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SEASONAL SETTLEMENT OF OLYMPIA OYSTER LARVAE, *OSTREA LURIDA* CARPENTER 1864 AND ITS RELATIONSHIP TO SEAWATER TEMPERATURE IN TWO SOUTHERN CALIFORNIA ESTUARIES

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ABSTRACT The continued lack of recovery of the United States west coast populations of the Olympia oyster, *Ostrea lurida*† Carpenter 1864, has piqued recent interest in restoration projects. Because local population persistence is influenced by many factors, including larval settlement, information about the magnitude and timing of settlement will provide valuable contributions to such restoration efforts. We examined larval settlement as a function of season and also monitored water temperature, which is reported to influence settlement timing by cueing synchronized male spawning and subsequent larval settlement. Previous literature, based on an anomalous open coast population, found that settlement of *O. lurida* in La Jolla, CA occurred once seawater reached a temperature of 16°C. To observe variation over seasons in larval settlement density relative to temperature within the more common estuarine habitat in southern California, we placed ceramic tiles in two locations within Upper Newport Bay, Newport, California and in two locations within Aqua Hedionda Lagoon, Carlsbad, California. Temperature data were also collected at each site throughout the sampling period. Tiles were collected and oyster spat counted every two weeks during spring tides to pinpoint pulses in settlement. Settlement in Upper Newport Bay occurred from May until November with peak settlement in June and ranged from 0.0 oysters/m^2 to 1,179 ± 344.8 oysters/m^2 at Coney Island and 0.0 oysters/m^2 to 511 ± 216.4 oysters/m^2 at Newport Wall. In Aqua Hedionda Lagoon, settlement occurred from June until February with peak settlement in June and ranged from 0.0 oysters/m^2 to 339 ± 53.7 oysters/m^2 at Aqua Hedionda site 1 and 0.0 oysters/ m^2 to 108 ± 37.3 oysters/ m^2 at Aqua Hedionda site 2. Whereas oyster settlement did occur at all of our study sites, we did not observe a universal temperature that correlated with the initiation and termination of oyster settlement, nor any significant correlations linking water temperature with peaks in settlement.

KEY WORDS: Olympia oyster, settlement, temperature, *Ostrea lurida*, native oyster

INTRODUCTION

The Olympia oyster, *Ostrea lurida*, ranges from Baja California to Sitka, Alaska to (Dall 1914, Baker 1995) more frequently inhabiting estuaries and bays than open coast regions (Couch & Hassler 1989, Baker 1995, Baker et al. 1999, Cook et al. 2000). *Ostrea lurida* oysters were commercially harvested since the 1850s in California, Oregon, and Washington but suffered severe population declines in the mid-1900s (Wallace 1966, Couch & Hassler 1989, Cook et al. 2000, Kirby 2004, Shaffer 2003). In addition to over-harvesting, Wallace (1966) reported pollution as a primary cause of native oyster decline in estuarine habitats. Sulfite waste liquor from pulp mills caused severe population declines because of decreased reproduction, body weight, and increased oyster mortality (McKernan et al. 1949, Shaffer 2003). Alteration of estuary or bay habitats by removing sediment through dredging or the addition of sediment also contributed to the decline of oysters by changing the hydrodynamics of the region and possibly affecting the magnitude and delivery of larvae to sites (Wallace 1966). These past reductions in *O. lurida* local population densities made continued harvest unprofitable. Currently, there is renewed interest in restoring populations of *O. lurida* because many populations have failed to recover on their own.

Facilitating the recovery of a population requires an understanding of factors constraining current population densities. Because local population density is directly influenced by the magnitude of larval settlement, identifying factors that can influence timing of larval delivery and the extent of settlement success might aid in understanding why adult population densities remain limited in some locations. For example, understanding the hydrodynamics of estuaries might reveal if eddies exist that could retain larvae, if neighboring estuaries are linked such that currents could deliver larvae from one to another, or if the larvae are permanently swept out of the estuary (Pineda 2000). Also, for locations lacking adequate substrate on which larvae can settle, maximal potential settlement might not occur because larvae remaining in the water column would eventually be lost to predation and other sources of mortality. *Ostrea lurida* does prefer to settle on hard substrate (Baker 1995) and the orientation and dimensionality of the surface can influence the magnitude of settlement because they settle most abundantly on the undersides of objects (Hopkins 1935). Identification of these and other factors that influence larval settlement may help pinpoint bottlenecks that are inhibiting population recovery in some locations.

One factor that appears to play a key role in *O. lurida* reproductive success is temperature, which is believed to cue spawning and seems to determine the length of the setting season (Coe 1930, Coe, 1931a, Coe 1931b, Coe, 1932a, Hopkins 1936, Hopkins 1937). Understanding how temperature influences the succession of *O. lurida* setting seasons could aid in pinpointing when larvae are most abundant in the water and

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†The taxonomy of the Olympia oyster has been in dispute since Harry (1985) proposed synonymy of *Ostrea lurida* Carpenter 1864 and *Ostrea conchaphila* Carpenter 1857. Polson et al. 2009 provide molecular evidence that the Olympia oyster refers to the nominal species, *Ostrea lurida* Carpenter 1864. In view of their genetic data, and for consistency, the original taxon, *Ostrea lurida*, is used throughout this volume to refer to the Olympia oyster, which is distributed from approximately Baja California (Mexico) to southeast Alaska.

ready to settle. Shellfish companies take advantage of such knowledge to maximize capture of oyster spat during setting events, and such knowledge could also aid those interested in catching spat (e.g., researchers and citizen groups) for restoration attempts (Bonnot 1937, Shaw 1967, Cook et al. 2000, Lok & Acarli 2006).

In southern California, Coe (1931a, 1931b, 1932a) noted that male oysters begin spawning once water temperatures reached 16°C, though ripe gonads of males and females can be found year-round (Coe 1931a). Female oysters brood larvae for about 9–12 days (Coe 1931a, Hopkins 1936) before releasing veliger larvae that remain in the water column for an estimated period of 2–8 wk (Hopkins 1937, Breese, 1953, Couch & Hassler 1989). As a rough estimate, then, larval settlement may be apparent as early as one month after water temperatures reach 16°C. In areas where the water temperature remains above 16°C for extended periods of time, adult oysters can theoretically release sperm and brood larvae throughout this extended time frame, resulting in a longer setting season (Coe 1931a, Coe 1932a, Coe 1932b). Importantly, whereas the relationship between temperature and settlement dynamics for this species has never been carefully determined in a controlled experimental setting, Coe (1932a) noted that settlement initiated once sea water temperatures rose above 16°C and terminated once temperatures fell below 16°C, and suggested that the temperature can be used as a predictor for initiation and termination of settlement as well as for the length of the setting season. In southern California, the reproductive season occurs for about seven months from April to October or November, depending on the temperature of the water (Coe 1931a, Coe 1932a, Coe 1932b). In British Columbia, where waters are colder, Hopkins (1937) reported a shorter spawning season of about three months from May until July.

Coe's (1932a) studies on the seasonal settlement of *O. lurida* spat focused on a single open-coast population in La Jolla, CA, anomalously located outside of an estuarine setting. Because water temperature can differ dramatically between open coast and estuarine habitats in southern California (NOAA Tides & Currents 2006), it is an open question whether Coe's findings could be representative of southern California oyster populations. Thus, we investigated spatial and temporal settlement patterns in the southern California estuarine habitats where oysters are more commonly found and examined whether temperature could be used as an accurate predictor of settlement initiation and termination, as suggested in Coe's (1932a) study. We examined variation in settlement density among sites and as a function of season and simultaneously measured temperature at two separate locations within Upper Newport Bay, California and at two locations within Aqua Hedionda Lagoon, CA from June 2005 to June 2006. We further searched for correlations in the magnitude of settlement with substrate availability, salinity, tidal height, and water temperature.

METHODS

Field Sites

We measured oyster spat settlement within two southern California estuaries: Upper Newport Bay in Newport, Orange County, and Aqua Hedionda Lagoon in Carlsbad, San Diego County (Fig. 1). Upper Newport Bay is part of the Newport Bay watershed and is a 752 acre (3.04 km^2) estuary that receives freshwater runoff from its north-eastern end in Orange County and opens up to the Pacific Ocean to the south-west. Aqua Hedionda Lagoon is part of the Carlsbad watershed and is a 350 acre (1.42 km^2) estuary with freshwater input to the east; it opens up to the Pacific Ocean to the west. Two sites within each estuary were chosen to observe settlement, Coney Island (CI, N33°37.176′, W117°53.542′) and Newport Wall (NPW, N33°37.144′, W117°53.644′) in Upper Newport Bay and AQ1 (N33°08.583′, W117°19.37′) and AQ2 (N33°08.69′, W117°19.747′) in Aqua Hedionda Lagoon (Fig. 1). Sites were chosen based on the presence of adult Olympia oyster populations and accessibility during low tides. Preliminary demographic surveys of adult populations using quadrat (0.25 m^2) survey techniques ($n = 10$ quadrats) indicated that one site within each estuary, CI and AQ1 (Table 1), had greater adult densities than the other, NPW and AQ2, respectively, though the difference in density for the Upper Newport Bay sites was not significantly different (T-test, $n = 10$, $P = 0.3922$).

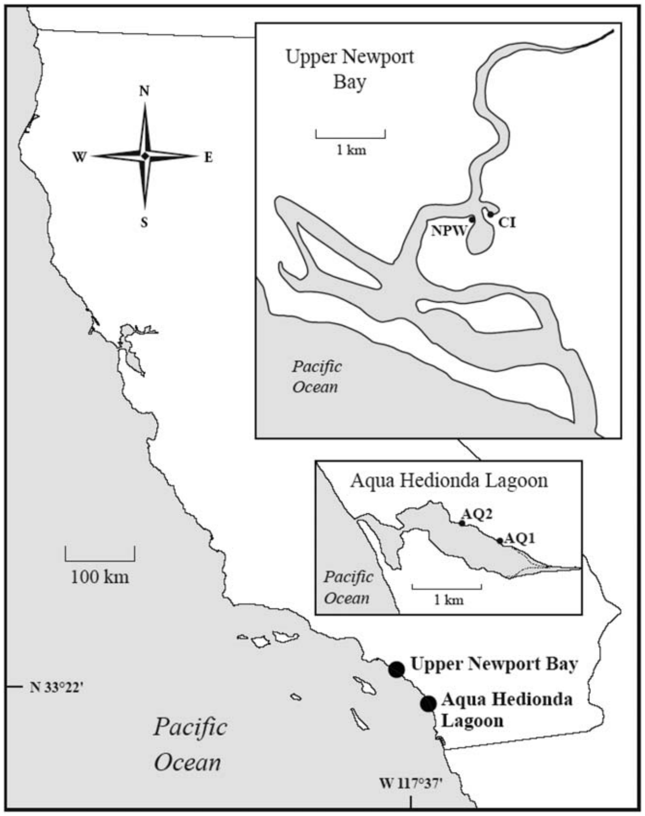

Figure 1. Field sites within Upper Newport Bay, Newport, CA: Newport Wall ("NPW") and Coney Island ("CI") and Aqua Hedionda Lagoon in Carlsbad, CA: Aqua Hedionda site 1 ("AQ1") and Aqua Hedionda site 2 ("AQ2"). The linear distance between NPW and Coney Island is 170 m and the linear distance between AQ1 and AQ2 is 610 m.

Field Measurements

To quantify settlement densities, 15.24 cm × 15.24 cm ceramic tiles were deployed into the intertidal habitat. Shaw (1967) compared oyster settlement of *Crassostrea virginica* onto asbestos plates *versus* onto oyster shells and found a similar pattern of spat settlement on each, with slightly greater

TABLE 1.

Mean adult oyster (*Ostrea lurida)* densities ($n = 10$) at Upper Newport Bay, California and Aqua Hedionda Lagoon, California. Significant findings in bold.

	Upper Newport Bay		Aqua Hedionda Lagoon	
	CI	NPW	AQ1	AQ2
# Oysters/0.25 m^2 (1 SE)	4.8 (1.8)	3.4 (1.3)	10.7 (3.0)	0.7 (0.4)
p ($T \leq t$) two-tail	0.39		**0.0057**	

settlement occurring on oyster shells during the largest overall peak in settlement. Because the varying surface areas of oyster shells do not allow accurate settlement densities to be obtained, ceramic tiles were used in this study to standardize surface area. On one side of each tile, a grid was drawn with a fine tip Sharpie to create 36–2.54 cm squares on the tile to facilitate accurate counting of spat after collection. Ceramic tiles were placed in heavy duty plastic netting with 1-cm square holes to protect tiles from human disturbance. Tiles were placed with the grid side face down inside the plastic netting, as *O. lurida* larvae preferentially settle on the undersides of substrate (Hopkins 1935, 1937). Tiles placed inside netting were attached to tees made of schedule 80 gray 1.91 cm (¾”) polyvinyl chloride pipe (PVC), (Fig. 2). Rebar was placed inside the horizontal arm of the PVC tee to keep tees weighted while submerged during high tides. The horizontal arm of the tee was 0.61-m long and the vertical portion placed into the sand or mud was also 0.61 m long. When deployed, tiles were approximately 0.15–0.2 m above the substrate. We placed four tees at each of two sites within each estuary. Tees were randomly placed along a 20-m transect parallel to the water line at an intertidal height in the midst of adult native oysters observed at that site.

We collected and replaced tiles during spring tides from June 2005 to May 2006. Tiles were collected twice a month during spring tides from June 2005 to August 2005, and during June 2006. Tiles were collected once a month during spring tides from September 2005 to May 2006. We counted spat on each tile and calculated settlement densities. Tidal heights (m) were measured at the point where the vertical base of the tee was inserted into the ground in February 2006 for each tee placed at each site, and the average tidal height was calculated per site within each estuary. Tidal heights were recorded relative to MLLW. Two Tidbit temperature loggers attached to settlement tees were deployed per site; they sampled seawater temperature (°C) every 15 min. We measured salinity within 0.3 m of the water surface in parts-per-thousand (ppt) with a YSI salinity meter during each tile collection. At each site, we also measured the percent cover of available substrate for multiple substrate types using a point-contact method (Murray et al. 2006). A 20-m transect was placed parallel to the tees. At every 2-m interval along the parallel transect tape, we laid a 2-m transect perpendicular to the tape, extending 1 m above and below it, and then measured percent cover of available substrate every 20 cm along the perpendicular transect. In this way, 100 points of available substrate were identified per site. Substrate type was categorized as large, medium, and small rock, pebble, sand, mud, shell, or wall (cement reinforcement wall).

Laboratory Settlement Counts

Once collected from the field, ceramic tiles were stored frozen at 0°C or air dried until counted. When tiles could not be counted immediately after collection, they were placed in a freezer and stored in racks preventing the settlement surface from coming in contact with other tiles to prevent spat loss. Tiles that could be counted after collection were laid to dry before counting. Tiles stored in the freezer were also air dried before counting. Oyster spat were counted per tile using an Olympus dissecting scope (Model SZ61). We then calculated mean spat settlement (spat per m^2) for each site within each estuary and overall density per estuary.

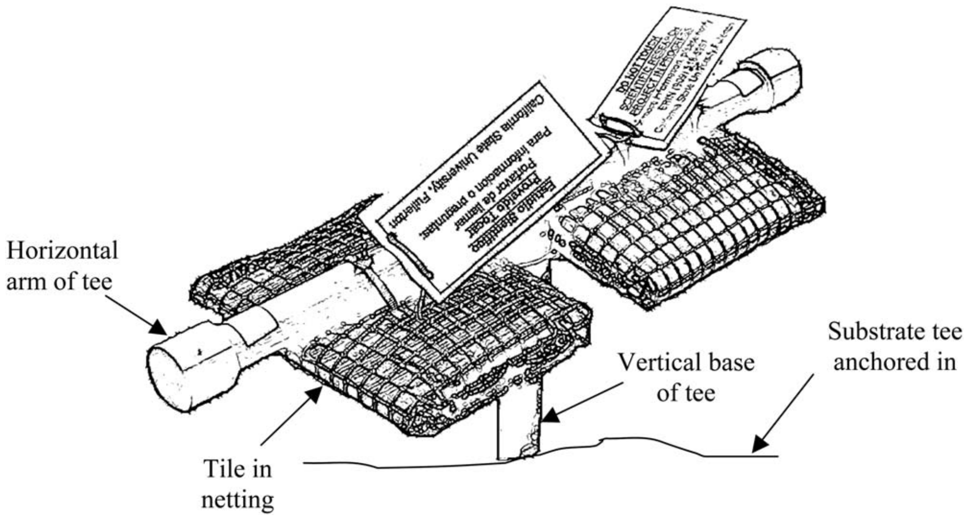

Figure 2. PVC tees were deployed with ceramic tiles attached to assay *Ostrea lurida* larval settlement density. One ceramic tile was encased face down in plastic netting to prevent human disturbance, yet to allow larval settlement. Black military grade zip ties were used to secure tiles in netting as well as plastic netting to PVC arms and base to restrict movement. Tees were marked with laminated signs with contact information and a purpose statement for public awareness.

We transformed all settlement data using log $(x + 1)$ to correct for heteroscedasticity. Within each estuary, we then tested for differences in settlement among months and between sites using a 2-way ANOVA with subsequent Bonferroni-corrected posthoc contrast tests.

RESULTS

Settlement

In Upper Newport Bay, settlement varied significantly as a function of both site and date ($P < 0.05$ and $P < 0.0001$; Table 2); overall settlement within Upper Newport Bay occurred from May until November and ranged from 0.0 oysters/m^2 to 1,179 ± 344.8 oysters/m^2 at Coney Island and 0.0 oysters/m^2 to 511 ± 216.4 oysters/m^2 at NPW, with peak settlement in June (Fig. 3). Settlement was consistently higher at Coney Island than at NPW (Fig. 3).

Overall settlement within Aqua Hedionda Lagoon occurred from June until February and ranged from 0.0 oysters/m^2 to 339 ± 53.7 oysters/m^2 at AQ1 and 0.0 oysters/m^2 to 108 ± 37.3 oysters/m^2 at AQ2, with peak settlement in June (Fig. 4). There was a significant interaction between site and date ($P = 0.0071$, Table 2) where settlement was higher at AQ1 than at AQ2 (Fig. 4), but only during peaks in settlement.

Within each estuary and at each site, settlement was always significantly higher in June of 2005 and 2006 when compared with other collection dates, with no other peaks in settlement ($P \leq 0.004$; Fig. 3, Fig. 4).

Temperature

In Upper Newport Bay, from May 2005 to June 2006 the overall average monthly water temperature was 19.12°C, with a maximum monthly water temperature of 22.78°C in June 2006 and a minimum monthly water temperature of 14.44°C in January 2006 (Table 3). In Aqua Hedionda Lagoon, the overall average monthly water temperature was 18.93°C with a maximum of 23.17°C in July 2005 and a minimum of 14.21°C in January 2006 (Table 3).

TABLE 2.

ANOVA table and test statistics testing the hypothesis that there was no effect of site, date and interaction effect between site and date on larval settlement of *Ostrea lurida* within Upper Newport Bay, CA and Aqua Hedionda Lagoon, CA. Significant findings are in bold.

Source	SS	DF	F ratio	Prob >F
	Upper Newport Bay			
Site	38.1017	1	14.8541	**0.0002**
Date Collected	699.5628	11	24.7934	**<0.0001**
Date Collected X Site	45.8716	11	1.6257	0.1009
Error	287.2870	112		
C. Total	1080.5987	135		**<0.0001**
	Aqua Hedionda Lagoon			
Site	6.26444	1	2.6683	0.1052
Date Collected	412.47919	11	15.9722	**<0.0001**
Date Collected X Site	65.0624	11	2.5194	**0.0071**
Error	262.9435	112		
C. Total	751.5370	135		**<0.0001**

Substrate, Salinity and Tidal Heights

Substrate type varied between estuaries and among sites. Within Upper Newport Bay, mud, wall and oyster shell substrate dominated NPW site (Table 4). At NPW, cement reinforcement wall of approximately 1.5 m tall and >50 m in length served as a vertical substrate upon which oysters would settle. This "wall" only occurred at the NPW site. At the CI site, pebble, mud, and small rock dominated (Table 4). Within Aqua Hedionda Lagoon, small rock, pebble and shell dominated at AQ2. Small, medium, large rock, pebble, and shell all dominated at AQ1 (Table 4). A regression correlation matrix was used to compare the settlement peaks of June 2005 and June 2006 to percent cover of each substrate type found at each site within each estuary, for a total of 4 data points per settlement peak. Although no statistically significant correlations were observed, percent cover of sand (%S) showed the strongest negative correlation with June 2005 settlement data ($r = -0.81$, Table 5).

Salinity (ppt) measurements were acquired by taking point samples from each site on all tile collection dates. In Upper Newport Bay, salinity ranged from 20.6 ppt to 32.1 ppt at CI and 21.0 ppt to 31.9 ppt at NPW; in Aqua Hedionda Lagoon, salinity ranged from 21.5 ppt to 32.8 ppt at AQ1 and 26.2 ppt to 32.8 ppt at AQ2 (Table 6). A regression correlation matrix was used to compare settlement peaks of June 2005 and June 2006 to average salinity found at each site. No statistically significant correlations were observed, though salinity showed a strong negative correlation with June 2005 peak settlement data ($r = -0.73$, Table 5).

Tidal heights (m) were measured in February 2006 for each tee within each site of each estuary and are reported relative to MLLW (mean lower low water), defined as the average of the lower low water height of each tidal day observed over a fixed time period. Tidal heights were measured at the point where the vertical base of the tee was inserted into the ground. Thus, the height of the settlement tiles averaged about 0.18 m above this reported tidal height. In Upper Newport Bay, tidal heights ranged from –0.08 m to –0.12 m for CI tees and –0.05 m to –0.17 m for NPW tees; in Aqua Hedionda Lagoon, tidal heights ranged from 0.29 m to 0.39 m for AQ1 and 0.31 m to 0.45 m for AQ2 tees (Table 7). There were no statistically significant correlations between peaks in settlement for June 2005 and June 2006, but in June 2005 a strong negative correlation was found for average tidal heights ($r = -0.79$, Table 5).

DISCUSSION

Seasonal Settlement

Settlement varied significantly throughout the year within both estuaries. Contrary to previous findings of multiple settlement peaks (e.g., Hopkins 1937) only one major peak in settlement was observed throughout the setting season in our study. Significantly greater settlement occurred during June 2005, with minimal settlement through the rest of the year. Another settlement peak did not occur until the next year at the same time, in June 2006 (Fig. 3, Fig. 4). Previous studies examining larval settlement of *O. lurida* and other oyster species (e.g., *Crassostrea virginica*, Shaw 1967, Lok & Acaeli 2006), have observed settlement typically occurring in two main successive waves, with one major peak in June and one minor peak in August for *O. lurida* (Hopkins 1937). We only observed one large

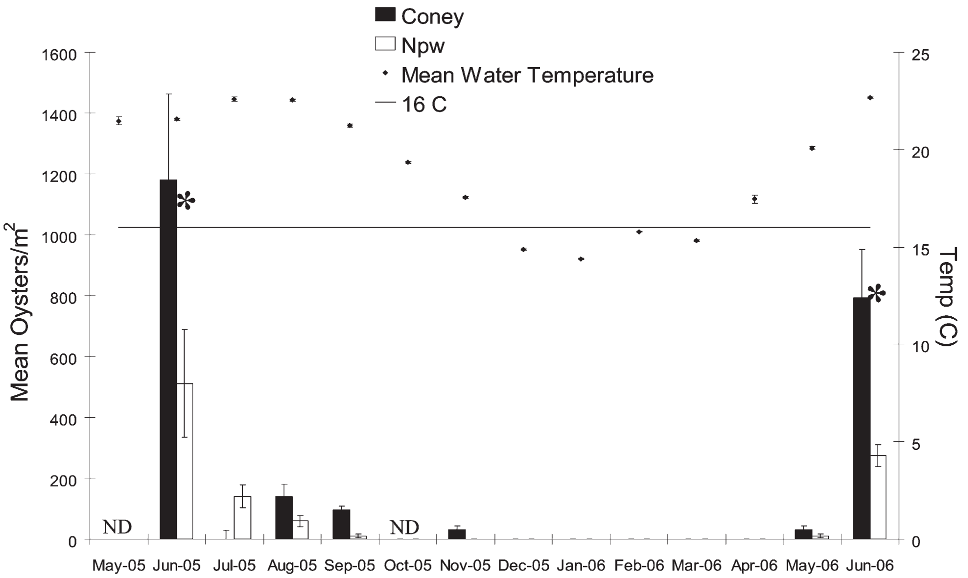

Figure 3. Mean *Ostrea lurida* settlement (per m^2) and water temperature (°C) for two sites within Newport Bay, CA (Coney and NPW) from June 2005 to June 2006. Settlement averages for June 2005 to August 2005, December 2005 and June 2006 are averages of twice-monthly collections. Solid line indicates 16°C, below which Coe (1932a) hypothesized settlement should cease. * indicates significant difference in spatfall between sites, $P \leq 0.004$, ANOVA, corrected *P* value for contrast tests. ND = no data. Error bars are ±1 SE.

peak in settlement per estuary; it is difficult to assess whether this is the general rule in southern California, or rather an anomalous finding, because so far our finding is based upon one year's worth of settlement data. Further monitoring of settlement will reveal if a single peak in settlement is the exception or the rule in the setting season of *O. lurida* in southern California populations.

Temperature as a Predictor of Settlement

Interestingly, settlement ceased at both sites within Upper Newport Bay from December 2005 to April 2006 when water temperatures fell below 16°C (Fig. 3), consistent with Coe's findings (1930, 1932a). Further, and also consistent with Coe's data, water temperatures reached an average of 16°C in early April 2006 (Fig. 3) and the first settlement events occurred at CI and NPW shortly after, in May 2006.

However, we did not observe the same pattern in Aqua Hedionda Lagoon where settlement did not cease once temperatures dropped below 16°C. Settlement continued for both sites within Aqua Hedionda Lagoon from June 2005 until December 2005 for AQ1 until February 2006 (Fig. 4). Beginning in November 2005, average water temperatures dipped below

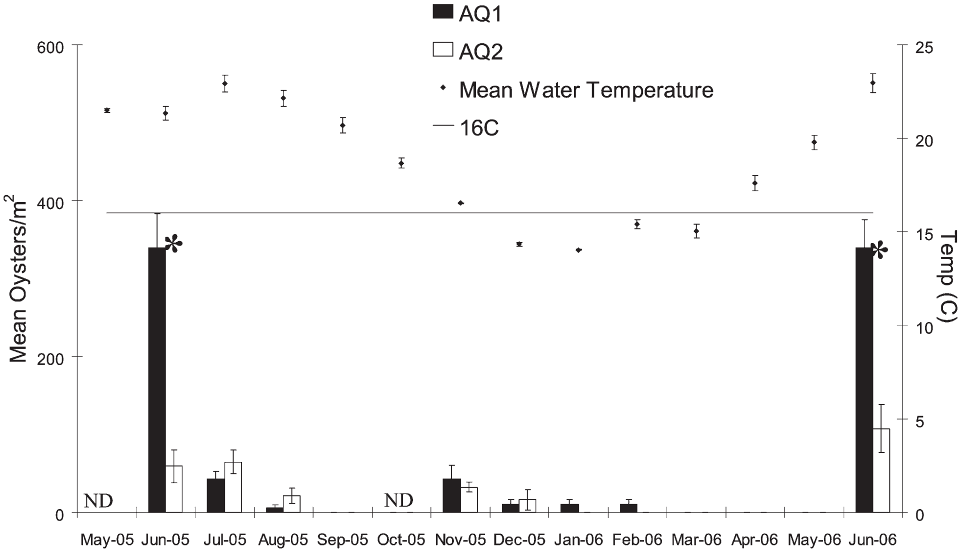

Figure 4. Mean *Ostrea lurida* settlement (per m^2) and water temperature (°C) for two sites within Aqua Hedionda Lagoon, CA (AQ1 and AQ2) from June 2005 to June 2006. Settlement averages for June 2005 to August 2005, December 2005, and June 2006 are averages of twice-monthly collections. Solid line indicates 16°C, below which Coe (1932a) hypothesized settlement should cease. *indicates significant difference in spatfall between sites, $P \leq 0.004$, ANOVA, corrected *P* value for contrast tests. ND = no data. Error bars are ±1 SE.

TABLE 3.

Average monthly, maximum monthly, and minimum monthly water temperatures (°C) for both estuaries and sites within Upper Newport Bay and Aqua Hedionda Lagoon, CA from May 2005 to June 2006.

Source	Average ($n = 14$)	SD	SE	Max	Min
	Estuaries				
Upper Newport Bay	19.12	3.11	0.83	22.78	14.44
Aqua Hedionda Lagoon	18.93	3.25	0.87	23.17	14.21
	Sites within estuaries				
CI	19.14	3.11	0.83	22.85	14.49
NPW	19.11	3.11	0.83	22.79	14.38
AQ1	19.18	3.41	0.91	23.56	14.19
AQ2	18.50	3.21	0.86	22.78	14.23

16°C and did not rise above 16°C until early April 2006. Also contrary to our Upper Newport Bay data and to Coe's findings, settlement was first observed in June 2006, although water temperatures were already above 16°C as of April (Fig. 4).

Water temperatures were extremely similar between estuaries (Table 4), suggesting that water temperature cannot account for the differences in the timing of settlement between the two estuaries. Hopkins (1937) also questioned the universality of temperature controlling *O. lurida* settlement in Oyster Bay, Washington, pointing out that there was no apparent link between water temperature and settlement in his study. Despite the congruency of our Upper Newport Bay findings with Coe's, the comparison between estuaries in our study suggests that temperature is not the predictable cue, at least for spat settlement, that has previously been assumed by Coe, and that other factors may account for the spatial and temporal variation in spatfall observed in this study.

Temperature not only affects spawning initiation and termination (Hori 1933) but also larval development time and larval survival (Breese 1953) for *O. lurida* and other oysters in general (Coe 1930, Coe 1931a, Coe 1931b, Coe 1932b, Prytherch 1934, Hopkins 1937, Lok & Acarli 2006). Our study did not measure larval availability or survival nor did we assay gonadal indices of ripening, though Coe (1931a) points out that at least some males and females have ripe gonads year-round in southern California. Given that temperature is expected to affect most stages of reproduction, it seems exceedingly unlikely that a simple cutoff temperature could indicate anything more than a general window of time within which to expect settlement activity, and our data seem to support this more complex view of the effects of temperature on settlement dynamics. Some of the observed differences in spatfall timing between our study and Coe's (1932a) study, for example settlement in Aqua Hedionda Lagoon in November and December 2005, may also simply be attributable to delayed settlement in larvae, which somehow were retained within the estuary until they found a suitable settlement habitat. Further, there may have been shallow water sources in each estuary where temperatures remained elevated above 16°C for a more extended period than our temperature loggers indicated. Future studies should examine all phases of the reproductive cycle when attempting to tease out the temperature effect.

Spatial Variation in Settlement

We observed large differences in settlement density between sites within estuaries, where one site within each estuary typically showed higher settlement throughout the year, with especially pronounced differences during the peaks in settlement in June 2005 and June 2006 (Fig. 3, Fig. 4). CI had significantly greater settlement than NPW in Upper Newport Bay, even though the sites were only 170 m apart (Fig. 1, Fig. 3); similarly, in Aqua Hedionda Lagoon, AQ1 showed significantly greater settlement compared with AQ2 during peaks in settlement; these two sites were 610 m apart (Fig. 1, Fig. 4). Future studies will help to determine whether the observed differences among nearby sites constitute a consistent pattern. If so, such large variation in settlement observed over such small spatial scales suggests that there must be some mechanism influencing settlement success that operates over very small spatial scales. For example, conspecific chemical cues and changes in the hydrodynamics within an estuary can influence larval settlement in a particular area throughout the year (Pineda 2000), and these sorts of factors could operate on a small scale. Gregarious settlement using chemical cues has been known to influence settlement in other oyster species (Turner et al. 1994, Baker et al. 1999) but little is known about the influence of such cues on the settlement behavior of the *O. lurida*. Settlement and intertidal adult oyster densities were greatest at CI and at AQ1 (Table 1), allowing for the possibility that conspecific chemical cues may have aided in the increased settlement. We did not survey subtidal adult populations so it is unknown whether any of our sites had additional nearby sources of larvae that could have further contributed to increased local settlement densities.

As a preliminary investigation to pinpoint whether adult density and other factors influenced settlement rates, we

TABLE 4.

Percent cover of available substrate at each site within each estuary. For substrate type: LR: large rock, greater than 30 cm; MR: medium rock, approximately 30 cm; SR: small rock, less than 30 cm; P: pebble, about 2.54 cm; S: (sand); M (mud); W: wall-cement, at NPW only; SH: oyster shell, alive or dead.

	Hard Substrate						Soft Substrate		
Site	LR	MR	SR	P	W	SH	S	M	% Hard
CI	2	3	15	38	na	0	0	42	58
NPW	0	5	6	0	14	18	0	57	43
AQ1	12	25	35	13	na	0	14	1	85
AQ2	5	3	39	29	na	0	24	0	76

TABLE 5.

Correlation coefficients between peaks in settlement and percent substrate (LR: Large rock, MR: Medium rock, SR: small rock, P: pebble, S: sand, M: mud, W: cement wall, SH: shell, Hard substrate includes LR, MR, SR, P, W and SH), adult oyster density, salinity, tidal height, and water temperature from June 2005 and June 2006 for all sites. R values are shown, none are significant.

	June-05	June-06
%LR	–0.43	–0.22
%MR	–0.26	–0.11
%SR	–0.65	–0.46
%P	0.38	0.49
%S	–0.82	–0.69
%M	0.65	0.45
%W	–0.02	–0.24
%SH	–0.02	–0.24
%Hard substrate	–0.49	–0.27
Adult density	0.14	0.28
Salinity	–0.73	–0.65
Tidal height	–0.79	–0.62
Temp 2005	0.44	0.43
Temp 2006	–0.08	0.08

searched for correlations between peaks in settlement in June 2005 and June 2006 and factors measured in this study by averaging each factor per site ($n = 4$ sites). Correlation analysis using the F statistic ($F_{0.05(2),\ 2}$, Cacoullous, 1965) showed no statistically significant relationship between settlement and adult density, type of substrate, tidal height, salinity, and mean monthly temperature. However, with only four sites, the power of our correlation analysis was very low. The most compelling, albeit nonsignificant, findings were the relationships between settlement and tidal height ($r = –0.79$), percent sand ($r = –0.82$) and salinity ($r = –0.73$).

These comparisons between sites within estuaries are preliminary, but even so, our study clearly points to the importance of broadly sampling the settlement dynamics within each estuary by encompassing a wider range of sampling sites. Further, our results indicate large variation in settlement over very small spatial scales. Therefore, to accurately reflect the overall estuary-wide variation in settlement density, future studies should broaden the number of sample sites within estuaries and also ensure that study sites are not constrained to a limited part of each estuary.

TABLE 6.

Average, maximal and minimal salinity (ppt) per site from point samples taken during each field collection from June 2005 to June 2006.

Site	Average	SD	SE	Max	Min
CI	29.2 ($n = 15$)	2.87	0.74	32.1	20.6
NPW	29.1 ($n = 14$)	2.83	0.76	31.9	21.0
AQ1	29.8 ($n = 14$)	3.34	0.89	32.8	21.5
AQ2	31.9 ($n = 15$)	2.36	0.61	32.8	26.2

TABLE 7.

Average, maximal and minimal tidal heights (m) of tees per site measured in February 2006.

Site	Average ($n =$ 4)	SD	SE	Max	Min
CI	–0.09	0.02	0.008	–0.12	–0.08
NPW	–0.10	0.05	0.021	–0.17	–0.05
AQ1	0.35	0.05	0.024	0.39	0.28
AQ2	0.39	0.06	0.027	0.45	0.31

CONCLUSION

From our studies observing seasonal and spatial settlement of *O. lurida* in southern California, there appears to be no universal temperature useful for predicting the initiation and termination of oyster settlement. Continued monitoring of larval settlement while simultaneously measuring factors thought to play a role influencing reproductive success in general will enable researchers to determine if peaks in settlement change with, for example, changes in water temperature, hydrodynamics, or adult population density. Prytherch (1934) and Couch and Hassler (1989), among others, have discussed how oystermen experimentally determine how they can ‘‘catch’’ the greatest number of spat over the years to increase their production. Valuable information from further studies will help to determine which factors have the greatest influence in cuing peaks in settlement in both time and space, and would aid in pinpointing the best time-frame and locations in southern California for placing settlement arrays into the water for future restoration attempts. Lastly, southern California estuaries have largely been overlooked in monitoring and restoration efforts focused on the Olympia oyster, but they clearly support populations that regularly recruit, thus providing highly favorable conditions for population persistence and restoration.

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