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Authors

Chang, Andrew L
Deck, Anna K
Sullivan, Lindsay J
et al.

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Upstream—Downstream Shifts in Peak Recruitment of the Native Olympia Oyster in San Francisco Bay During Wet and Dry Years

Andrew L. Chang[1,2,3,4] · Anna K. Deck[2,3,4] · Lindsay J. Sullivan[5] · Steven G. Morgan[4] · Matthew C. Ferner[2,3]

Abstract Understanding the conditions that drive variation in recruitment of key estuarine species can be important for effective conservation and management of their populations. The Olympia oyster (*Ostrea lurida*) is native to the Pacific coast of North America and has been a target of conservation efforts, though relatively little information on larval recruitment exists across much of its range. This study examined the recruitment of Olympia oysters at biweekly to monthly intervals at four sites in northern San Francisco Bay from 2010 to 2015 (except 2013). Mean monthly temperatures warmed at all sites during the study, while winter (January–April) mean monthly salinity decreased significantly during a wet year (2011), but otherwise remained high as a result of a drought. A recurring peak in oyster recruitment was identified in mid-estuary, in conditions corresponding to a salinity range of 25–30 and >16 °C at the time of settlement (April–November). Higher average salinities and temperatures were positively correlated with greater peak recruitment. Interannual variation in the timing of favorable conditions for recruitment at each site appears to explain geographic and temporal variation in recruitment onset. Higher winter/spring salinities and warmer temperatures at the time of recruitment corresponded with earlier recruitment onset within individual sites. Across all sites, higher winter/spring salinities were also correlated with earlier onset and earlier peak recruitment. Lower winter salinities during 2011 also resulted in a downstream shift in the location of peak recruitment.

Keywords Larval supply · Oyster · Salinity · Larval settlement · Recruitment · Estuary

Introduction

Variation in recruitment is a key factor determining the population dynamics and structure of many coastal marine and estuarine species, including sessile foundation species. This is especially true in rapidly changing and dynamic environments, such as estuaries, where many species of benthic invertebrates retain sufficient larvae within the estuary to maintain self-sustaining populations (e.g., Bousfield 1955; Bennett et al. 2002; Kunze et al. 2013). A greater understanding of factors governing larval recruitment in these systems would aid in modeling population dynamics, predicting responses to abiotic changes including climate change, and assisting managers with conservation and restoration efforts.

Numerous factors have been proposed to explain temporal and spatial variation in recruitment dynamics, including geographic or temporal differences in larval production, delivery, and settlement onshore. Variation in per-capita reproductive output is often controlled by parental exposure to environmental conditions (e.g., Leslie et al. 2005) and cues stimulating

✉ Andrew L. Chang
changal@si.edu

[1] Smithsonian Environmental Research Center, Tiburon, CA, USA

[2] San Francisco Bay National Estuarine Research Reserve, Tiburon, CA, USA

[3] San Francisco State University, San Francisco, CA, USA

[4] Bodega Marine Laboratory and Department of Environmental Science and Policy, University of California Davis, Bodega Bay, CA, USA

[5] Dominican University of California, San Rafael, CA, USA

reproduction or larval release, such as temperature (e.g., Southward et al. 1995), phytoplankton (Starr et al. 1990), or turbidity (e.g., Gyory et al. 2013). Delivery of larvae to a specific geographic region may be affected by a range of physical oceanographic processes, such as differences in boundary currents around the lee of headlands (Graham and Largier 1997; Wing et al. 2003; Roughan et al. 2005; Morgan et al. 2012). Estuarine species face several challenges in maintaining populations, as some proportion of larvae produced inside an estuary must be retained, and larvae transiting the open ocean must find and return to an estuary for settlement (Ketchum 1954; Gaines and Bertness 1992). Larval behaviors such as vertical migration to take advantage of inflowing or outflowing tidal currents have been demonstrated for a number of estuarine species (Forward and Tankersley 2001), including Olympia oysters (Peteiro and Shanks 2015). Meanwhile, larval settlement from the water column to habitats onshore and subsequent microhabitat selection is stimulated by a variety of cues, which may be physical (tactile stimulus, changes in water flow) or chemical in nature (e.g., conspecific cues often serve as an attractant, while predator cues may repel settlers) (Crisp 1976; Pawlik 1992; Koehl and Hadfield 2010; Prairie et al. 2012).

Estuaries encompass strong environmental gradients that may impose temporal and geographical variation in physiological constraints on reproduction and recruitment of resident species (Remane and Schlieper 1971; Attrill 2002). These strong gradients are good candidates for potential drivers of recruitment peaks or areas where many larvae recruit in aggregate. The geographic location of these peaks and the timing, magnitude, and duration of recruitment are all potentially influenced by environmental gradients.

The Olympia oyster (*Ostrea lurida*) is a native bivalve inhabiting intertidal and shallow subtidal rocky shores in estuaries along the North American Pacific coast. Oyster beds support a diverse community of species, provide a variety of ecosystem services, and are a focus of conservation and restoration efforts (Kimbro and Grosholz 2006; Wasson et al. 2014). Relatively little is known about abundance patterns for most life stages of *O. lurida* (Peteiro and Shanks 2015). Recent field surveys and genetic analyses have established a current range for *O. lurida* as British Columbia–Baja California, where it approaches, but does not overlap, with its southern congener *Ostrea conchaphila* (Polson and Zacherl 2009; Raith et al. 2016). Reproduction is seasonal, with females brooding larvae for up to 2 weeks in the spring and summer (Strathmann 1987; Baker 1995). Upon release, larvae then spend 1–8 weeks in the water column before settling onto hard substrates; the sources of variation in these estimates remain unclear, but may include temperature, food availability, and latitude (Strathmann 1987; Baker 1995).

Spatial and temporal patterns of settlement are poorly documented across much of *O. lurida's* range, especially in relation to environmental conditions (Pritchard et al. 2015). The seasonality and months during which *O. lurida* is known to settle have been reported for numerous locations throughout its geographic range (reviewed in Pritchard et al. 2015), but relatively few reports include information on physical environmental conditions such as temperature and salinity, and almost none have statistically examined the relationship between major environmental variables and settlement (but see Seale and Zacherl 2009). Using an experimental population of oysters from a non-estuarine outer coast site in southern California, Coe (1931) found that settlement commenced when water temperature reached 16 °C. Bonnot (1937) and Hopkins (1937) reported Olympia oyster settlement along with environmental parameters for Humboldt Bay and southern Puget Sound, respectively. While neither study examined these relationships quantitatively, Bonnot (1937) reported that peak settlement roughly corresponded to peak temperatures of 18–20 °C. Settlement patterns show no clear relationship with salinity at the time of settlement, although examination of Bonnot's data suggests that lower winter salinity could be linked to delayed and reduced settlement (Bonnot 1937, Fig. 20). The only recent report on settlement in relation to temperature (Seale and Zacherl 2009) concluded that there was no threshold temperature corresponding with initiation or termination of settlement or with any settlement peaks. Meanwhile, although neither Bonnot (1937) nor Hopkins (1937) linked the onset of settlement to a specific temperature, both studies found that the onset of settlement followed tidal cycles to some degree, starting with a run of neap tides, with peak settlement during successive spring tides.

Significant spatial variation in recruitment and fecundity in San Francisco Bay populations of *O. lurida* was previously documented in several short-term studies, each lasting about 2 years (Wasson et al. 2014). Here, we examine trends in recruitment in 5 years (over a 6-year period) at four sites along the axis of the northern section of San Francisco Bay, which encompasses a substantial gradient in temperature and salinity. Prior to this study, little was known about the spatial or temporal variation in adult or juvenile oyster abundances along this gradient, although physical conditions at these sites spanned a range of values that seemed likely to influence oyster biology based on the literature (reviewed by Pritchard et al. 2015) and previous observations (Grosholz et al. 2007; Wasson et al. 2014). These sites also encompassed significant variation in oyster population density, including one site (China Camp State Park) that at times had both the densest population and densest recruitment in the entire species range (Wasson et al. 2014). We hypothesized that environmental conditions would be correlated with the magnitude and timing of peak recruitment of *O. lurida* in San Francisco Bay, as well as the onset of recruitment. Specifically, we hypothesized that both temperature and salinity at each site would be both

Fig. 1 Map of four study sites in San Francisco Bay showing locations of salinity monitoring stations and sites where *Ostrea lurida* had previously been found. Site codes are in Table 1; salinity monitoring station codes are in Online Resource 1. Data on presence of *O. lurida* from Grosholz et al. (2007)
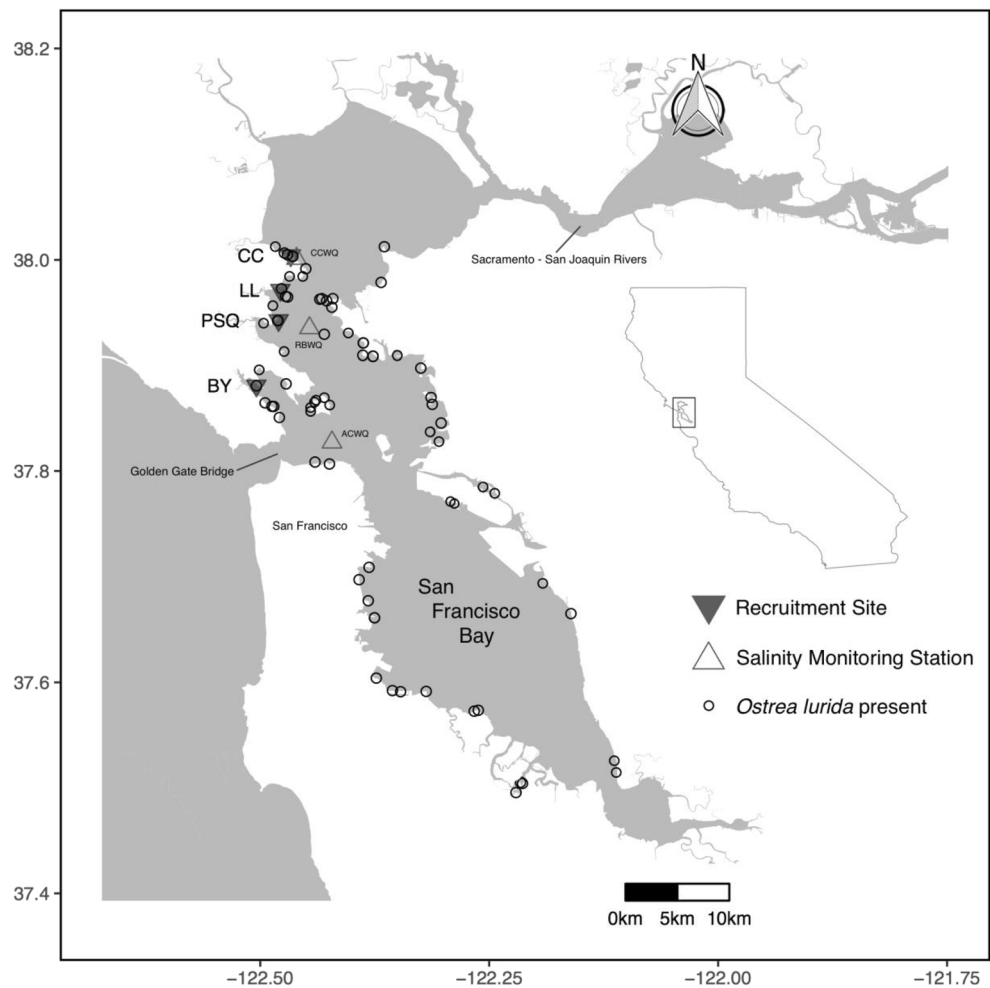
positively correlated with the magnitude of peak recruitment and inversely correlated with the timing of the onset of recruitment and its peak. We modeled the correlations between environmental conditions and recruitment to determine whether there are specific conditions linked with high recruitment rates.

Methods

Recruitment

We assessed Olympia oyster recruitment at four sites along the axis of the northern brackish-to-saline region of San Francisco Bay, 2010–2015; the northernmost site (China Camp State Park) is within the San Francisco Bay National Estuarine Research Reserve (SF Bay NERR; Fig. 1; Table 1). A major salinity gradient is consistently present in this region of the estuary, which is sensitive to seasonal and inter-annual changes in weather, such as temperature and precipitation, presenting an ideal area for assessing the responses of the oyster population.

The San Francisco Bay region has a Mediterranean climate, with a dry summer/fall season (June–October) when there is almost no precipitation, and a wet winter/spring season (November–May), with great interannual variation in precipitation (Conomos 1979; Cloern and Jassby 2012). The major sources of freshwater entering the estuary are the Sacramento and San Joaquin Rivers, which join in an inland delta before passing through the Carquinez Strait into San Pablo Bay, which forms the upper portion of San Francisco Bay, and then exit through the Golden Gate. South of the Golden Gate, the South Bay ends in a lagoonal embayment. This geography results in two distinct subregions of the estuary: a river-dominated northern half, and a relatively low-inflow southern half. While the northern half of the estuary can become stratified during higher flow periods in the winters of wet years, the estuary is generally well-mixed in the summer (Conomos 1979). The estuary is highly modified, as previously marshy shorelines have been drained and filled, and over half of the mean annual freshwater flow is diverted for agriculture and drinking water (Conomos et al. 1985; Nichols et al. 1986).

We focused most intensely on the spring-to-fall period, when we expected *O. lurida* to settle most heavily based on

Table 1 Four study sites in San Francisco Bay with information on annual maximum recruitment rate of Olympia oysters, *O. lurida*, and annual temperature and salinity ranges.

Site name	Abbreviation	Latitude	Longitude	Year	Annual maximum recruitment rate (oysters m^{-2} day^{-1})	Annual temperature range (°C)	Annual salinity range[a]
China Camp State Park	CC	38.00415	−122.46669	2010	644.4	8.6–21.9	8.5–27.4
				2011	223.8	6.9–22.4	1.7–24.1
				2012	344.3	8.1–21.1	9.9–27.6
				2014	907.8	9.0–23.1	12.4–29.0
				2015	668.4	9.5–23.6	14.8–29.6
Loch Lomond	LL	37.97208	−122.47683	2010	293.2	10.8–20.3	15.5–28.4
				2011	271.4	8.1–19.6	1.7–26.2
				2012	150.2	9.1–22.4	19.7–28.6
				2014	80.7	9.4–23.9	23.3–29.4
				2015	18.2	9.9–24.7	23.9–30.1
Point San Quentin	PSQ	37.94211	−122.48099	2010	834.3	9.9–20.3	18.2–29.9
				2011	194.5	8.3–20.4	11.9–28.0
				2012	54.6	10.4–19.4	20.3–29.6
				2014	453.9	10.6–22.4	21.0–30.8
				2015	94.2	16.5–22.9	24.1–30.9
Brickyard Park	BY	37.88085	−122.50425	2010	4.8	9.5–23.1	22.1–30.9
				2011	21.2	7.7–22.5	11.5–30.9
				2012	12.3	9.6–21.8	22.8–32.1
				2014	54.6	9.5–22.8	24.5–31.8
				2015	21.4	9.8–22.5	26.5–32.3

[a] Annual salinity range given here is distinct from the mean daily winter/spring (February–May) salinity used in several analyses and figures

preliminary data, but the duration of collection effort varied yearly due to changing availability of funding and human resources. We targeted significant rocky shoreline or riprap areas that serve as potential oyster habitat. At each site, we deployed two PVC frames consisting of a 1-m crosspiece and two 0.5-m legs staked into the sediment with rebar, so that the crosspiece was at 0 m, mean lower low water (MLLW) parallel to the waterline. On each frame, we attached three white porcelain 110-cm^2 tiles to the crosspiece of the frame with the rough, unglazed sides facing down. The unfinished side acted as the collecting surface, because larvae of oysters and other sessile invertebrates preferentially settle on rougher surfaces (Crisp 1976) and *O. lurida* larvae specifically prefer downward-facing surfaces (Hopkins 1935; Bonnot 1937). We replaced the tiles with new ones ~biweekly 2010–2013 and monthly in 2014 and 2015. We omitted data from 2013 due to infrequent sampling. We counted the number of recruits on each tile using a dissecting microscope and calculated recruitment rates for each sampling period as the number of settlers per square meter per day. Thus, for the purposes of this study, we define recruitment as the settlement and post-settlement survival of oyster larvae during 2- or 4-week deployments.

In 2012 for logistical reasons, we moved the Loch Lomond site approximately 200 m to the south to a location with similar physical characteristics. Later, shoreline construction in early 2014 necessitated an additional move 200 m still further south to a partially sheltered cove.

Environmental Measurements and Data Preparation

We measured temperature every 15 min at each site using loggers (Tidbit and Tidbit v2, Onset Computer, Bourne, Massachusetts) that were attached either to the settlement frames or to an adjacent rebar stake. Loggers, like settlement tiles, were placed at 0 m MLLW. For each site, we processed logger data as daily mean values of air and water temperatures using the SiteParser program (Gilman et al. 2006). We calculated daily mean salinity values for each site using data from nearby continuous water-quality monitoring stations that were maintained by the US Geological Survey (USGS 2015) and the SF Bay NERR (NERR 2015), and compared these daily means with measurements that were taken during biweekly or monthly site visits using a YSI-85 multimeter (YSI, Yellow Springs, Ohio; Online Resource 1). We summarized these mean daily temperature and salinity values as biweekly (or monthly) means during the corresponding settlement tile deployments for each site.

The temperature data record (Table 1) included some gaps due to logger failure. In these cases, we filled in gaps using

data from nearby continuous water quality monitoring stations (NERR 2015; USGS 2015). To accurately estimate missing intertidal logger data, we regressed existing logger data against continuous monitoring data from overlapping time periods where data from both sources were available, and we used the resulting model to correct continuous monitoring data for periods corresponding to the missing logger data (see Online Resource 1).

Statistical Analyses

We assessed trends in temperature and salinity across sites and years using linear mixed models. For temperature, we compared mean monthly temperature across sites and years with month specified as a random factor nested within site to account for autocorrelation. For salinity, we compared mean winter/spring (February–May) salinity levels across sites and years, again with month as a random factor nested within site. Analyses were conducted in the R statistical programming environment (R Core Team 2015) using the package lme4 (Bates et al. 2015).

We analyzed the relationship between recruitment and conditions at the time of recruitment using generalized linear mixed models (GLMM) with negative binomial distributions with logit links. The response variable was oyster recruitment rate standardized as number of individuals per square meter per day for a given biweekly or monthly time period. Mean water temperature and salinity for the given biweekly or monthly time period, and their interaction, were considered predictors. We used sampling date as a random factor nested within site to account for repeated measures within each site, and we used year of sampling as a blocking factor. Models were evaluated based on Akaike Information Criteria (AIC). Analyses were conducted in R using the package glmmADMB (Bolker et al. 2013; Skaug et al. 2015), an implementation of the AD Model Builder fitting engine (Fournier et al. 2012).

We examined the relationship between environmental conditions and both the timing of the onset of recruitment and time to peak recruitment rate using ordinary least squares (OLS) regression. When there were two statistically indistinguishable peaks at a site in a given year (e.g., China Camp, 2012: $t_{2.98} = -0.58$, $p = 0.60$), we used the earlier peak in our analysis. As above, we assessed conditions at the time of recruitment, but because recruitment may be influenced by severe environmental disturbances that cause adult mortality and may suppress reproduction, we also tested the effect of winter/spring low salinity, the most severe such stressor believed to affect San Francisco Bay oysters (Wasson et al. 2014). The response variables were the number of days since 1st January to the retrieval date of tiles marking either recruitment onset or peak recruitment rate. The predictors were mean daily water temperature and salinity for the biweekly or monthly time period corresponding to either onset or peak recruitment at each site, along with their interaction (all at the time of recruitment onset or peak recruitment). In a separate set of models, we evaluated mean daily salinity during the winter/spring season (February–May) as a predictor of the number of days to the onset of recruitment or peak recruitment. For all models, before adding site as a blocking factor, we first considered timing of recruitment across all four sites to examine the relationships between the predictors and recruitment timing within each site. Lastly, we evaluated the relationship of environmental variables to the location of earliest recruitment, and the highest peak recruitment within each year.

Results

Environmental Conditions

Physical conditions varied significantly among sites both within and across years (Figs. 2 and 3; Online Resources 2 and 3). Across all sites, in most months, mean daily water temperature increased over the years from 2010 to 2015 (Table 2; Fig. 3; Online Resource 3). The average observed increase was highest during late spring to early fall (May–October), and lowest in the winter months (December–February). Mean daily winter/spring salinity varied significantly among sites (Table 3) and was consistently lowest at China Camp, which is farthest upstream in the estuary, and highest at Brickyard Park, which is farthest downstream (Fig. 2; Online Resource 2). Mean daily winter/spring salinity also varied among years (Table 3), as did the salinity ranges among sites. The greatest spread in mean daily winter/spring salinity was in 2011, which was a wetter year, and with lower salinities occurring farther downstream than in other years (Fig. 2; Online Resource 2). During a record drought (2013–2015), the salinity gradient shifted upstream, and salinities were more similar among sites (Fig. 2; Online Resource 2).

Magnitude of Recruitment

Within each year, we observed significant geographic variation in the magnitude of recruitment rates, with distinct peaks appearing each year (Fig. 4). Across all years, China Camp generally had the highest recruitment rates, reaching a maximum of 907.8 ind. m^{-2} day^{-1} in 2014, but there was some variation in which site had the highest (peak) recruitment rate, with slightly higher rates at Point San Quentin in 2010 and Loch Lomond in 2011 (Table 1; Fig. 4). Brickyard Park consistently had the lowest peak recruitment rates, with a maximum of 54.6 ind. m^{-2} day^{-1} in 2014. There was no significant difference in recruitment at Loch Lomond before (2010, 2011, 2012) and after
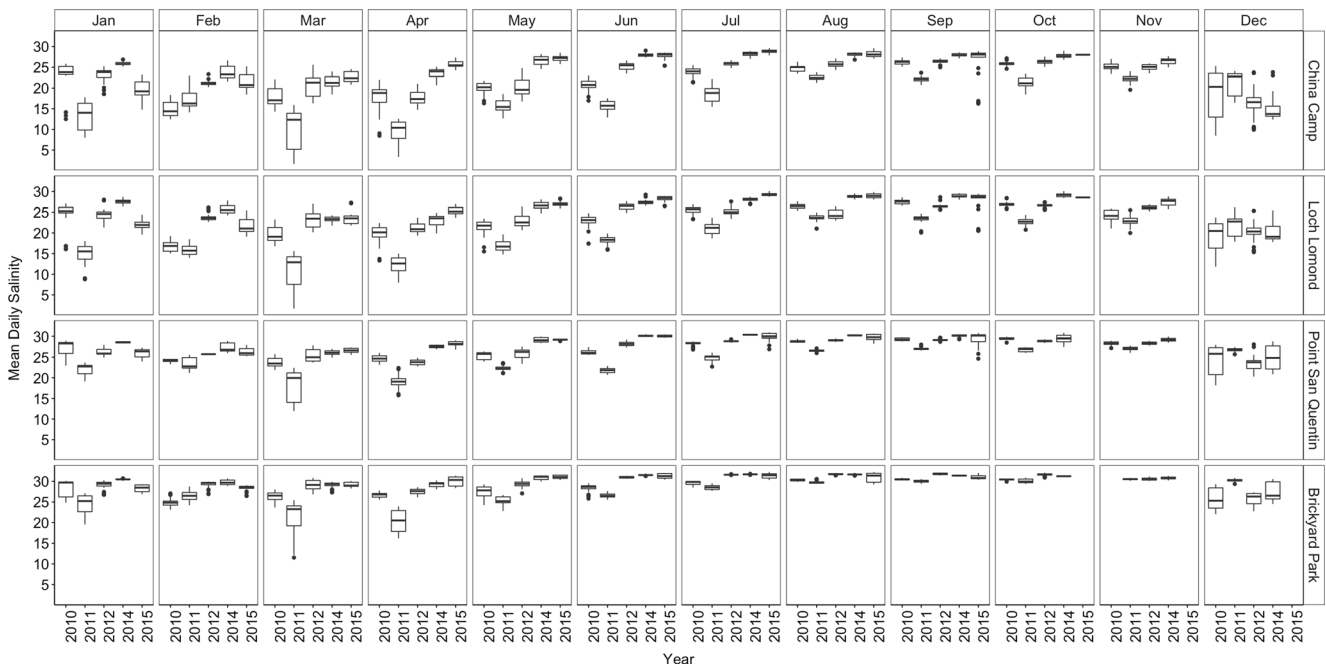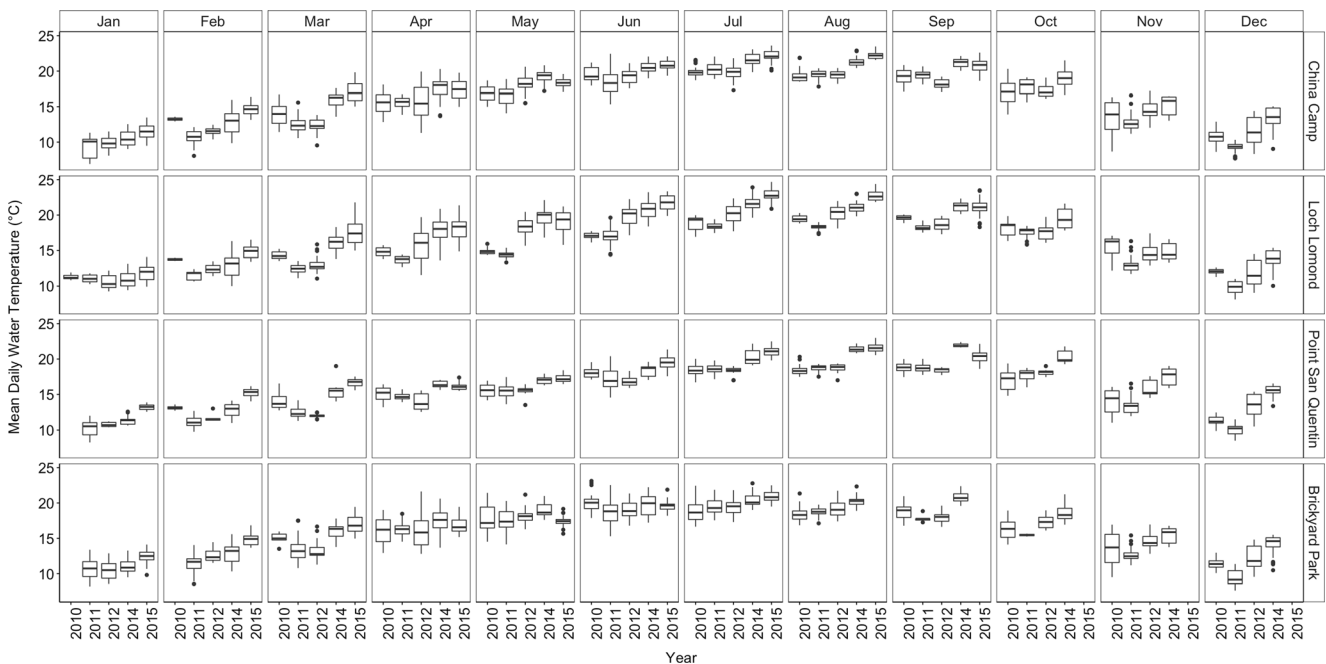
Fig. 2 *Boxplots* of reconstructed mean daily salinity by month at four study sites in San Francisco Bay, 2010–2015 (except 2013). *Box* represents interquartile range (25th–75th percentile), *horizontal line inside box* represents median, *whiskers* extend to minimum and maximum values, up to 1.5 times the interquartile range, beyond which outliers are marked with *circles*. See Online Resource 1 for derivation of site-specific salinities from nearby continuous monitoring stations. Analysis of winter–spring (February–May) trends is summarized in Table 3

(2014, 2015) the site was moved to a partially sheltered cove (Online Resource 4). The previous winter's freshwater flow to the estuary did not predict the locations of either the earliest recruitment or the recruitment peak.

Fig. 3 *Boxplots* of mean daily temperature by month at four study sites in San Francisco Bay, 2010–2015 (except 2013). *Box* represents interquartile range (25th–75th percentile), *horizontal line inside box* represents median, *whiskers* extend to minimum and maximum values, up to 1.5 times the interquartile range, beyond which outliers are marked with *circles*. Analysis of trends across years is summarized in Table 2

Table 2 Results of linear mixed model comparing mean monthly temperature across sites and years at four study sites in San Francisco Bay, 2010–2015 (except 2013)

| Parameter	Number	Chisq	df	p value	Variance
Fixed					
Site	4	6.049	3	0.1092	
Year	5	144.965	1	<0.0001	
Site × year		2.973	3	0.3958	
Random					
Month	–	–	–		11.577
Residuals	–	–	–		1.093

The magnitude of peak recruitment was correlated with mean temperature and salinity conditions at each site, with a significant interaction between mean temperature and mean salinity (Tables 4 and 5). Warmer temperatures and higher salinities correlated strongly with higher recruitment rates, regardless of site (Figs. 5 and 6).

Timing of Recruitment

The onset of recruitment occurred earlier each year across all sites, advancing from late June/early July in 2010 to April by 2015 (Fig. 5). When considering all four sites together, first recruitment occurred significantly earlier in years when mean daily winter salinities were higher ($F_{1, 9} = 9.264$, $p = 0.014$). Peak recruitment across all sites also occurred significantly earlier following higher mean daily salinities during the preceding winter ($F_{1, 4} = 25.297$, $p = 0.0007$) (Tables 6 and 8). Mean water temperature and salinity conditions during recruitment were not correlated with timing of first recruitment across all sites ($F_{1, 6} = 0.156$, $p = 0.707$ for temperature; $F_{1, 6} = 2.762$, $p = 0.148$ for salinity). Nor were conditions during recruitment correlated with timing of peak recruitment ($F_{1, 2} = 0.407$, $p = 0.589$ for salinity), although there was a positive correlation with mean daily temperature ($F_{1, 2} = 16.176$, $p = 0.0566$). Recruitment onset was earlier in later years despite the switch from biweekly to monthly tile deployment periods for 2014–2015, which would tend to bias toward later

Table 3 Results of linear model comparing mean winter/spring salinity levels across sites and years at four study sites in San Francisco Bay, 2010–2015 (except 2013)

Parameter	df	Sum sq	Mean sq	F value	p value
Site	3	193.896	64.632	14.089	<0.0001
Year	1	79.874	79.874	17.412	0.0007
Site × year	3	12.740	4.247	0.926	0.4509
Residuals	16	73.398	4.587		
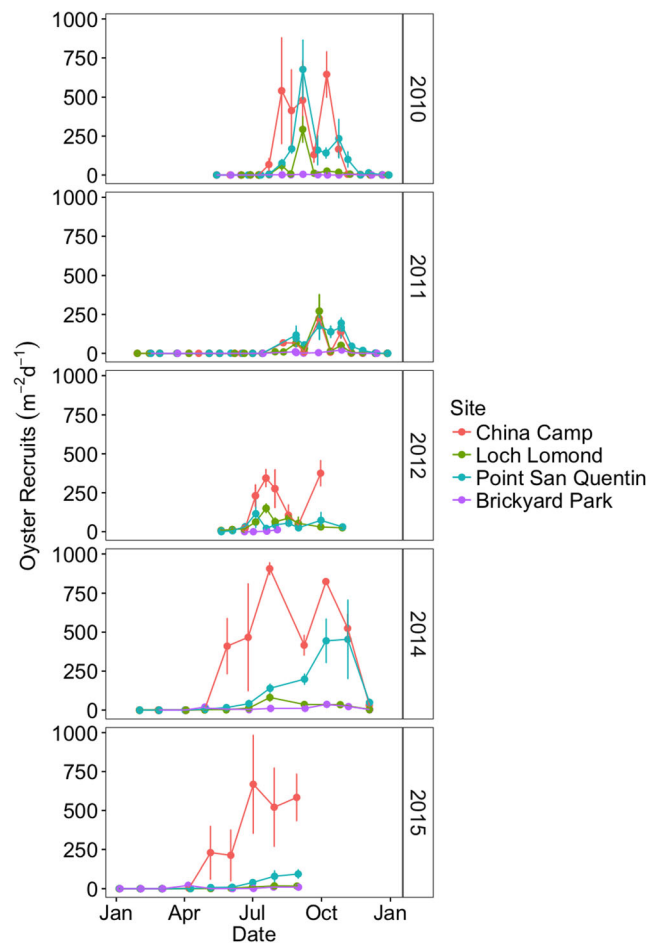
Fig. 4 Time series of oyster recruitment rate at four study sites in San Francisco Bay, 2010–2015 (except 2013). Biweekly recruitment was measured in 2010–2012, and monthly recruitment was measured in 2014 and 2015. *Error bars* are ±1 standard deviation

observed onset of recruitment because the longer deployment times result in later retrieval dates.

The timing of the arrival of warmer temperatures (>16 °C) and more saline conditions (>25) that we linked to increased recruitment in the spring and summer varied from year to year at a given site (Fig. 5). In 2010, these conditions began in June, but especially July, which coincided with the onset of recruitment. In 2011, a wetter year, these conditions did not occur until August. In 2014 and 2015, these conditions appear earlier, by April (Fig. 5). Within each site, the onset of recruitment was positively correlated with the arrival of warmer water temperatures ($F_{1, 8} = 12.255$, $p = 0.0081$), but there was no relationship with salinities at the time of recruitment ($F_{1, 8} = 2.662$, $p = 0.141$) (Tables 7 and 8; Fig. 7). However, the onset of recruitment was inversely related to the previous winter's salinity regime ($F_{1, 16} = 8.749$, $p = 0.0093$), as well as to site ($F_{3, 16} = 10.552$, $p = 0.0004$) (Tables 7 and 8; Fig. 8). Thus, interannual variation in the timing of favorable conditions for recruitment at each site appears to explain geographic and temporal variation in recruitment onset. In contrast, within

Table 4 Model selection for generalized linear mixed model analysis of recruitment rate magnitude at four study sites in San Francisco Bay, 2010–2015 (except 2013)

Parameter	Number	AIC	Deviance	*p* value
Temperature × salinity × site + year	282	1921.5	0	
Temperature × salinity + year	282	1950.1	52.578	>>0.0001
Salinity × site + year	282	2001.6	96.112	>>0.0001
Temperature × site + year	282	2006.9	101.36	>>0.0001

Model comparisons show that the full model including mean daily water temperature ("temperature"), mean daily salinity ("salinity"), and site is the best model (lowest AIC score). *p* values are given for likelihood ratio tests comparing nested models

each site, none of the environmental variables was significantly correlated with the timing of peak recruitment ($F_{1, 7} = 0.041$, $p = 0.845$ for temperature at recruitment, $F_{1, 7} = 1.129$, $p = 0.323$ for salinity at recruitment, $F_{1, 16} = 2.183$, $p = 0.159$ for previous winter/spring mean daily salinity).

Discussion

Predicting peaks in recruitment is key for conservation and restoration of Olympia oysters because these efforts rely on natural spatset in many areas, either in siting construction of restoration structures or for collection of natural spat used to seed other locations (Wasson et al. 2014; Pritchard et al. 2015). Our results suggest that peak recruitment for Olympia oysters occurs in predictable temperature and salinity conditions each year (>16 °C and salinity 25–30) and that continued monitoring of those conditions would enable forecasts of the timing, location, and magnitude of peak recruitment. In addition, the geographic location of the recruitment peak along the estuarine gradient in northern San Francisco Bay was broadly

Table 5 Results of best fit generalized linear mixed model analysis of recruitment rate magnitude at four study sites in San Francisco Bay, 2010–2015 (except 2013)

Parameter	Estimate	S.E.	*p* value	Variance
Fixed				
Intercept	146.0757	171.3900	0.394	
Temperature	5.4208	2.2104	0.014	
Salinity	3.9459	1.5573	0.011	
Temperature x Salinity	−0.1662	0.0803	0.038	
Year	−0.1320	0.0819	0.107	
Random				
Site	–	–	–	2.061×10^{-9}
Date	–	–	–	1.232

Mean daily water temperature ("temperature"), mean daily salinity ("salinity"), and their interaction were all significantly related to recruitment rate

predicted by the winter/spring salinity regime (i.e., winter/spring freshwater input to the estuary). These results confirmed our hypotheses of positive relationships between temperature and salinity conditions and the magnitude of oyster recruitment at each site. Earlier onset of recruitment was correlated with warmer temperatures and higher mean daily winter/spring salinity. Considering all sites together, higher winter/spring salinity was also correlated with earlier peak recruitment, but contrary to our hypothesis, peak recruitment was not predicted by either temperature or salinity at the time of recruitment.
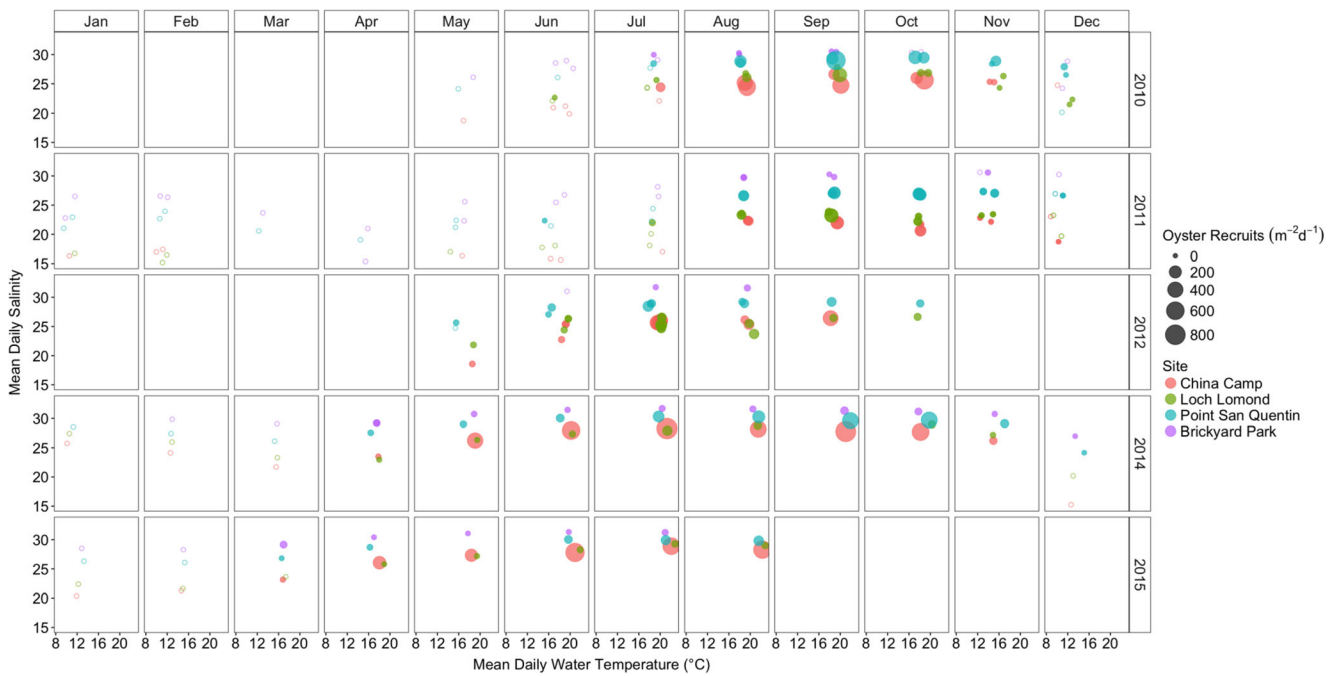
Because the hard substrate required for larval oyster settlement is in limited supply in many regions, restoration efforts frequently rely on spreading shell or installing artificial structures such as oyster "reef balls" to provide greater substrate area (Wasson et al. 2014). These efforts must be timed so as to capture the settlement of oysters, and if possible, to avoid the preemptive settlement of other species such as barnacles or tubeworms that may compete for space (e.g., Trimble et al. 2009; Wasson et al. 2014; Pritchard et al. 2015). Our results suggest that potential oyster recruitment could be maximized by timing the deployment of restoration structures to occur when conditions reach 16 °C and 25–30 salinity, and by adjusting timing and location of substrate deployment based on winter/spring salinity conditions. These results are a significant advance in understanding the population biology of Olympia oysters and will allow oyster conservation and restoration to take maximum advantage of the natural cycles of resident populations.

Over the 6-year study period, the optimal conditions for recruitment occurred at radically different times—even in different seasons—due to significant interannual variation in environmental conditions linked to larger-scale climate patterns and regional hydrological cycles. By 2015, we observed oyster recruitment several months earlier than in the first 2 years of the study, which was likely a result of record drought conditions that led to generally warmer and drier conditions across western North America (Diffenbaugh et al. 2015; Swain 2015). Meanwhile, during the wetter year (2011), higher freshwater outflow from storms and snowmelt resulted in the persistence of slightly cooler temperatures throughout the spring. However, the key factor in delayed settlement in

Fig. 5 Oyster recruitment rate by month as a function of salinity and temperature at four study sites in San Francisco Bay, 2010–2015 (except 2013). Points are located at the mean daily temperature and salinity that occurred at each site in a given month and are sized in proportion to the rate of recruitment observed. *Open circles* indicate zero recruitment. Absence of points indicates no data available, except for Loch Lomond and China Camp from March and April 2011 (not shown; salinity <<15, zero recruitment)

Fig. 6 Oyster recruitment rates as a function of salinity and temperature at the time of recruitment at four sites in San Francisco Bay, 2010–2015 (except 2013). Points are located at the mean daily temperature and salinity that occurred at each site in a given month and are sized in proportion to the rate of recruitment observed. *Open circles* indicate zero recruitment
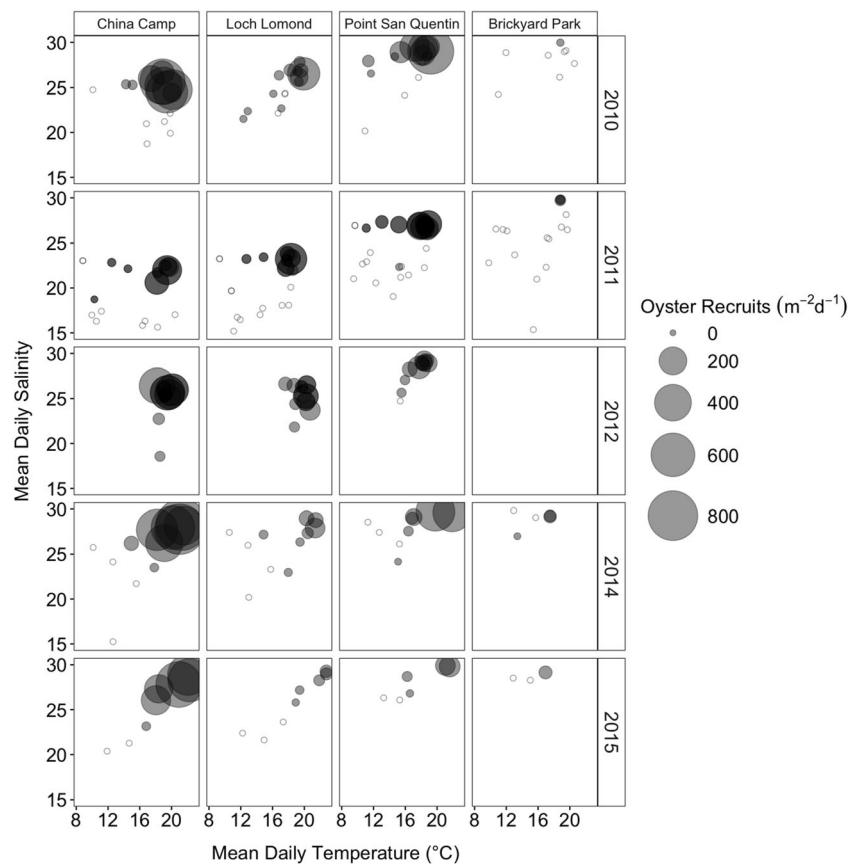
Table 6 Results of linear models relating timing of onset of first recruitment and peak recruitment (as day of year) across four study sites in San Francisco Bay (2010–2015, except 2013) to the previous winter/spring (February–May) mean daily salinity conditions

Response	Parameter	df	Sum sq	Mean sq	F value	p value
Day of year of first recruitment (across all sites)	Winter/spring salinity	1	2441.3	2441.3	11.3268	0.01199
	Site	3	1181.6	393.86	1.8274	0.23006
	Residuals	7	1508.8	215.54		
Day of year of peak recruitment (across all sites)	Winter/spring salinity	1	4218.9	4218.9	26.8420	0.01396
	Site	1	457.0	457.0	2.9078	0.18669
	Residuals	3	471.5	157.2		

this year appeared to be salinity levels that were <25 until July 2011 (Fig. 2). The wetter spring also caused significant oyster mortality, especially at China Camp, which previously had the densest oyster population in the entire species range, and five times greater than the next most densely populated site in San Francisco Bay (Wasson et al. 2014). This drastic reduction in adult populations likely resulted in substantially lower larval output, which would reduce available larvae for settlement; if the populations at our sites received larvae from these areas, then the magnitude of subsequent recruitment onshore would be reduced. Peak recruitment in 2011 was approximately half as much as in 2010.

Within years, recruitment fluctuated from tidal cycle to tidal cycle, likely reflecting the ebb and flow of reproductive activity and larval release by adults (Coe 1931; Hopkins 1936; Bonnot 1937). At a monthly scale, these biweekly fluctuations tend to even out, presenting the appearance of a steady increase in recruitment during spring and summer toward a peak in early fall (September–October), followed by a gradual decline in winter (November–December) (Figs. 4 and 5). The finer-scale variations in recruitment visible at the resolution of biweekly tidal cycles suggest an approximately monthly schedule of larval release among adults, consistent with findings by Bonnot (1937) and Hopkins (1937) that the onset of

settlement follows tidal cycles to some degree, starting with a run of neap tides and followed by peak settlement during successive runs of spring tides (Bonnot 1937; Hopkins 1937). Further investigation should examine the influence of tidal cycles on settlement relative to the temperature and salinity effects documented here.

In addition to temperature and salinity, a number of other factors may play a role in driving the observed patterns of oyster recruitment, such as physical aggregation of larvae by currents, shifts in reproductive patterns, and variation in cues and habitat availability. Current-driven aggregations of larvae in the lee of headlands are well documented for several marine invertebrate species, leading to higher recruitment on the open coast (Graham and Largier 1997; Roughan et al. 2005; Mace and Morgan 2006; Morgan et al. 2011). In San Francisco Bay, the Loch Lomond and Point San Quentin sites are both in the lee of headlands relative to the prevailing river flow exiting the estuary, whereas China Camp and Brickyard Park are not (Fig. 1), offering only equivocal support for the importance of leeward aggregations to settlement patterns in an estuarine setting. In a previous shorter study encompassing the entire estuary, we observed much greater oyster recruitment on the western than eastern shore of San Francisco Bay. However, the timing and location of greatest recruitment along the axis

Table 7 Results of linear models relating timing of onset of first recruitment (as day of year) *at each site* (of four study sites in San Francisco Bay, 2010–2015, except 2013) to temperature and salinity at the time of recruitment, or to salinity conditions during the previous winter/spring (February–May)

Response	Parameter	df	Sum sq	Mean sq	F value	p value
Day of year of first recruitment at site	Temperature	1	13,735.3	13,735.3	12.2554	*0.00807*
	Salinity	1	2983.4	2983.4	2.6619	0.14142
	Site	3	4807.5	1602.5	1.4298	0.30417
	Temperature × salinity	1	852.4	852.4	0.7605	0.40858
	Temperature × site	3	3935.3	1311.8	1.1704	0.37965
	Salinity × site	3	1181.1	393.7	0.3513	0.78960
	Temperature × salinity × site	3	4425.1	1475.0	1.3161	0.33487
	Residuals	8	8966.0	1120.8		
Day of year of first recruitment at site	Winter/spring salinity	1	5969.3	5969.3	8.7490	*0.00925*
	Site	3	21,598.8	7199.6	10.5521	*0.00045*
	Winter/spring salinity × site	3	2401.3	800.4	1.1732	0.35093
	Residuals	16	10,916.6	682.3		

These results correspond to Figs. 7 and 8, respectively. Factors are mean daily water temperature ("temperature"), mean daily salinity ("salinity") at the time of recruitment, or mean daily salinity during the previous winter/spring (February–May) ("winter/spring salinity")

Table 8 Summary of significant and non-significant relationships between environmental variables and timing of recruitment onset and peak recruitment across all sites and within each site

	Timing across all sites		Timing within each site	
	Onset	Peak	Onset	Peak
Mean temperature during settlement	NS	NS	+	NS
Mean salinity during settlement	NS	NS	NS	NS
Previous winter/spring mean daily salinity	–	–	–	NS

Direction (positive or negative) of relationship is given, if significant. Previous winter/spring mean daily salinity refers to mean daily salinity (February–May) during the same calendar year

NS not significant

of the estuary on the eastern shore followed a similar pattern to that documented in this study for the western shore (Chang et al., unpublished data). The prevailing summer winds blow to the southwest, driving surface and subsurface waters against the western shore of the estuary (Conomos 1979), which could deliver more larvae to the western shore.

Water column conditions also affect reproductive output, which can indirectly affect patterns of settlement by influencing larval supply (Carson 2010; Pritchard et al. 2015). In a previous work, we have found that sites exposed to warmer
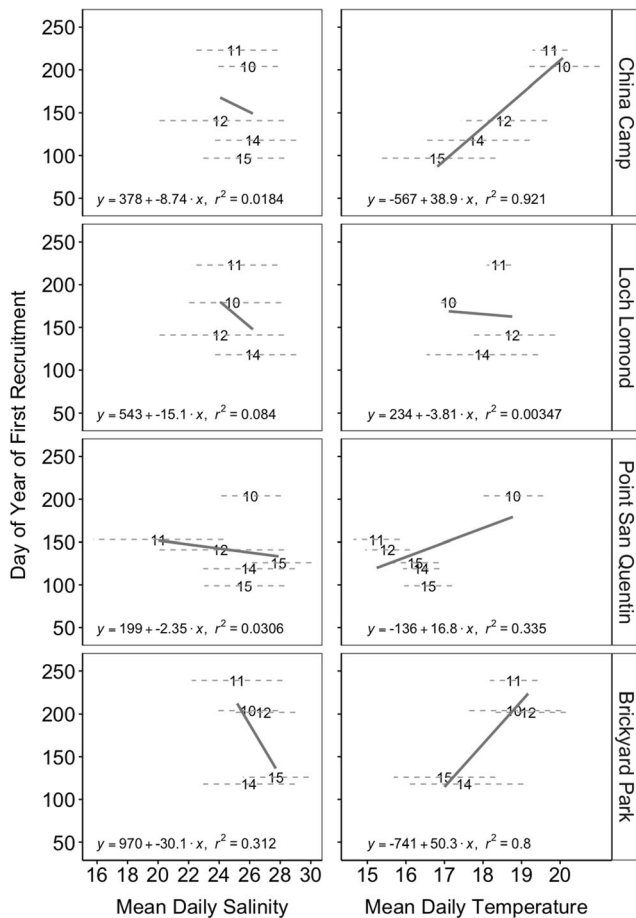
Fig. 7 Timing of *first* recruitment (i.e., onset) at four study sites in San Francisco Bay, 2010–2015 (except 2013) is predicted by average temperature (but not salinity) conditions at the time of recruitment. See Table 7 for linear model results. The last two digits of each year are used to represent the day of first recruitment at each site in that year, and the mean daily salinity (*left*) or temperature (*right*) is shown for the corresponding the biweekly or monthly tile deployment when recruitment was first detected. *Dashed horizontal lines* represent mean daily salinity or temperature ±1 SD. See Online Resource 1 for derivation of site-specific salinities
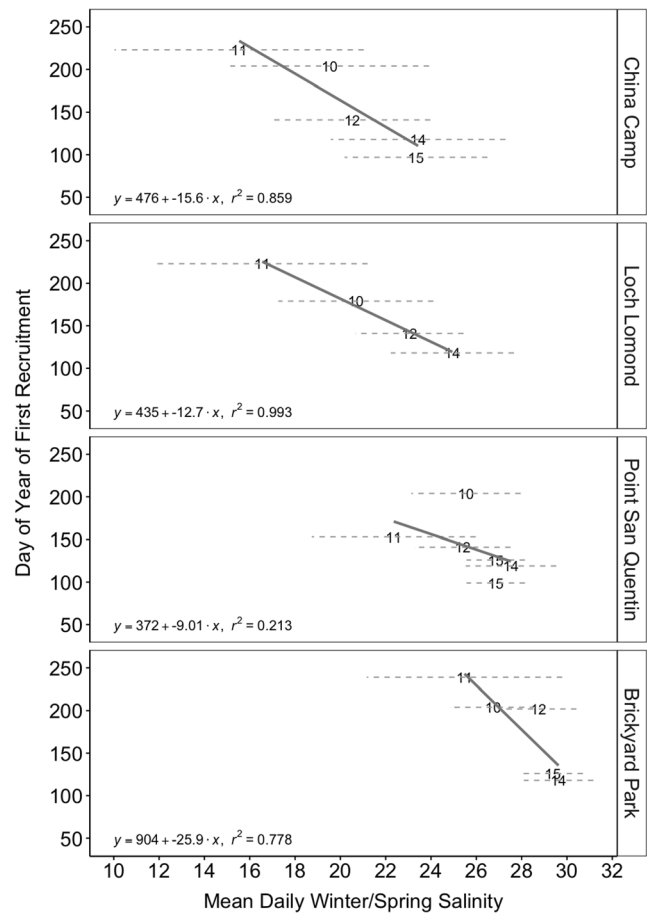
Fig. 8 Timing of *first* recruitment (i.e., onset) at four study sites in San Francisco Bay, 2010–2015 (except 2013) is predicted by the previous winter/spring (February–May) salinity. The last two digits of each year are used to represent the day of first recruitment at each site in that year, and the corresponding mean daily winter/spring salinity. Mean daily winter/spring salinity levels at each site are inversely related to the number of days to first recruitment in the same calendar year (Table 7). *Dashed horizontal lines* represent mean daily salinity ±1 SD. See Online Resource 1 for derivation of site-specific salinities

conditions for longer periods of time have a greater proportion of the oyster population reproducing earlier (Chang et al., unpublished data). These patterns, in turn, may influence local settlement if more larvae are retained in close proximity to the source. Habitat availability and settlement cues also influence larval settlement patterns via larval behaviors that affect substrate selection (e.g., Fuchs and Reidenbach 2013 for *Crassostrea virginica*), though little is known about these factors in *O. lurida* (Pritchard et al. 2015).

Across broad latitudinal gradients, mussel and barnacle recruitment are related to regional differences in sea surface temperature (Broitman et al. 2008), producing regional peaks in recruitment for several invertebrate species. These peaks span several orders of magnitude that track temporal and spatial shifts in oceanographic conditions spanning >1000 km of the Pacific coast (Broitman et al. 2008). Here, we documented comparable variation in recruitment rate tied to physical oceanographic conditions on a much smaller scale of just 10 km inside northern San Francisco Bay. Larvae can be retained in the upper, middle, or lower estuary depending on the species (Carriker 1951; Newman 1953; Bousfield 1955; Kunze et al. 2013). Physical oceanographic patterns may also influence both reproduction and recruitment more indirectly by producing good food conditions (Leslie et al. 2005), and further work should examine this possibility for Olympia oysters.

Changing climate regimes and water management policies will likely shift the focal points for settlement peaks such as the ones documented here, with numerous implications for populations and communities (Harley et al. 2006; Cloern and Jassby 2012) as well as for conservation and restoration programs. The regional climate in northern California is predicted to shift toward warmer, drier conditions (Cloern et al. 2011; Cloern and Jassby 2012) with modest changes in mean precipitation (Neelin et al. 2013; Seager et al. 2015) and an increase in the frequency of both very dry and very wet years (Das et al. 2013; Berg and Hall 2015; Yoon et al. 2015). The Olympia oyster population's center of distribution in San Francisco Bay and other estuaries may move upstream as warmer and drier (and consequently more saline) conditions shift settlement peaks upstream and earlier in the year, on average. Conversely, in wetter years, settlement peaks are likely to shift downstream. The modestly wetter winter of 2010–2011 led to near complete mortality of adult populations at China Camp, and the center of recruitment shifted downstream to Loch Lomond; greater shifts would be expected in response to more extreme wet years. The detection and tracking of such peaks is important for effective management and conservation strategies in the face of continuing anthropogenically driven climate change, particularly as such strategies often rely on natural spatset (Wasson et al. 2014), and because large-scale control of hydrological factors is infeasible in larger estuaries. Although warming appears to lengthen the

recruitment season, creating the opportunity for greater accumulation of individuals onshore, these effects occurred most strongly at sites furthest upstream (e.g., China Camp) that are also vulnerable to mass die-offs in wetter years (Wasson et al. 2014). The net implications for the population dynamics of *O. lurida* remain to be explored. Detailed information on occurrence patterns for different life history stages will enable more comprehensive modeling of likely changes to the population dynamics of Olympia oysters and many other estuarine species.

Long-term, standardized sampling programs, such those espoused by the NERR System, including the NERR System Wide Monitoring Program (SWMP) (Buskey et al. 2015), are critical to detecting spatial and temporal environmental and ecological variation that might otherwise appear random. Salinity and temperature are relatively easily assessed by researchers and managers and are monitored continuously by every NERR SWMP water quality station, as well as by similar stations run by USGS and other organizations. A network of such stations enables broad coverage of regions important to conservation and management, but even highly studied regions like San Francisco Bay have limited coverage in some areas, and would benefit from an expansion of existing monitoring networks.

Studies in which detailed, fine-grained measurements of environmental conditions are coupled with measurements of recruitment across a spatial gradient remain relatively rare. With more systematic studies such as this one, we are likely to see greater evidence for predictable recruitment patterns that map across spatial gradients in accordance with environmental conditions. This knowledge, in turn, will enable a more detailed understanding of the impacts of large-scale environmental changes, including water management regimes and global climate.

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