and  $z_i$  is the mid-depth of the  $i$ th interval (Pearre 1973). WMD values close to the averaged mid-depth of the water column (~5 m) would indicate equal horizontal distribution of the larvae, while WMD values closer to the mid-depths of the upper (~2.5 m) or lower (~7.5 m) sampling intervals would indicate asymmetrical distribution.

The relationship water density vs. water depth was evaluated with GAMs for each sampling date. When this analysis was significant, the inflexion point of the curve describing the partial effect of depth on water density was used to estimate the depth of the pycnocline ( $D_p$ ; m). The relationship chl *a* vs. water depth was evaluated in the same way, and the depth of the main chl *a* discontinuity ( $D_{\text{chl } a}$ ; m) was estimated for each sampling date following the same protocol.

GAMs were used again to test the influence of tide (R or F), Sp, position of physical discontinuities ( $D_p$ ,  $D_{\text{chl } a}$ ) and depth of maximum chl *a* concentration ( $D_{\text{Max chl } a}$ ; m) on Olympia oyster larvae WMD. Tide was included as a factor, and continuous variables were considered as smoothed terms.

Akaike's information criterion was used to select the optimal set of variables for inclusion in every regression model. Model validation included the verification of homogeneity (lack of structure of the residuals) and normality (quantile–quantile plot of the residuals). The independence assumptions were tested using the Ljung-Box test to verify lack of autocorrelation on the residuals for the first 7 lags according to the function:

$$Q = N(N+2) \sum_{j=1}^{k-p} \frac{1}{N-j} \hat{\rho}(j)^2 \quad (2)$$

where  $Q$  is the Ljung-Box statistic,  $N$  is the length of the time series,  $k$  is the number of lags being tested,  $p$  is the number of parameters estimated by the model and  $\hat{\rho}(j)$  is the sample autocorrelation at lag  $j$  (Zuur et al. 2009). All statistical analyses were carried out using R 2.15.2 (R Development Core Team 2012).

## RESULTS

Salinity profiles collected in the bay during the sampling period clearly illustrate the transition between wet and dry seasons (Fig. 2). As the summer progressed, the increased salinity reflects the decrease in runoff characteristic in mid-summer and early fall. A progressive increase in atmospheric

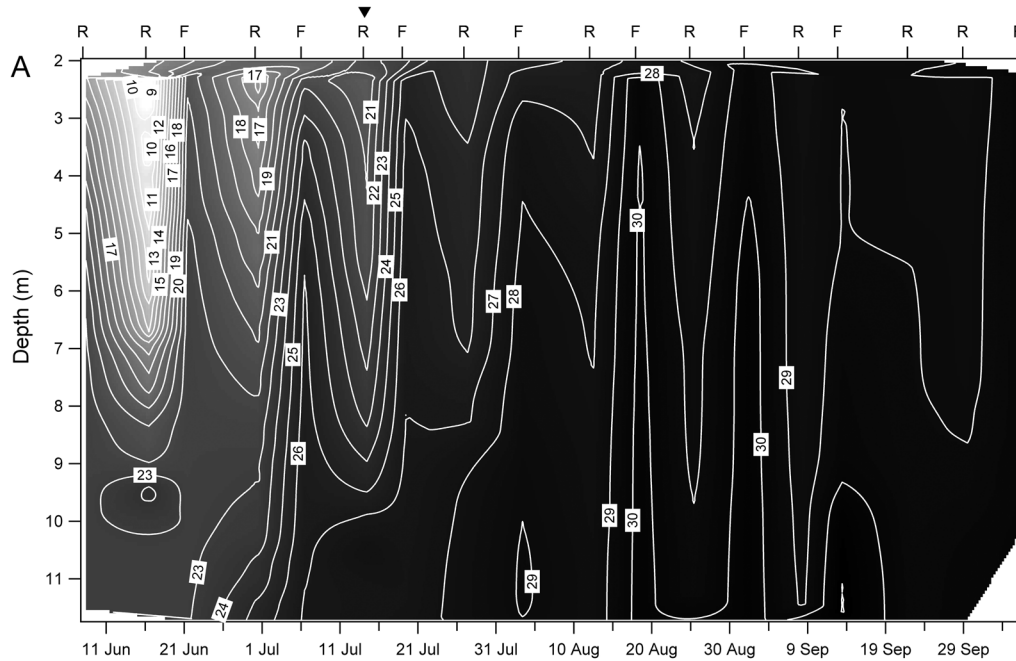


Fig. 2. (Above and following 2 pages.) Contour plots of hydrographic variables (A) temperature ( $^{\circ}\text{C}$ ), (B) salinity, (C) density ( $\text{kg m}^{-3}$ ) and (D) chl *a* concentration ( $\text{mg m}^{-3}$ ) in Coos Bay, Oregon, during the sampling period. Sample dates are marked with F (falling) or R (rising) to represent the tidal cycle during the sampling. The symbol  $\blacktriangledown$  on the top x-axis indicates the date of the first occurrence of Olympia oyster larvae



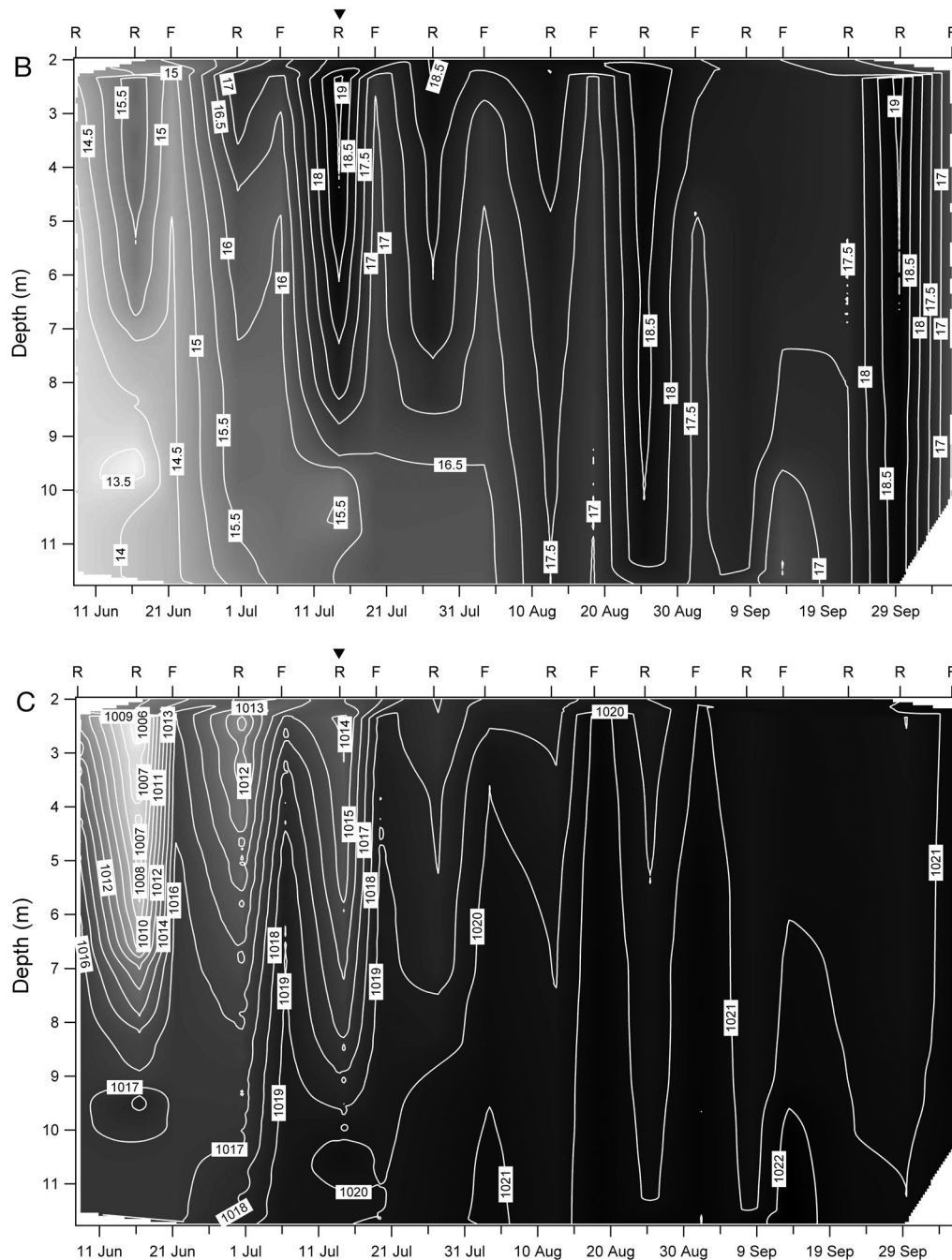


Fig. 2. (continued)

temperature, which is reflected in rising water temperature (Fig. 2A,B), is associated with the seasonal decrease in runoff. In the dry season, low river discharge decreased the amount of buoyant water entering the estuary, weakening stratification, which allowed mixing to occur more easily such that the water column was homogeneous or weakly stratified with seasonally higher density (Fig. 2C). Maximum concentrations of chl *a* were observed during the dry

season, when values  $>2 \text{ mg m}^{-3}$  were consistently observed (Fig. 2D).

Olympia oyster larvae were only present during late summer and early fall (Fig. 3). Larvae were found in the water column for the first time on July 14 and were consistently present after this date. Throughout that period, larval abundance fluctuated, with 2 peaks, one in mid-August and the other in mid-September (Fig. 3). The evolution of the size

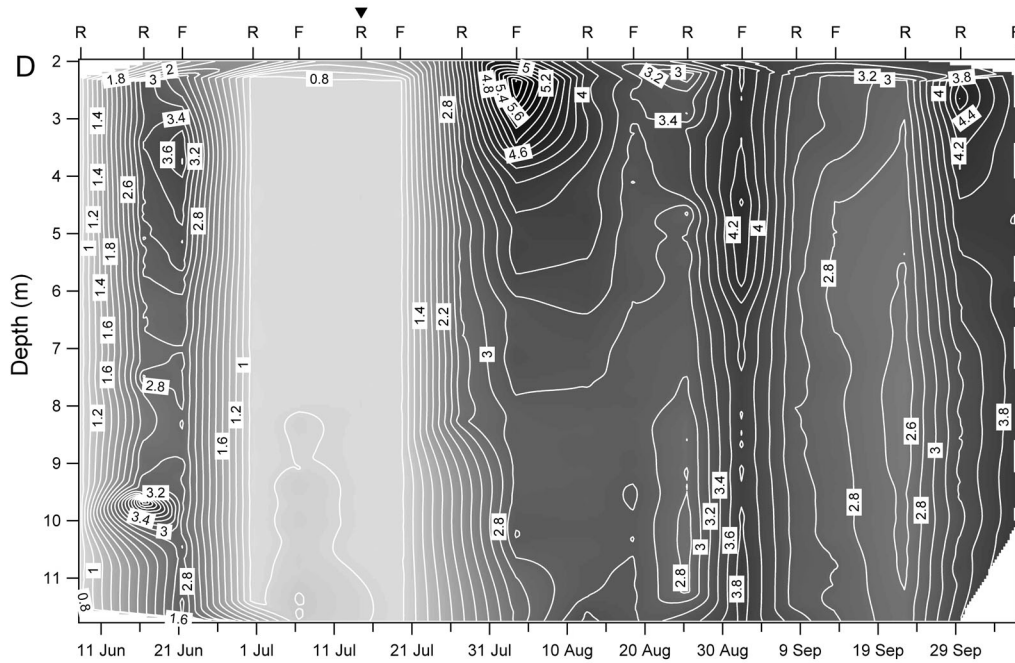


Fig. 2. (continued)

frequency distribution during the sampling period illustrates the progress and simultaneous presence of different cohorts (Fig. 4). Larval length through the sampling period ranged from 194 to 281  $\mu\text{m}$  ( $N = 808$  measured), covering the whole larval size range.

The variability in larval presence was best explained by the effects of water temperature and Brunt-Väisälä frequency (Table 1, Fig. 5), although p-values revealed a larger effect of temperature (Table 1). Water temperature was positively related to larvae presence (Fig. 5A), while B-V showed an inverse relationship (Fig. 5B). The probability of

Olympia oyster larvae presence drops dramatically with temperatures under  $16^\circ\text{C}$  and B-V values over 0.1 (Fig. 6).

During the time of year when the larvae are present, the model that best explains larval abundance includes the effects of salinity and current speed (Table 2, Fig. 7). High current speeds during falling tides ( $Sp < 0$ ) had a negative effect on larval abundance, while increasing current speeds during rising tides ( $Sp > 0$ ) had a positive effect (Fig. 7A). Salinity also positively affected larval abundance, especially for salinity values over 26 (Fig. 7B). Since we were sam-

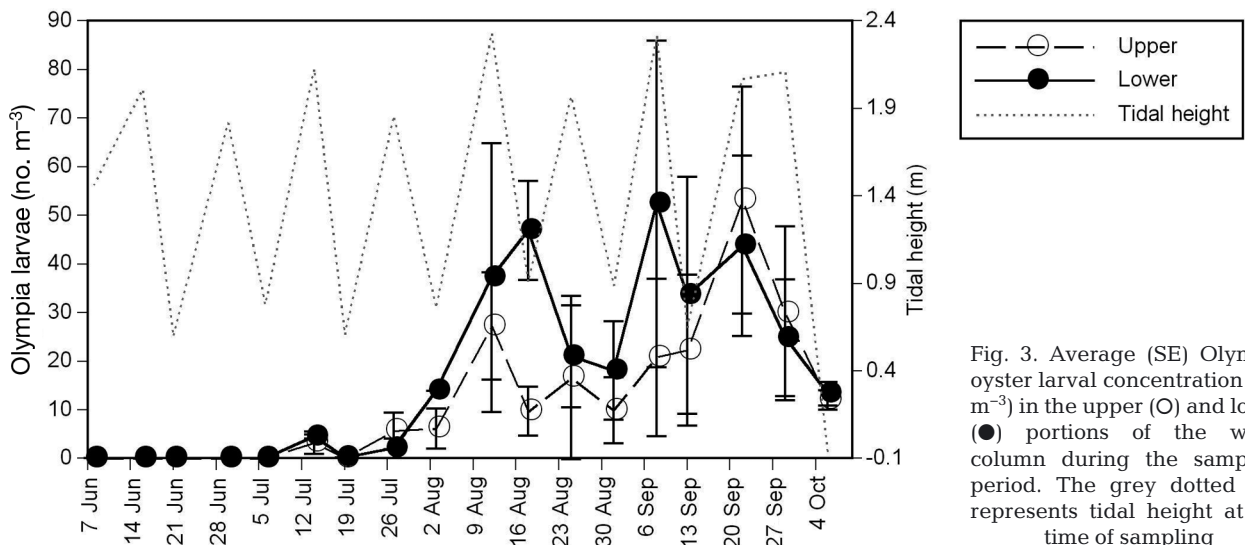


Fig. 3. Average (SE) Olympia oyster larval concentration (no.  $\text{m}^{-3}$ ) in the upper (○) and lower (●) portions of the water column during the sampling period. The grey dotted line represents tidal height at the time of sampling

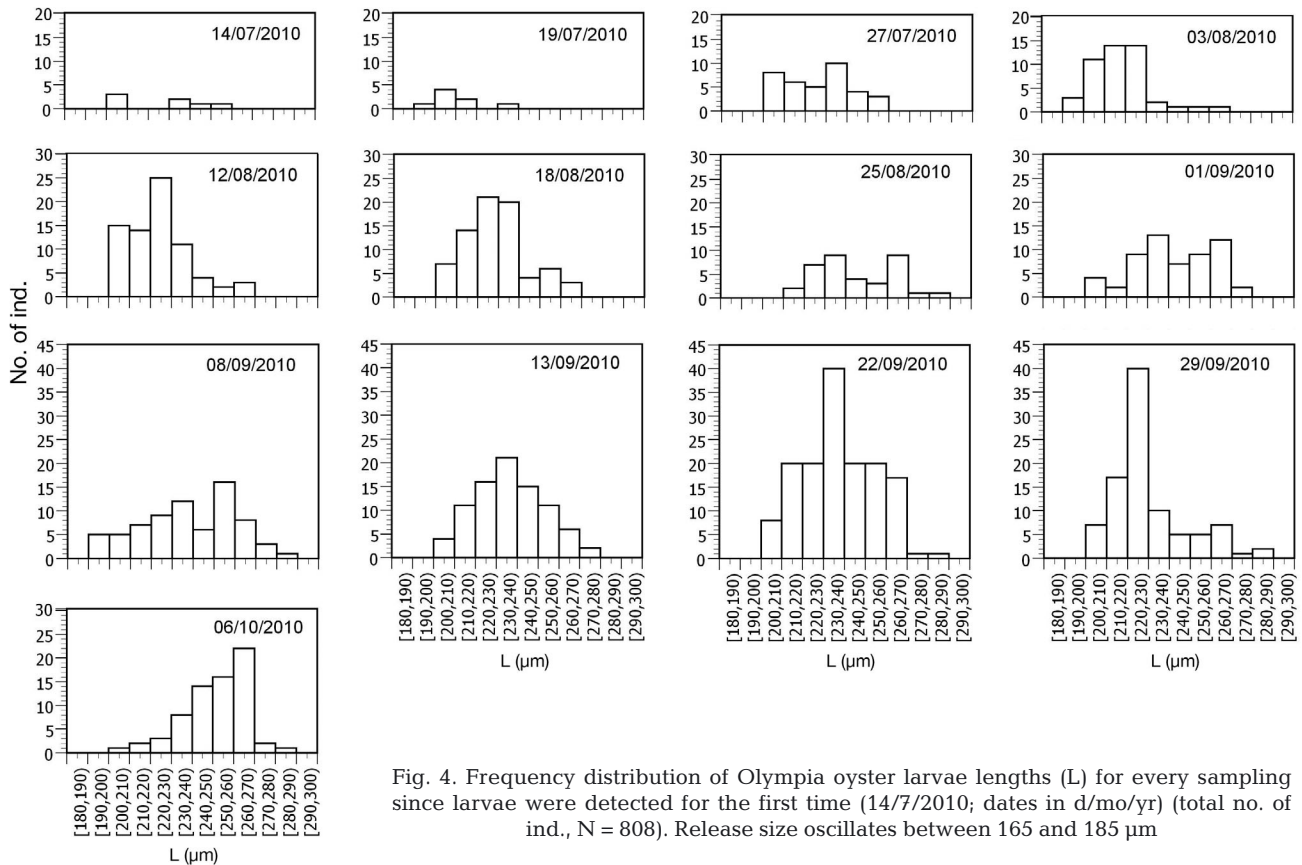


Fig. 4. Frequency distribution of Olympia oyster larvae lengths (L) for every sampling since larvae were detected for the first time (14/7/2010; dates in d/mo/yr) (total no. of ind., N = 808). Release size oscillates between 165 and 185  $\mu\text{m}$

pling at a fixed station, these results indicate that larvae were being dragged back and forth with the tide.

The variables that best explained the WMD of larvae were stage of the tide and current speed (Table 3, Fig. 8). The WMD estimate for rising tide ( $-3.43$  m; Table 3) is significantly shallower than the estimate for falling tide ( $7.22$  m; Table 3). Differences in the vertical distribution of larvae between falling and rising tides were only maintained during low current speeds (Figs. 8 & 9); otherwise, larvae were equally distributed in the water column (Figs. 8 & 9). Current speeds below  $0.5$  m  $\text{s}^{-1}$  have a slight effect (Fig. 8) over the estimated intercepts for rising and falling tides ( $7.22 \pm 0.43$  and  $3.79 \pm 0.69$  m, respectively; Table 3), allowing for the maintenance of differences in vertical distribution between tidal phases. High current speeds cause variations of  $\sim 2$  m around the estimated WMD but in opposite directions during rising and falling tides (Fig. 8; positive and negative effect over the estimated WMD values for  $\text{Sp} > 0$  and  $\text{Sp} < 0$ , respectively). Therefore, high current speeds tend to counter-effect the differences observed in WMD (Figs. 8 & 9, Table 3) and homogenise the distribution of the larvae through the water column (WMD  $\approx 5$  m; Fig. 9).

## DISCUSSION

The size-frequency distribution of the larvae suggests larval retention in the estuary during their entire development (Fig. 4). Olympia larvae are re-released in the water column at lengths between 165 and 185  $\mu\text{m}$  and become competent to settle at 275 to

Table 1. Structure of the model selected to describe Olympia larvae presence/absence. The inverse of the logit function has been applied to get the estimated values and SE on the scale of actual probability. edf: estimated degrees of freedom; B–V: Brunt-Väisälä frequency; Q: Ljung-Box statistic testing independence assumption on the residuals

Parametric coefficients				
Parameter	Estimate	SE	Z	p
Intercept	0.816	0.199	1.469	0.142
Smooth terms (non-parametrics)				
Parameter	edf	$\chi^2$	p	
Temperature	1.43	12.65	0.0012	
B–V	1	5.04	0.0248	
R <sup>2</sup> adjusted: 0.893		% deviance explained: 87.3		
		Q = 7.723; df = 3.6 ; p = 0.057		



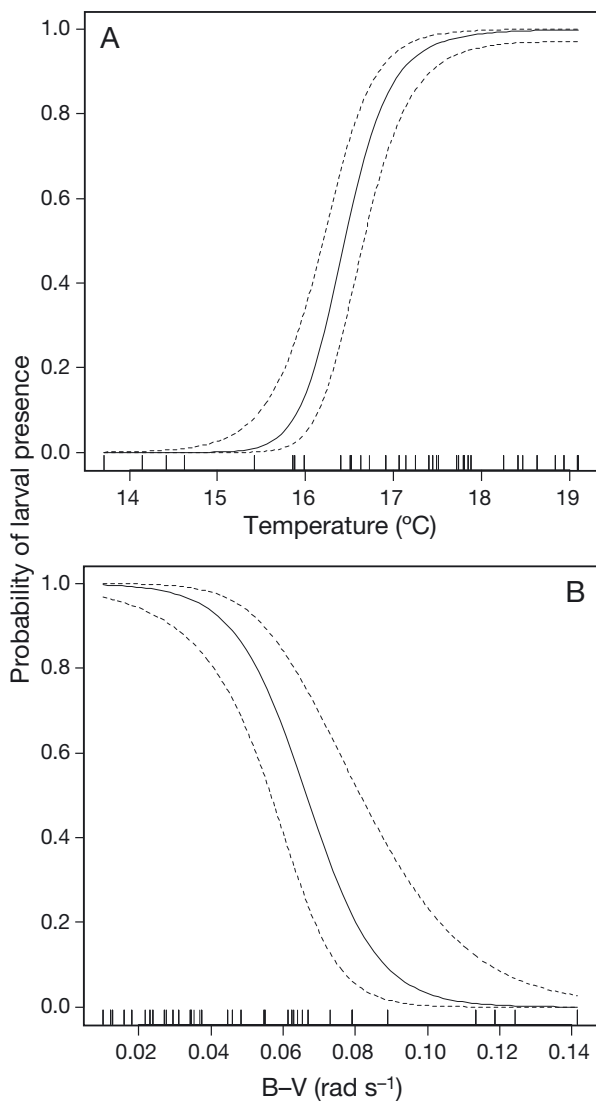


Fig. 5. Generalized additive model results showing the partial effect on the probability of Olympia oyster larval presence of the variables (A) temperature and (B) Brunt-Väisälä frequency (B-V). Dotted lines indicate 95% confidence intervals, and tick marks along the x-axis below each curve represent effect values where observations occurred

290  $\mu\text{m}$  (Hori 1933, Loosanoff et al. 1966, Strathmann 1987). Although the abundance of early released larvae might be underestimated because of our visual identification limitations, the size-frequency evolution through the reproductive season illustrates the presence of the rest of the size classes and the progress and co-existence of different cohorts (Fig. 4). In addition, even when our ability to visually identify Olympia larvae was limited to umbonate stages, the umbo becomes prominent 4 to 6 d after spawning ( $\sim 200 \mu\text{m}$ ; Hori 1933, Loosanoff et al. 1966,

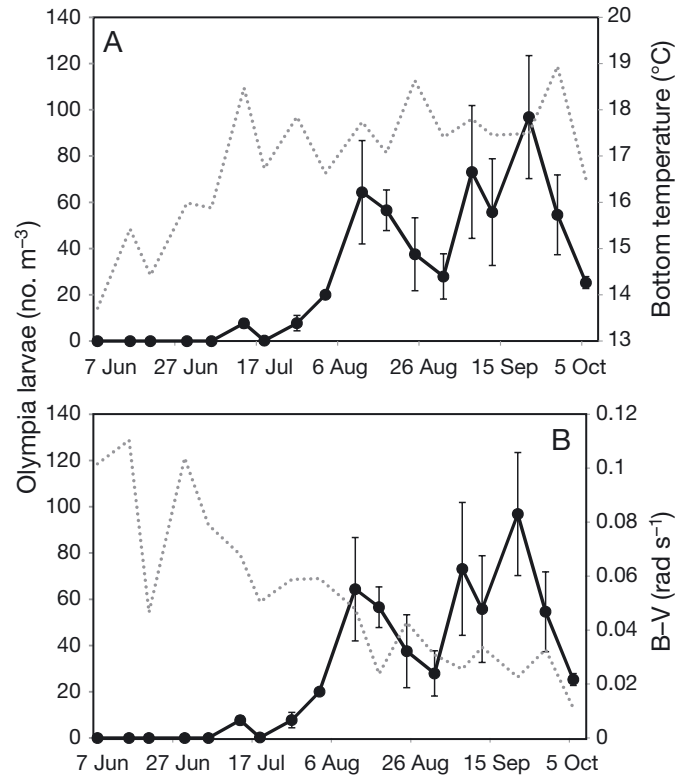


Fig. 6. Average (SE) Olympia oyster larval concentration (no. m<sup>-3</sup>) in the water column during the sampling period. The grey dotted line represents (A) bottom temperature and (B) Brunt-Väisälä frequency (B-V).

Strathmann 1987) and starts to develop as early as 2 d after spawning ( $\sim 185$  to  $190 \mu\text{m}$ ; Loosanoff et al. 1966). That period is below the minimum water residence time estimated for the bay (6 d; Arneson 1976) and should not bias our results, which indicate larval retention in the estuary during the entire development.

Table 2. Structure of the model selected to describe Olympia larval abundance (log-transformed). edf: estimated degrees of freedom; Q: Ljung-Box statistic testing independence assumption on the residuals; Sp: current speed

Parametric coefficients				
Parameter	Estimate	SE	Z	p
Intercept	1.202	0.038	31.830	<2 × 10 <sup>-16</sup>
Smooth terms (non-parametrics)				
Parameter	edf	F	p	
Sp	1.32	21.31	8.63 × 10 <sup>-7</sup>	
Salinity	1.82	17.32	1.17 × 10 <sup>-6</sup>	
R <sup>2</sup> adjusted: 0.436		% deviance explained: 46.3		
		Q = 5.336; df 2.9; p = 0.139		

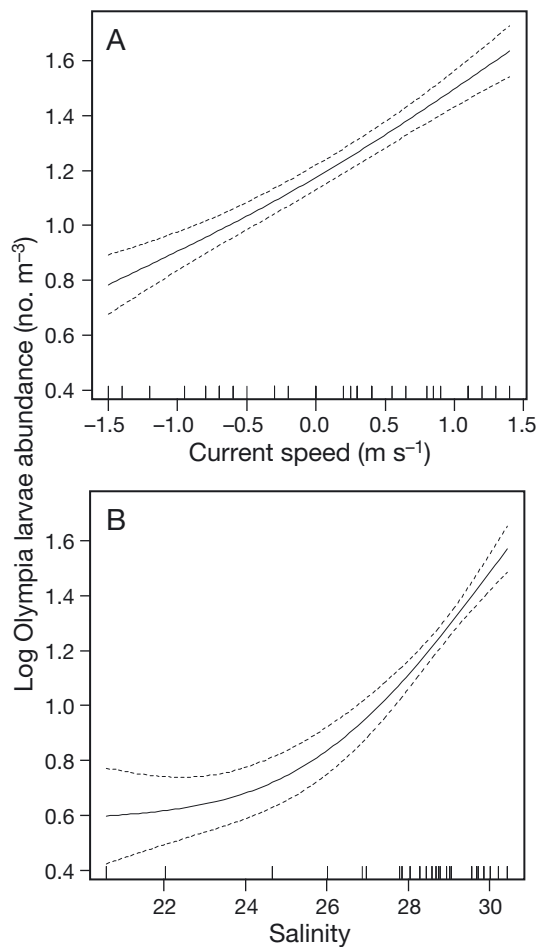


Fig. 7. Generalized additive model results describing the partial effect on Olympia oyster larval abundance of the variables (A) current speed and (B) salinity. Dotted lines indicate 95% confidence intervals, and tick marks along the x-axis below each curve represent effect values where observations occurred

Table 3. Structure of the model selected to describe Olympia larvae weighted mean depth. edf: estimated degrees of freedom; Q: Ljung-Box statistic testing independence assumption on the residuals; Sp: current speed

Parametric coefficients				
Parameter	Estimate	SE	Z	p
Intercept	7.217	0.4336	16.646	$1.16 \times 10^{-15}$
Tide (rising)	-3.428	0.689	-4.976	$3.30 \times 10^{-5}$
Smooth terms (non-parametrics)				
Parameter	edf	F	p	
Sp	3.18	5.18	0.0034	
R <sup>2</sup> adjusted: 0.444		% deviance explained: 51.9		
		Q = 0.5186; df = 1.8; p = 0.72		

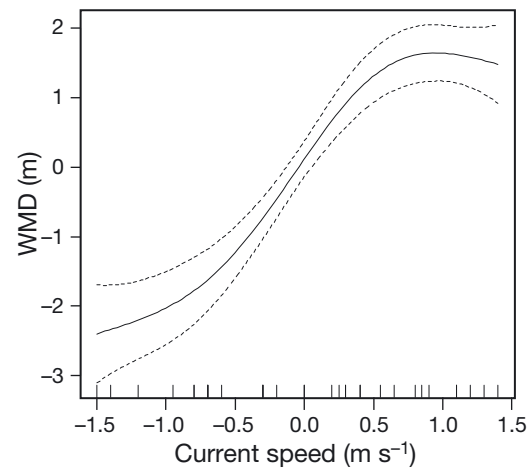


Fig. 8. Generalized additive model results describing the partial effect of current speed ( $\text{m s}^{-1}$ ) on Olympia oyster larvae weighted mean depth (WMD; m). Dotted lines indicate 95% confidence intervals, and tick marks along the x-axis below each curve represent effect values where observations occurred

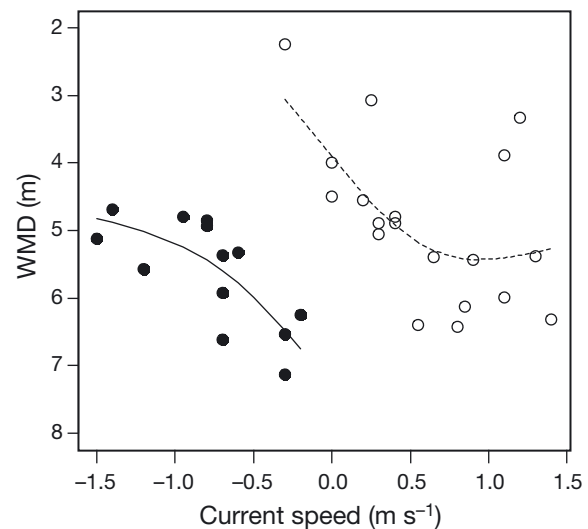


Fig. 9. Weighed mean depth (WMD; m) of Olympia oyster larvae vs. current speed (Sp;  $\text{m s}^{-1}$ ) during rising (O) and falling (●) tides through the sampling period. Lines represent generalized additive model fitted values for WMD (Table 3) during rising (dashed line) and falling (solid line) tides

Since all size classes were present (Fig. 4), the larvae appear to have been retained in the estuary during their development even though this is a highly dynamic environment and they are weak swimmers. How is retention accomplished? There are 2 possible mechanisms for retention: (1) the larvae vertically migrate to exploit the vertically stratified tidal currents in the bay, or (2) spawning matches environ-

mental conditions coincident with the long residence time of water within the estuary.

Our results suggest a combination of both mechanisms. Olympia oyster larvae have some capacity to perform tidal-timed vertical migrations during periods of low current speeds (Fig. 8, Table 3). Averaged larval depth was significantly deeper during falling tides than rising tides, but when current speed increased, larvae were found distributed equally in the water column independent of the tidal phase (Fig. 8, Table 3). These results are consistent with previously observed bivalve larvae distribution in weakly stratified estuaries, where changes in the depth distribution of larvae relative to the tidal cycle have been identified but just around slack tide or during low current speeds (Carriker 1951, Nelson 1954, Wood & Hargis 1971, Hidu & Haskin 1978, Roegner 2000, Knights et al. 2006, Kim et al. 2010). Residing on or near the bottom during falling tide and in the water column during rising tide has been described for many marine invertebrate larvae and interpreted as an effective mechanism to maintain their position in an estuary against predominant outflowing currents (Forward & Tankersley 2001, Gibson 2003, Kunze et al. 2013). But our results suggest that this mechanism of retention is only viable for Olympia larvae during low current speeds.

Physical discontinuities and food patch distribution have also been documented as factors affecting larval vertical distribution both in the laboratory and in the field for different species (Tremblay & Sinclair 1990, Raby et al. 1994, Gallagher et al. 1996, Kingsford et al. 2002, Sameoto & Metaxas 2008, Daigle & Metaxas 2011). We did not detect any effects of those variables on WMD in the present study, but during the period that larvae were present, stratification was weak, river inflow was low and the estuary was well mixed (Fig. 2). Vertical mixing might dilute the signal of environmental cues, activating certain behaviours, as has been suggested for different species (Tremblay & Sinclair 1990, Pearce et al. 1998, Sameoto & Metaxas 2008, Breckenridge & Bollens 2011, Morgan et al. 2014). Nonetheless, our results detected an effect of the tidal phase on larval vertical position when current speeds were weak, suggesting that flow intensity and turbulence might be playing a more relevant role. Under situations of high water flows or strong turbulence, bivalve larvae usually behave as inert particles (Andrews 1983, Tremblay & Sinclair 1990, Roegner 2000, Pernet et al. 2003, Kim et al. 2010, Narvaez et al. 2012). Even stronger swimmers, such as certain species of crustacean larvae, lost their capability to perform vertical migrations

under turbulent flows and well-mixed situations in shallow estuaries (Morgan et al. 2014). Particle-tracking models in partially mixed estuaries also suggest tidal-timed migration as an effective retentive strategy but just under low to moderate flows (Kimmerer et al. 2014). Although recent studies suggest that oyster larvae are able to develop active swimming even in strong turbulent flows (Fuchs et al. 2013, Wheeler et al. 2013), our results suggest that this is not the case for *Ostrea lurida* (Fig. 8, Table 3). Therefore, even though Olympia oyster larvae can and do make tidally timed vertical migrations, their swimming capabilities are usually overcome by the prevalent currents in the estuary.

The inability of the larvae to overcome high current speeds is also reflected in the relationships between total larval abundance, current speed and salinity at our fixed station (Fig. 7, Table 2). There is an inverse relationship between larval abundance and current speed during falling tides but a direct relationship between both variables during rising tides (Fig. 7A) as well as a positive effect of salinity on larval abundance (Fig. 7B), suggesting that larvae are transported back and forth with the tide as inert particles.

Therefore, matching their pelagic development to less dispersive periods might be crucial to minimize larval wastage out of the estuary. Our results on the presence of Olympia oyster larvae suggest that larval release is synchronized with the high temperatures and low levels of stratification characteristic of the dry season (Figs. 5 & 6), when water residence time is annually maximal and, hence, the likelihood of larval retention in the bay is annually highest. Those environmental variables may be acting as spawning triggers or conditioning seasonality of reproduction. Temperature has been traditionally described as one of the main factors determining gametogenesis, spawning and larval release in *O. lurida* and many other invertebrates (Hori 1933, Hopkins 1936, Strathmann 1987, Young et al. 1998, O'Connor et al. 2007, Oates 2013). This effect has been mainly attributed to an increase in survival because of a reduction in PLD (O'Connor et al. 2007). Although there is not always a direct relationship between PLD and dispersal distance (especially if larvae behave in a way that affects their dispersal), planktonic duration can affect dispersal distance (Shanks 2009). In Coos Bay, higher water temperatures in the upper estuary are coupled with seasonally low values of stratification (Fig. 2), and it is during this period that *O. lurida* larvae are released (Fig. 6). Larvae released under these conditions should experience shorter PLDs due to faster

development at higher temperatures and longer water residence times, both of which should increase the likelihood that larval development is completed in the estuary, minimizing larval wastage. By timing their spawning and larval release to the dry season, adult oysters increase the probability of larval survival and retention in a suitable habitat.

Matching planktonic life to the dry season might provide the best possible scenario for larval retention inside the estuary. The major influence affecting seasonal changes in the circulation of Coos Bay is freshwater inflow; low runoff during mid-summer and early fall changes the estuary circulation from partially mixed to well mixed (Blanton 1964, Arneson 1976, MacCready 1999, Ji et al. 2001; Fig. 2). Andrews (1983) described 2 types of estuaries based primarily on morphology and freshwater discharge: trap-type (tortuous geography and low freshwater inflow) and high freshwater flow estuaries. The different circulation patterns in these 2 types of estuaries drive differences in the quantity of larvae retained and regularity of spat falls. Roegner (2000) also suggested that larval retention in weakly stratified, tidally dominated estuaries is restricted to refugia from strong horizontal velocities. Coos Bay is characterized by a complex morphology (Fig. 1) which contributes to longer residence times in certain areas (Arneson 1976).

According to Arneson's classification, Coos Bay might be considered a trap-type estuary in its more intricate areas but just during the dry season. Residence time of water in the upper part of the estuary (head of the tide 43.5 km from the mouth of the bay) increases as much as 2.5 times during the dry season (from 15.9 to 40.3 d in March and September, respectively). Even in areas closer to the mouth of the bay (Isthmus Slough; 23.8 km from the mouth of the bay; Fig. 1), flushing time varies seasonally (from 14.4 to 22.9 d in March and September, respectively). Areas fairly close to the estuary mouth (airport; 12 km from the mouth of the bay; Fig. 1) have similar water residence times throughout the year (8.2 and 9.7 d in March and September, respectively; Arneson 1976). PLD for the Olympia oyster varies from 10 to up to 30 d (Strathmann 1987) for the range of temperatures observed (16 to 19°C; Fig. 2B) in our study area. Differences in the residence time of water in different segments of Coos Bay might be responsible for the distribution of adult Olympia oyster; adults are restricted to the area of the bay where residence times are seasonally long enough that larvae can complete their pelagic development within the bay (Fig. 1). Therefore, matching larval release to hydrodynamics

favourable for larval retention might play a key role in maintaining the Olympia oyster population in Coos Bay, as has been suggested for other estuarine bivalve species (Young et al. 1998, Carson 2010, Carson et al. 2010, Fodrie et al. 2011, López-Duarte et al. 2012).

A retentive dispersal pattern is consistent with the high levels of genetic structure in Olympia oyster populations along the coasts of Oregon, Washington and British Columbia (Stick 2012), which suggests strong isolation between estuaries and predominance of self-recruitment within estuaries. However, Carson (2010), using larval shell microchemistry, reported larval exchange between estuaries in California located as far as 75 km apart, although self-recruitment was still dominant in some estuaries, and the degree of larval exchange was dependent on seasonal hydrographic patterns. Differences in the amount of self-recruitment/exchange between estuaries have been attributed to the morphology and seasonality of prevailing currents at each particular bay (Andrews 1983, North et al. 2008, Carson 2010).

In summary, even though tidally timed migration to the bottom during falling tides was detected in *O. lurida*, current speeds in the bay usually overcome the swimming capability of the larvae, limiting the effectiveness of this retentive behaviour. Since the Olympia oyster population in Coos Bay seems to be quite isolated from neighbouring estuarine populations (Stick 2012), timing planktonic life with predictable hydrodynamics that favour larval retention in the bay and subsequent self-recruitment appears to be the main factor determining population sustainability. Our results also point out how sensitive the Coos Bay population may be to alterations of the circulation regime within the bay. Manmade alterations, such as further deepening of navigation channels, may alter the hydrography of the bay, decreasing the residence time of water, which may decrease the capability the Coos Bay population of *O. lurida* to sustain itself. Restoration efforts in Coos Bay as well as other estuaries should focus on sections of the estuaries where water residence time is seasonally long enough to allow larvae to complete their development within the estuary, leading to high self-recruitment to the population.

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