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Multi-decade changes in the condition index of adult Pacific oysters (*Crassostrea gigas*) in response to climate in a US west coast estuary

Brett R. Dumbauld[a,*], Xiuning Du[b], Mary Hunsicker[c], Zachary Forster[d]

[a] U.S. Department of Agriculture, Agricultural Research Service, Hatfield Marine Science Center, 2030 S.E. Marine Science Drive, Newport, OR 97365, USA
[b] Oregon State University, Cooperative Institute for Marine Ecosystem and Resources Studies, 2030 S.E. Marine Science Drive, Newport, OR 97365, USA
[c] Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Newport, OR 97365, USA
[d] Washington State Department of Fish and Wildlife, Willapa Bay Field Station, PO Box 190, Ocean Park, Washington 98640, USA

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ABSTRACT

Pacific oysters (*Crassostrea gigas*) were introduced to the US west coast in the early 1900's, but only regularly spawned in several discrete estuarine locations like Willapa Bay where conditions allowed for adult oyster gametogenesis as well as larval survival, retention, and settlement. Oyster industry participants have long recognized that the condition of marketable oysters was related to proximity of their growing areas to the ocean. This prompted resource managers to routinely collect data and identify trends in oyster condition index (CI) in this estuary. An analysis of this almost seven- decade long CI record revealed consistent trends across four sampling locations in Willapa Bay where 50–70% of the variability in CI was explained by a single component. This component of variability in CI was related most strongly to variability in the upwelling index (UI) which was positively correlated with CI during the summer upwelling season. A relationship with the Pacific Decadal Oscillation (PDO), a broader basin-scale index of temperature was also significant, but weaker and PDO was negatively correlated with CI. Shifts or breaks in the long-term CI record occurred in 1977/78 and 1999/2000 with another shift related to the second component of variation in CI that occurred in 1988/1989. The change in 1977/78 has previously been shown to correspond with a shift in the basin scale PDO, but more recent shifts appear to be correlated with local fluctuations in both temperature and upwelling intensity. Further investigation into shifts in the seasonal timing of temperature and phytoplankton as variables that control the oyster gametogenic cycle seem warranted.

1. Introduction

Responses of marine invertebrates to long-term changes in climate are less well documented than those of their terrestrial counterparts, but there is strong evidence that recent climate warming has influenced their distribution and abundance, especially where their populations can be more readily assessed along intertidal shorelines or for commercially fished species (Cloern et al., 2010; Edwards et al., 2010; Helmuth et al., 2006; Menge et al., 2011). While there is a rich historical dataset on the physiology and seasonal phenology for some marine invertebrates, fewer long-term records have been maintained. Recent recognition of the anthropogenic contribution to changes in marine climate and obvious shifts due to more extreme climate warming events have resulted in new efforts to collect such data in order to make comparisons with these historical records (Moore et al., 2011; Sainz et al., 2019).

Due to their commercial value and widespread distribution in coastal marine waters, bivalve molluscs represent marine invertebrates for which long-term records have often been maintained. This is particularly the case for Pacific oysters (*Crassostrea gigas* Thunberg 1793), recently reclassified as *Magallana gigas* (but see Bayne et al., 2017, 2019), which have been widely introduced and cultured along many coastlines around the world (Minchin, 2007; Ruesink et al., 2005). The value of these oysters as a sentinel species for examining effects of climate change and variability has also been recently recognized, in part due to concern over observed changes in their distribution outside culture (King et al., 2021; Thomas et al., 2018; Thomas et al., 2016).

Pacific oysters were introduced from Japan to several estuaries along the west coast of North America in the early 1900s where they were

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* Corresponding author.
E-mail address: brett.dumbauld@usda.gov (B.R. Dumbauld).

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cultured on tidelands and replaced the oyster native to this coast (*Ostrea lurida* Carpenter 1864) as the primary harvested species (Lindsay and Simons, 1997; Quayle, 1988; Steele, 1964; White et al., 2009). Pacific oysters only initially became "naturalized" in several discrete estuarine locations along this coast including Willapa Bay and Dabob Bay in Washington state, US where conditions were favorable for adult oysters to undergo gametogenesis and spawn, and for larvae to survive and settle on suitable benthic substrates (Chapman and Esveldt, 1943). The shellfish industry took advantage of this "wild" set at these locations and/or continued to import juvenile Pacific oysters as seed from Japan until the advent of shellfish hatcheries in the late 1970's (Chew, 1984; Clark and Langmo, 1979; Im et al., 1976; Nosho and Chew, 1991). Due to the importance of these two areas to the Washington state industry, programs were established to monitor oyster spawning, larval abundance, and forecast larval set at both of these locations (Lindsay et al., 1959; Packer and Mathews, 1980). A monthly sampling program was also initiated to examine the condition or "fatness" of adult Pacific oysters, recognizing its value for assessing both the seasonal reproductive cycle and relationships between potential market yield and the environment where the oysters were grown (Westley, 1964). This program was initiated in Willapa Bay in 1954 (Westley, 1959; Westley, 1961) and has been maintained with some gaps through present day because the natural spawning and recruitment cycle of these oyster stocks on state established reserves continues to be an important feature of Pacific oyster management in this estuary (Dumbauld et al., 2011). This data now comprises one of the longest biological records on the U.S. west coast.

Interannual trends in this long-term oyster condition index (CI) data have been previously examined in part due to a general decline in condition over time that was observed after the 1970s and concerns that this might be a result of large increases in the number of shellfish planted in Willapa Bay exceeding the estuaries carrying capacity. Several authors have explored relationships between CI and ocean climate indices. Schoener and Tufts (1987) found a significant inverse relationship between sea level height and CI using this data record for 1955–1985 with a coherent two-year frequency signal. They did not find a direct relationship with local seawater temperature, but suggested that broader temperature records for the NE Pacific ocean seemed to relate with large fluctuations in CI. Ebbesmeyer and Strickland (1995) found that CI varied with an integrated climate index – the Pacific Northwest Index (PNI) and that CI also generally declined with decreased outflow from the Columbia River. The physical and biological processes leading to these empirical relationships however remained largely unexplained and these authors were uncertain about whether these correlations would continue in the future. Hare and Mantua (2000) assembled a diverse set of climate and biological time series including CI from 1965 to 1997 to explore empirical evidence for common regime shifts after the 1989 climate event in the broader North Pacific ecosystem. Their analysis showed a decline of CI post-1977 which seemed to match a consistent large scale summertime west coast warming, a feature now recognized as the Pacific Decadal Oscillation (PDO). Finally, Litzow et al. (2020) found a nonstable relationship between the PDO and North Pacific Gyre Oscillation (NPGO) and several other biological indices including CI especially after 1989.

The effects of coastal upwelling on estuarine hydrography, water column properties and resultant effects on juvenile Pacific oyster growth in Willapa Bay have been previously examined and modeled (Banas et al., 2007; Ruesink et al., 2003; Wheat et al., 2019). On event and seasonal time scales, upwelling-driven coastal phytoplankton blooms and associated water properties are advected directly into the bay which along with the presence of oysters and other filter feeders results in a gradient of high phytoplankton biomass near the mouth and lower biomass and a slightly different phytoplankton community up-estuary, particularly during the summer upwelling season when river flow is minimal (Newton and Horner, 2003; Roegner et al., 2002). This estuarine gradient in water column properties has also been attributed to water residence time because water moves back and forth and is retained for longer periods away from the estuary mouth (Banas et al., 2007) and daily tidal exchanges cause a similar gradient from the channels across broad intertidal mudflats to shore (Wheat et al., 2019). These spatial gradients are well known to shellfish growers and have been previously related with juvenile oyster growth across summer months and general production of larger oysters in this estuary, but the seasonal cycle of condition and its well-known relationship with gametogenesis in older diploid oysters (Brown, 1988; Costil et al., 2005; Royer et al., 2008) less explored. Mechanistic models have been developed to describe growth and reproduction in Pacific oysters, (Bernard et al., 2011; Gasmi et al., 2017; Gourault et al., 2019) and link this to environmental drivers, but few studies have previously described these relationships in Willapa Bay (see Schumacker, 1999; Dumbauld et al., 2021).

Here we further examine the more than a half-century long record of oyster condition data collected from four locations in Willapa Bay, with a focus on relationships between CI and two climate indices for which similar long-term records exist. First, we chose the PDO to represent basin-scale marine climate forcing, due to the previously established relationship between CI and PDO and because PDO dynamics have been shown to be related and respond to the El Niño Southern Oscillation (ENSO), a second important basin scale climate indicator. The PDO also represents decadal scale variability in this system particularly north of 45°N where this data was collected (Litzow et al., 2020; Macias et al., 2012; Newman et al., 2003). Second, we chose and index of coastal upwelling (UI) to represent local environmental conditions due to its strong influence on temperature, salinity and phytoplankton availability for oysters in this estuary (Banas et al., 2004; Banas et al., 2007; Roegner et al., 2002).

2. Methods

2.1. Study sites

Willapa Bay, Washington, is the third largest estuary along the West coast of the continental US (46°40'N, 124°0'W, Fig. 1), but relatively small (358 km^2) and shallow with extensive intertidal mudflats that make up about half of this area and are therefore exposed on low tides (Dumbauld and McCoy, 2015; Hedgepeth and Obrebski, 1981). Most of the Pacific oysters in this estuary are farmed on these low to mid intertidal tidelands that growers either uniquely own or in relatively few cases lease from the state. While nine small rivers drain into the bay, the average monthly river flow ranges from only 17 m^3 s^{-1} to 390 m^3 s^{-1} and the majority of that input occurs during winter months when precipitation is highest (November–March) and/or during storm events in other seasons when river input is otherwise minimal (Banas et al., 2004; Hickey and Banas, 2003). Both river flow and ocean exchange are forced by large-scale winds, and wind-driven coastal upwelling provides the primary source of nutrients and resulting phytoplankton especially close to the estuary mouth during summer months (Banas et al., 2004; Banas et al., 2007; Hickey et al., 2002). The Willapa Bay estuarine gradient is well known to shellfish growers whom typically plant juvenile seed oysters south of an imaginary line (from just north of Nahcotta to just north of the Nemah River on the east side of the estuary, Fig. 1) where they reside for 1–2 years and then are transplanted to "fattening" beds located north of this "fattening" line for harvest after at least a second summer. This line also serves as a rough boundary for the locations of historically successful spawning and setting of Pacific oysters in this estuary, so growers often distribute oyster shell on beds south of this line to obtain a "natural" larval set and transplant these oysters to fattening beds north of the line (Dumbauld et al., 2011; Ruesink et al., 2018). Data from four sites include a location just east of the WDFW Willapa Bay Field station (designated as Parcel A; PA, 27.7 km from the estuary mouth, Fig. 1), a location closer to the estuary mouth along the east side of the North Beach peninsula (Stackpole; STK, 14.6 km from mouth), a

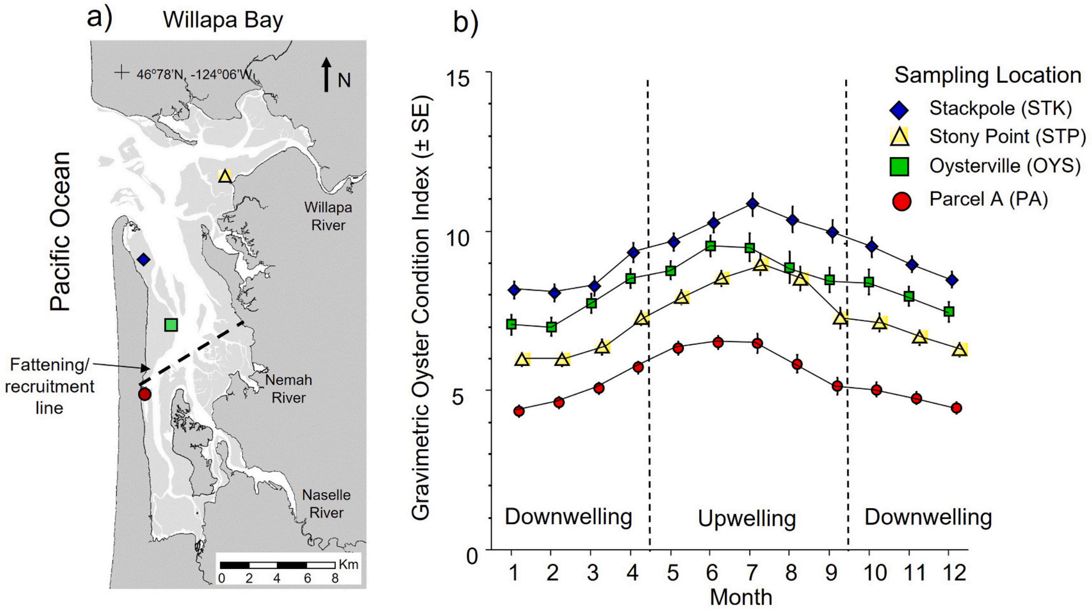


Fig. 1. (a) Map of four locations in Willapa Bay where oysters were sampled. (b) Average monthly values of gravimetric condition index (± SE) measured at these locations. Vertical dashed lines represent divisions between upwelling (May – September) and downwelling (October – April) seasons. Also shown is dashed line across the estuary known as the “fattening line” by shellfish growers.

location about halfway between STK and PA (Oysterville; OYS, 22 km from mouth), and a location on the east side of the estuary, but also close to the estuary mouth (Stony Point; SPO, 11.6 km from mouth).

2.2. Condition index (CI) calculation

Although several different methods have been used, bivalve condition relates a measure of the meat biomass to that of the shell or the volume of the shell cavity (Abbe and Albright, 2003; Crosby and Gale, 1990; Lawrence and Scott, 1982; Zeng and Yang, 2021). Condition of oysters in Willapa Bay from 1954 to 1998 was measured using the Westley method (Westley, 1961) which was adapted from original work by Medcof and Needler (1941) for eastern oysters *Crassostrea virginica*. Archimedes principle which assumes that oyster meats have approximately the same density as water is used to obtain the shell cavity volume and is calculated as follows:

$$CI = \frac{\text{Dry body wt x 100}}{[\text{whole wt.in air} - \text{whole wt.in water}] - [\text{shell wt.in air} - \text{shell wt.in water}]}$$

(all weights recorded in g)

Oysters were collected, all fouling organisms removed and then first weighed in air (whole weight = wet weight of whole animal in air), then suspended in seawater using a hanging balance and measured again (whole weight in water). Oysters were then opened and tissues removed, dried (48 h at 50° C followed by 48 h at 100 °C) and weighed (dry body wt). The shells were then weighed again both in air and submersed. This method was evaluated and standardized (Westley, 1961) and biologists collected 20 individual adult oysters of similar size (generally about 2 years old, volume = 125 cc.) at each location once every month. Oysters were pooled and measured together to make these monthly assessments for each location, so no estimate of error was obtained for each individual monthly value. After a detailed comparison with several other methods Schumacker (1999) found a consistent relationship between condition collected using this technique and the gravimetric method (Lawrence and Scott, 1982) which is less prone to error and much easier to conduct on individual oysters so that error can be estimated. Sample size was increased to 30 oysters of the same size which were collected at each of the same locations and the gravimetric technique was adopted thereafter, so all monthly values became averages from 1999 to 2021 and individual oyster condition was calculated as follows:

$$CI = \frac{\text{Dry body wt x 100}}{[\text{whole wt.}] - [\text{dry shell wt.}]}$$

(all weights recorded in g)

These measures are mostly the same as above so whole weight represents the weight of oysters in air before the tissue is removed, but dry shell weight now represents valves from each individual oyster that have been dried alongside meats in an oven. Pre- 1999 values were then converted to gravimetric equivalents using the relationship: Gravimetric = Westley-0.905/1.180 (n = 504, r^2 = 0.9126; Schumacker, 1999).

2.3. Data processing

The length of the condition index time series was slightly different at Parcel A (1955–2021), Stackpole (1960–2021), Stony Point (1954–2021), and Oysterville (1963–2016) due to differences in when data collection was initiated at each site and in the case of Oysterville when sampling program was terminated. Missing values were also prevalent in these records when sampling could not be conducted for various logistical and funding challenges. Missing values (>6 per year) were present primarily in 1979, 1982 and 1983 at all sites comprising 13.5%, 16.3%, 15.5% and 19.6% of the entire time series at PA, STK, SPO and OYS, respectively.

The annual seasonal pattern in this data set has previously been examined (Dumbauld et al., 2021) and we replicated that analysis here by first examining monthly means for the entire data set at each of the four locations. Then to characterize seasonal differences in long-term variability of CI at each site, we aggregated data into 3-month seasons to reduce the number of missing values due to irregular monthly sampling noted above, with winter representing December (of the previous year) – February, spring as March–May, summer as June–August, and autumn as September–November. Coastal upwelling and downwelling alternations are very periodic physical events outside Willapa Bay but annual occurrences produce consistent effects on nearshore biological variables (Banas et al., 2007). Considering this forcing and coupling, we also calculated seasonal averages and anomalies for two broader seasonal cycles (October of the previous year to April representing the downwelling season and May to September for the upwelling season). We then normalized these seasonal averages by removing corresponding long-term means and dividing by standard deviations to obtain standardized anomalies (Jones and Hulme, 1996) which provide an alternate visual representation of variation above or below the long-term average and explored interannual patterns in CI at each site by plotting both mean values and anomalies.

We examined relationships between CI long-term variability and two climate indices: 1) the Pacific Decadal Oscillation (PDO) which represents basin scale sea surface temperature variations (SST) for the North Pacific (north of 20°N) (data accessed at http://research.jisao.washington.edu/pdo/PDO.latest), and 2) the coastal upwelling index (UI, $m^3 s^{-1}$ per 100 m coastline at latitude 45°N) which represents local environmental forcing factors that impact oyster condition (NOAA Environmental Research Division, data accessed at https://oceanview.pfeg.noaa.gov/products/upwelling/dnld).

2.4. Statistical analysis

Analysis of variance (ANOVA) on mean CI values across years was first used to examine the effect of both calendar and upwelling downwelling season and location on CI (AOV in R, R development team 2020). We then analyzed temporal variability in CI using two statistical tools: 1) Principal Component Analysis (PCA), a more traditional tool used most often in community analyses and 2) Dynamic Factor Analysis (DFA), a more recently implemented method in ecological studies. Goals were to determine whether these two methods produced consistent results and to avoid mischaracterizing results due to limitations of each method.

While most often used to examine patterns in ecological community data, PCA has also been used to isolate the most dominant mode of variability patterns in time series variables (Hare and Mantua, 2000). For this study, multivariate PCA analyses were run using Primer (Clarke and Gorley, 2006) and PC scores were plotted against year to examine interannual variability of CI. The eigenvectors (loadings) quantify correlations between each of the time series and dominant PCs, primarily the first and second PC in this study. The eigenvalues determine the fraction of total data variance explained by each PC. We conducted PCA analysis separately for both CI data only and CI with environmental covariables PDO and UI. Correlations between the first PC score data series representing the most dominant temporal variability pattern across sites and corresponding PDO and UI data series were then examined using least squares linear regression models.

DFA is a multivariate statistical method similar to PCA, but it is specifically designed for time- series ordination (Holmes et al., 2018; Zuur et al., 2003). Here we follow the methods of Ward et al. (2019) and Hunsicker et al. (2022) and use a Bayesian implementation of DFA to (1) summarize the variability in oyster CI from the four sampling sites by estimating the number of temporal patterns (‘trends’) that best capture the observed variation, (2) identify relationships between variability in the CI and two climate variables, PDO and UI, and (3) determine the probability of regime shifts in the identified trend over time. All analyses were conducted using the bayesDFA package in R (Ward et al., 2019; Ward et al., 2022).

To summarize the variability in oyster CI, we used model selection tools to identify the best supported DFA model and number of shared trends. Specifically, we identified support for (1) the number of latent or shared DFA trends ($n = 1–2$), (2) a fixed versus estimated trend variance (using a prior on the standard deviation, σ_w, of $\sigma_w \sim \text{Normal}(0,1)$), (3) the most appropriate error structure for the oyster CI data (whether the times series had equal (shared) or unequal (unique) observation errors), and (4) and process errors drawn from a multivariate Student-t distribution or a normal distribution.

We identified the best-performing models for both upwelling and downwelling seasons based on the Leave-Future-Out Cross Validation Information Criterion (LFO-CV) because it properly accounts for time series structure (Burkner et al., 2020). For each model formulation, we applied the LFO-CV method by first fitting the model to all years of data prior to year T (i.e., training data, years 1, 2, …, (T-1)) and then using the fitted model to predict the trend value in year T (i.e., test data). We repeated this process for 10 years, starting with 2021 as year T and working back to 2012, and then calculated the expected log predictive density (ELPD) across those time steps. Models with the highest ELPD were deemed the best supported models. We used this same approach to evaluate whether the performance of the DFA model was improved when PDO or UI were included as covariates in the model. If one or both climate time series increased variability explanation in the models, it would indicate that variability in the CI is strongly correlated with the two climate variables (this methodology is similar to PCA including both CI and PDO, UI).

Once the best supported oyster condition DFA models for the upwelling and downwelling seasons were identified, we estimated the presence of different regimes or shifts in shared CI trends by applying hidden Markov models (HMM) to the estimated trends from the DFA, as described by Ward et al., 2019. We evaluated support for regimes by using the posterior trend estimates from each model as input. The Bayesian Leave-One-Out Cross Validation information criterion (LOO-CV, Vehtari et al., 2017) was used to identify the data support for the number of regimes ($n = 1–3$). The model with the lowest LOO-CV value was deemed the best model.

Finally, simple linear regressions were applied using the first PC score time series and most common trend values from the DFA models to examine consistency between the two methods.

3. Results

3.1. Seasonality

Oyster condition followed a similar seasonal pattern at the four sites with lowest CI in winter increasing over spring to the highest CI in summer and then declining again in autumn (Fig. 1). The peak CI value in summer appeared to occur slightly earlier (June) at PA and OYS than at STK and SPO (July). Univariate tests demonstrated significant site and season differences, but no interaction (ANOVA, site, $F = 232.70$, $df = 3$, $p < 0.001$, season, $F = 60.01$, $df = 3$, $p < 0.001$; interaction $F = 1.28$, $df = 9$, $p = 0.239$). Oysters at STK had the highest CI in all four seasons followed by Oysterville, Stony Point and the lowest CI was observed at Parcel A (Table 1). In general CI was about 2 units higher during the upwelling season at all sites than during the downwelling season at all sites (Table 1) and this difference was also significant with no significant interaction between factors (ANOVA, location $F = 122.954$, $df = 3$, $p < 0.001$, upwelling season, $F = 75.74$, $df = 1$, $p < 0.0.001$, interaction $F = 0.42$, $df = 3$, $p = 0.742$).

3.2. Interannual variability

Patterns of interannual change in oyster CI were coherent across all four sites ($r > 0.5$, $p < 0.0001$) and were observed in both mean CI values and the CI anomaly (Figs. S1 and S2). We therefore only display time series plots and contrast trends for STK and PA hereafter, because these two locations were closest and furthest to the estuary mouth (Fig. 1) and oysters had the highest and lowest average CI at these two sites, respectively (Table 1, Fig. S1). Visual analysis of average CI during the upwelling and downwelling season revealed similar interannual patterns at both PA and STK with multi-year decreases from the late 1970s through early 1980s and from the late 1980s to early 1990s and an increase from the late 1990’s through the early 2000’s (Fig. 2). These patterns were observed at both locations, but there was a multi-year decrease in the early 1970s at PA during the upwelling and summer

Table 1
Seasonal averages of CI (±SD), and number of monthly values (n) for each time series at four sampling locations in Willapa Bay.

Site	Winter	Spring	Summer	Autumn
Stackpole	8.2 (2.0), *n* = 170	9.1 (2.2), *n* = 159	10.5 (2.5), *n* = 143	9.4 (2.3), *n* = 153
Oysterville	7.2 (2.1), *n* = 136	8.3 (2.0), n = 136	9.3 (2.7), *n* = 128	8.2 (2.3), *n* = 126
Stony Point	6.1 (1.5), *n* = 179	7.1 (1.9), *n* = 181	8.6 (2.4), *n* = 167	7.0 (2.1), n = 167
Parcel A	4.5 (1.3), n = 179	5.6 (1.5), *n* = 178	6.3 (2.0), *n* = 169	4.9 (1.7), n = 167

	Downwelling	Upwelling
Stackpole	8.6 (2.1), *n* = 375	10.2 (2.4), *n* = 247
Oysterville	7.7 (2.2), *n* = 312	9.0 (2.5), *n* = 214
Stony Point	6.5 (1.7), *n* = 409	8.2 (2.4), *n* = 281
Parcel A	4.8 (1.5), n = 409	6.1 (2.0), n = 281

seasons only, and CI fluctuated more in summer and autumn seasons at STK than at PA (Figs. 2 and S3). Higher mean values of CI at STK than at PA were apparent throughout the entire time series, and the difference became gradually larger from the late 1970s on, and much greater after the mid-1990s (Figs. 2 and S3). While interannual variability was generally coherent between the two sites in each season, there were some years when the difference between locations changed in opposite directions. For example, CI remained low in the 1990s at PA, while it stayed high or even increased at STK.

Patterns in the CI anomaly could more easily be divided into three distinct time segments: mostly above the long-term mean before 1977, mostly below this mean during 1978–1999 (except for 1988/89, during the downwelling season), and above the mean again from 2000 onwards (Fig. 2). The long-term pattern in the CI anomaly was similar for both PA

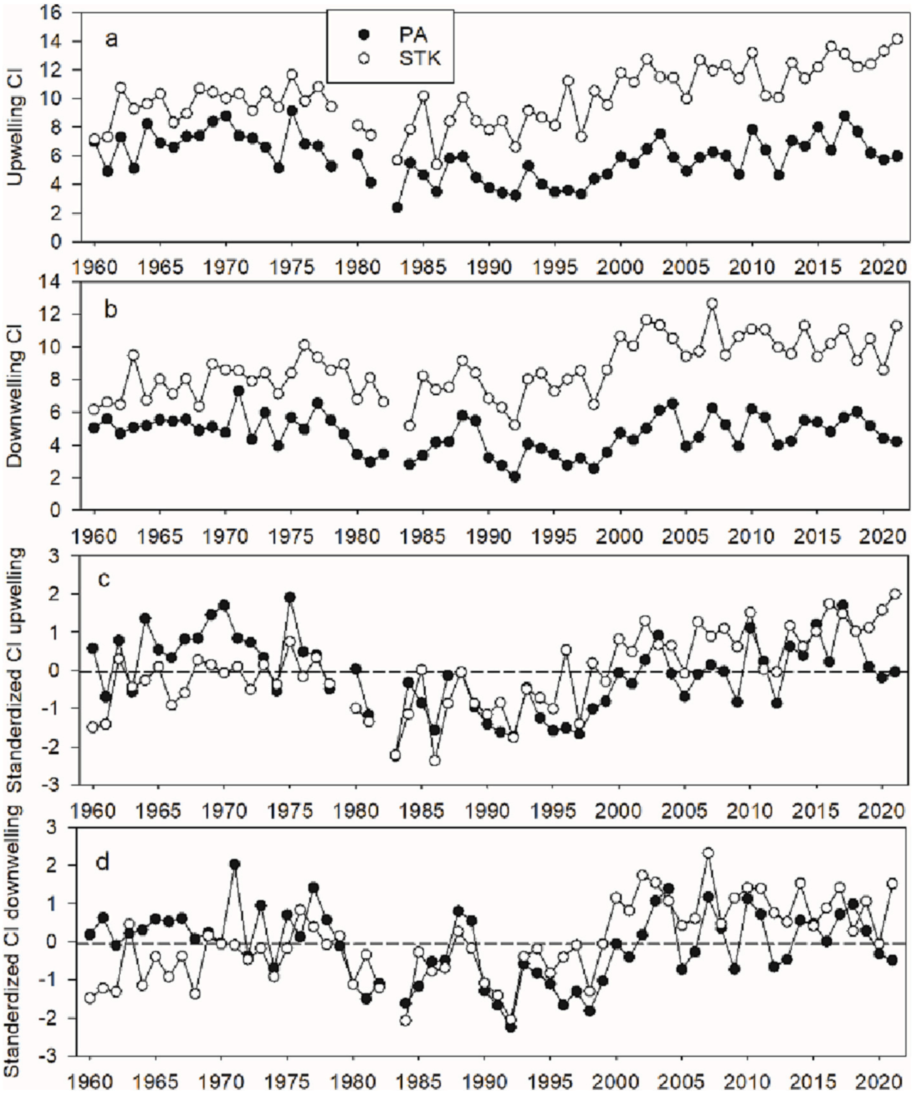


Fig. 2. Mean CI at Parcel A (PA) and Stackpole (STK) during (a) upwelling and (b) downwelling seasons. Standardized anomalies of CI at Parcel A (PA) and Stackpole (SP) during (c) upwelling and (d) downwelling seasons.

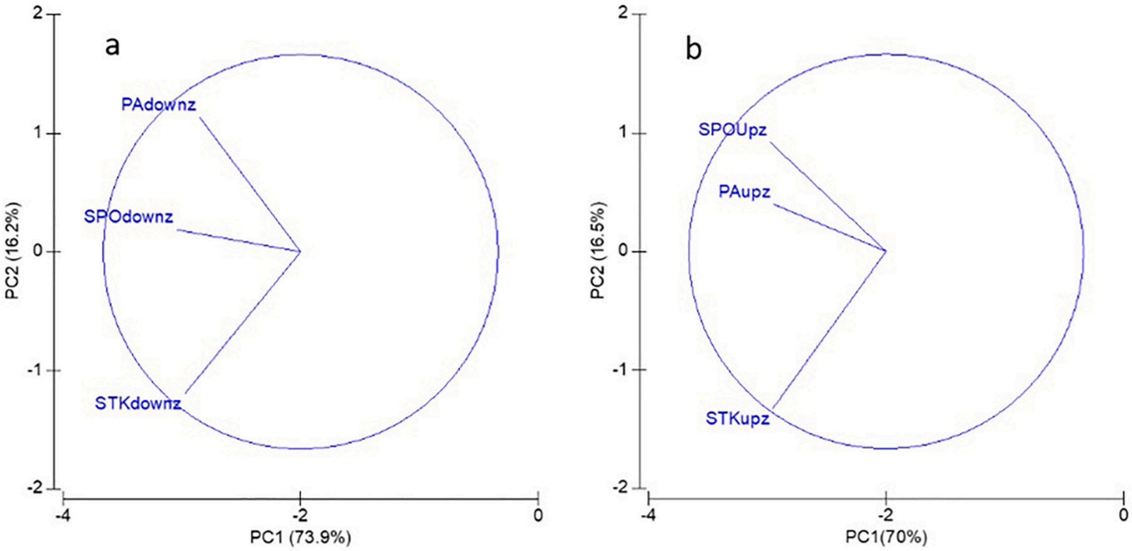


Fig. 3. Eigenvector patterns derived from Principal Component Analysis (PCA) of CI time series at three sites, PA, STK, and SPO in (a) downwelling and (b) upwelling aeasons.

and STK, but the above mean magnitude was lower pre-1977 at STK than that at PA, and higher post-1999. These patterns in the anomaly also held across conventional calendar seasons (Fig. S5).

3.3. Principal component analysis

Since the CI time series at Oysterville was shorter than that for the other sites, initial PCA analysis were conducted for three sites (PA, STK and SPO) and for all four sites at both four-season and two-season temporal resolutions. Results were similar, so we show only those for the longer time series at three sites here. The oyster condition time series from these 3 sites loaded similarly on the first axis (PC1) which explained 64 to 74% of the total variance (Figs. 3 and 4) while PC2 only explained 14–23% of total variance. The fraction of the variance explained by PC1 was slightly lower in autumn (64%) and summer (65.2%). Correspondingly, the eigenvector distribution showed that PA, STK and SPO had similarly sizable explanations (loadings) to PC1 variance in individual seasons. The PC2 fractions were all much lower than PC1 and ranged between 14 and 24%. In each of the vector plots (Figs. 3 and 4), STK had negative and sizable loadings while PA had positive and sizable loadings to PC2. SPO had negligible loadings to PC2 in most cases except upwelling, spring and autumn seasons when it had the highest positive and sizable loadings. Similar eigenvector patterns and PC component variances were derived in all-season data series (4-season and 2-season) combined PCA (Fig. S5).

Common dominant trends of CI change shared by the three sites are evident in the time series of PC1 scores where two time shifts are identifiable in 1977–1978 and in 1999–2000 for both upwelling downwelling and four calendar seasons (Figs. 5 and S6). Times series of PC2 scores revealed the same shift around 1977/1978, but a shift also seemed to occur around 1988–1989 (Figs. S7, S8). PC 1 and PC2 score time series patterns for all seasons combined showed the same time shifts (Fig. S9).

3.4. Dynamic factor analysis

The best models for oyster condition indices in Willapa Bay during the upwelling and downwelling seasons were one-trend models (Fig. 6, Table S1). The best model for the upwelling season included shared (equal) observation variances across the four time-series and support for heavy-tailed deviations (Student-t distribution) of the latent trend and a fixed trend variance. The best model for the downwelling season was the same as the upwelling season model except that it included support for unique (unequal) observation variances across time-series (Table S1). The estimated trends demonstrate potential shifts in oyster condition around 1980 and 2000 (Fig. 6, Table S1), and oyster condition time series from all four sites loaded strongly and negatively on the trends (Fig. 7, Table S1). The direction of the loadings indicates that there was an increase in oyster condition prior to 1980 and after 2000 and a decrease in oyster condition between 1980 and 2000. Evidence of these shifts in the trends is supported by our regime detection analysis, which demonstrated that two-state models best described the latent trends for the upwelling and downwelling seasons, based on the LOO-CV (upwelling season: one-state = 401.1, two-state = 7.8, three-state = 24.9; downwelling season: one-state = 450.8, two-state =5.7, three-state = 16.7, Fig. 8). The shifts coincide with switches between negative (cold) and positive (warm) PDO regimes in the northeast Pacific. However, in comparing models of oyster condition with and without climate covariates, we found that models without climate predictors outperformed models that included covariates (Table S1). This indicates that there is only a weak correlation between CI and the PDO and upwelling indices at the seasonal timescale.

3.5. Correlations between CI long-term variability and environmental variables

Relationships between CI and PDO/UI varied by season (Fig. 9). PDO and UI exhibited no changing relationships with CI during downwelling, winter and spring seasons. Both PDO and UI correlated with CI during upwelling, summer and autumn seasons. PDO values increased in in the opposite direction to CI while UI increased in the same direction.

Results of least squares linear regression analysis confirm these relationships between CI and environmental covariates. In the case with all-seasons combined, UI had significant effects on the dominant CI trend (PC1 score time series) ($p < 0.0001$ and $R^2 = 0.22, 0.24$, Table 2). Adding PDO only slightly enhanced model performance ($R^2 = 0.23$). In individual seasons, PDO and UI effects together explained most of the variance in CI during upwelling and summer seasons ($p = 0.004$ and 0.01) and $R^2 = 0.18$ and 0.16, respectively). During the upwelling season, the PDO effect was slightly higher than UI ($R^2 = 0.13$ vs 0.08). Finally, there was also a weak correlation between the PDO and CI in autumn ($R^2 = 0.08$, $p = 0.03$).

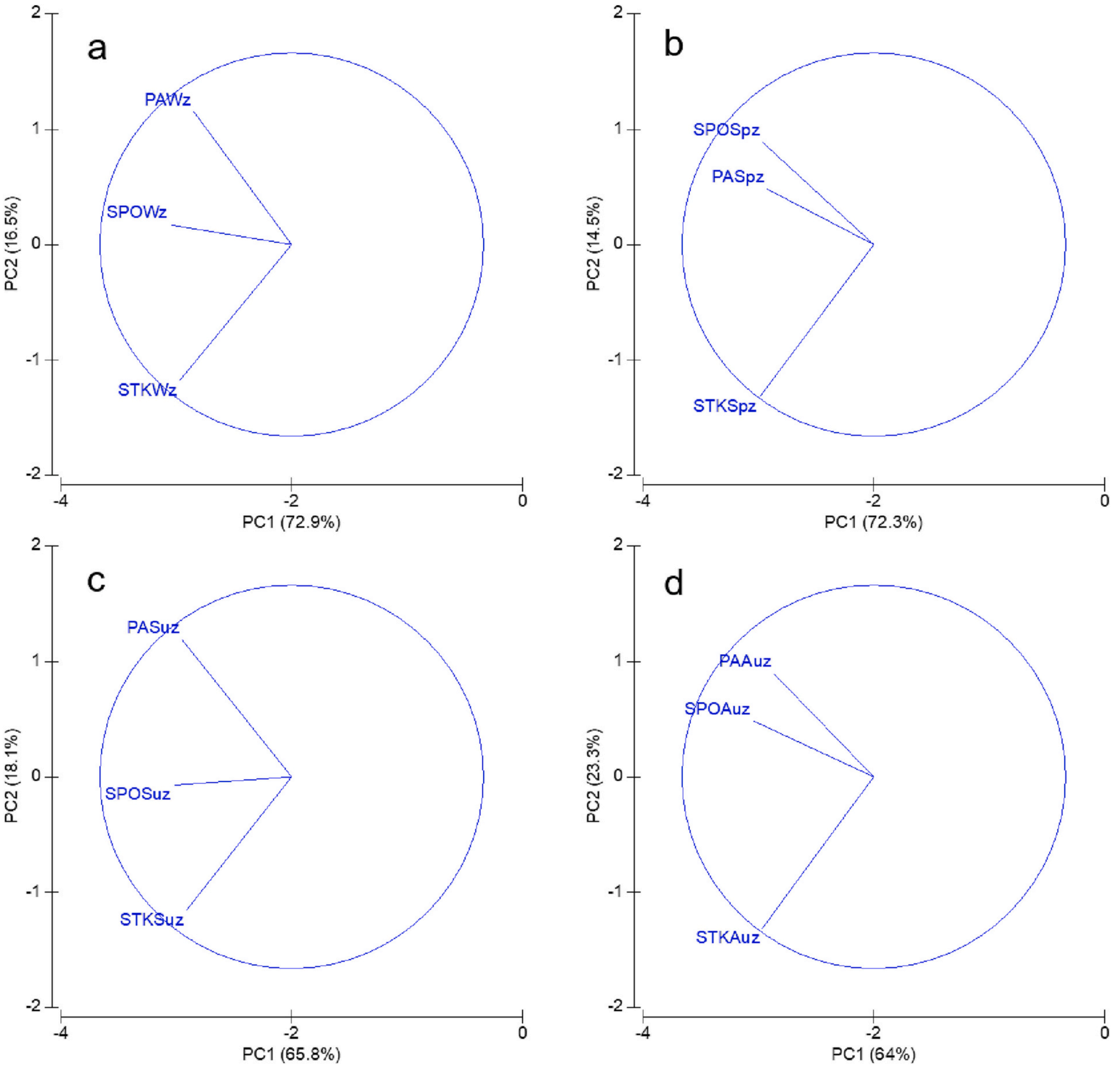


Fig. 4. Eigenvector patterns derived from Principal Component Analysis (PCA) of the CI time series at three sites, PA, STK, and SPO in: (a) winter (W), (b) spring (Sp), (c) summer (Su) and (d) autumn (Au), respectively.

3.6. *Comparisons between PCA and DFA*

Upwelling season PC1 scores time series correlated significantly with DFA derived mean trend values during the same time period ($R^2 = 0.86$, $p < 0.0001$). The same correlation result was found for downwelling season which indicates that both methods capture the dominant CI variation pattern.

Although PDO and UI as covariates did not produce the best model compared to models without them, least squares regression analysis found the most dominant trend value series (DFA) during upwelling season was significantly but weakly correlated with CI ($R^2 = 0.08$, $p < 0.03$) and with UI ($R^2 = 0.15$, $p < 0.002$). However, there was no significant correlation with either variable during the downwelling season. These results match those for correlations between CI and PC scores (Table 2).

4. Discussion

An analysis of the almost seven- decade long record of oyster condition index measured at four locations in Willapa Bay revealed consistent trends across sampling locations where 50–70% of the variability in CI was explained by a single component. Further analysis of two long-term indices of climate revealed that this component of variability in CI was related most strongly to variability in upwelling (UI) which correlated positively with CI during summer or during the upwelling period, while the relationship to the broader basin-wide PDO index was weaker and negative at the same time. Shifts in the long-term record occurred in 1977/78 and 1999/2000 with another possible shift related to the second component of variation occurring in 1988/1989. The change in 1977/78 has been previously identified and corresponds with a cold to warm phase shift in the basin scale PDO, but the more recent shift appears to be corelated with more local fluctuations in both temperature and upwelling intensity.

4.1. *Seasonal dynamics*

The seasonal cycle of CI we observed for *C. gigas* in Willapa Bay averaged across years was consistent with that widely documented for these bivalves and generally attributed to resource allocation with an increasing amount of energy devoted to reproduction during spring and

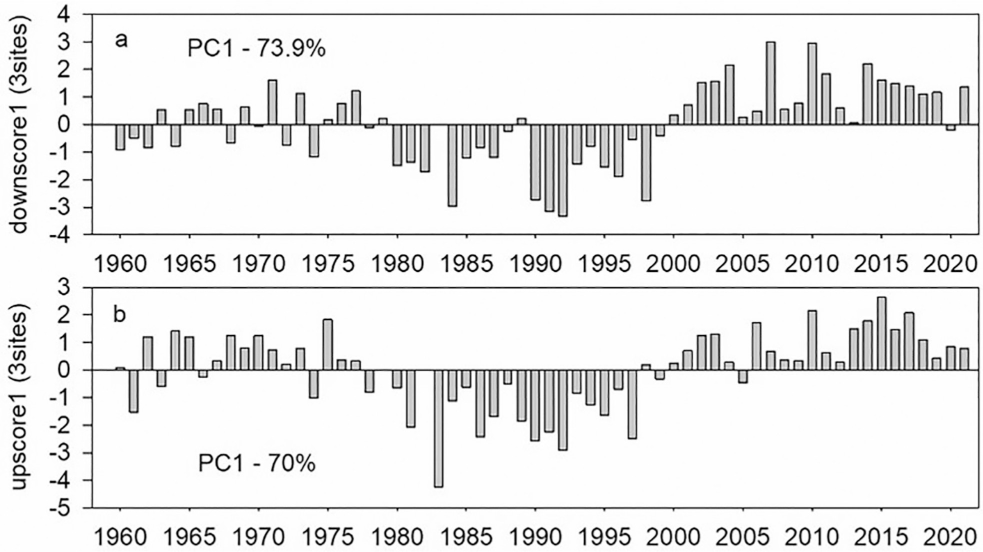
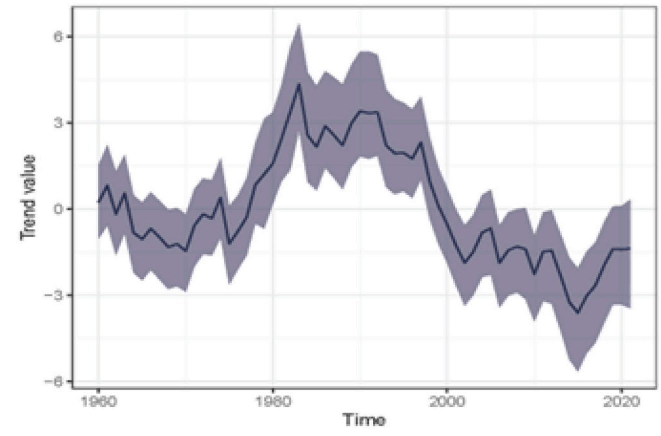


Fig. 5. Time series of PC1 scores showing the most dominant common trend pattern across three sites, PA, STK and SPO in (a) downwelling and (b) upwelling season. The fractions of overall variance explained by PC1 are shown.

a) Upwelling



b) Downwelling

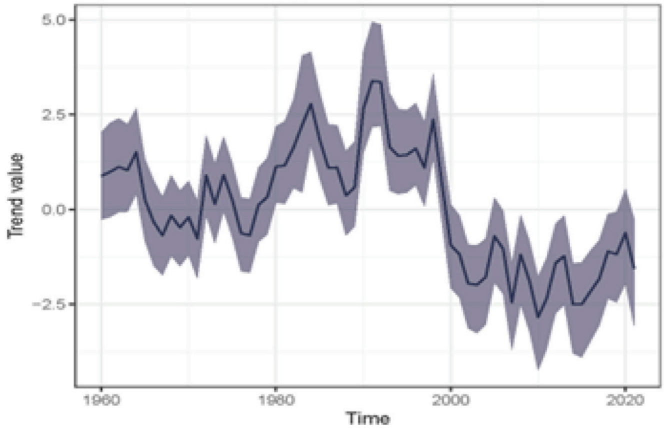


Fig. 6. Shared trend with 95% credible intervals of oyster condition variability during a) the upwelling period (May–September) and b) downwelling season (October–April) between 1960 and 2021.

summer, and subsequent decrease when gametes are spawned or partially spawned and later resorbed in the fall and winter (Grant, 1996; Royer et al., 2008; Steele and Mulcahy, 1999). This seasonal dynamic has been widely studied and modeled for both *C. virginica* (Abbe and Albright, 2003; Austin et al., 1993; Galtsoff, 1964; Medcof and Needler, 1941; Rainer and Mann, 1992; Rheault and Rice, 1996; Soniat et al., 1989) and *C. gigas* (Chavez-Villalba et al., 2003; Enriquez-Diaz et al., 2009; Kang et al., 2000; Mason and Nell, 1995; Ubertini et al., 2017).

4.2. Estuarine gradient and ocean influence in Willapa Bay

CI was higher at the three sites (Stackpole, Oysterville, and Stony Point) located closer to the mouth of Willapa Bay than at Parcel A, a site closer to the southern end of the estuary and just south of the feature recognized by shellfish growers as the “fattening line” (Chapman and Esveldt, 1943; Hedgepeth and Obrebski, 1981) where there was a greater drop in CI during summer, presumably due to spawning events. Shellfish growers traditionally plant small oysters or seed south of this line and then transplant them to areas north of the line after they reach market size to increase meat weight and avoid this spawning affect. This within estuary variation has also been previously documented elsewhere and related to environmental parameters like temperature, salinity and both quantity and quality of food (phytoplankton or chlorophyll) that influence growth and reproduction (Brown and Hartwick, 1988; Dutertre et al., 2009; Gasmi et al., 2017). Temperature and available food are likely the most important factors influencing oyster condition in Willapa Bay during summer months as well, with the intrusion of upwelled nearshore oceanic water into this estuary especially during relaxation events. This has been shown to result in a north to south gradient in temperature, chlorophyll *a* (Chla), phytoplankton production and phytoplankton species composition with colder but phytoplankton rich waters occurring near the estuary mouth (Newton and Horner, 2003; Roegner et al., 2002; Ruesink et al., 2003). Banas et al. (2007) used an oceanographic model to demonstrate that water residence time was much shorter north of a line stretching across the middle of the estuary, such that oysters grown north of this line regularly experienced these intrusions of oceanic phytoplankton while oysters grown south of the line did not. This model also suggested that oysters distributed farther from the mouth would potentially be subject to drawdowns of this food source by oysters and other benthic grazers distributed north of the line.

Seawater temperatures are also typically higher south of this line,

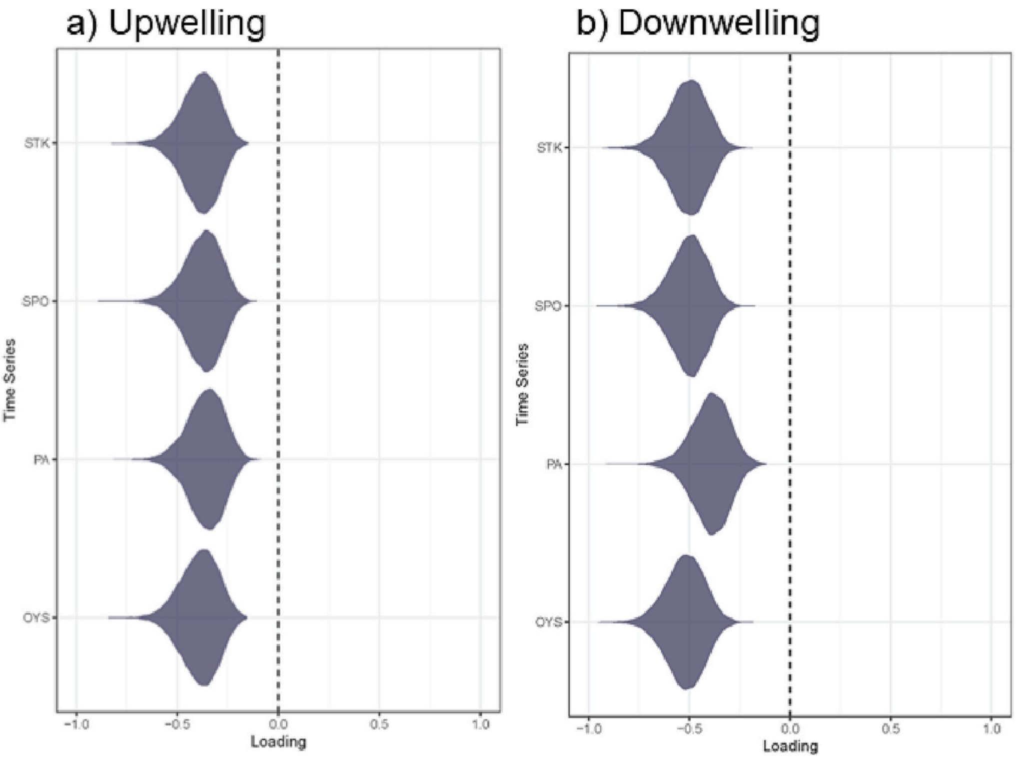


Fig. 7. Posterior distributions for loadings on all four time-series associated with the oyster condition index trend for (a) the upwelling season (May–September) and (b) the downwelling season (October–April).

oysters are more likely to spawn during summer months resulting in lower condition for several months thereafter. This gradient and effect is perhaps most evident in similar oyster condition data collected for a shorter period (1968–1978), but at a broader array of locations in Willapa Bay, that demonstrate a consistent drop in CI at several locations south of this fattening line including Parcel A (Dumbauld et al., 2021). Nonetheless, CI can also vary at smaller spatial scales as evidenced by results of a reciprocal transplant experiment where greatest CI was observed for oysters transplanted well away from the estuary mouth, but at a location along the Willapa River where Chla values were higher (Schumacker, 1999). Oyster growth and condition have also been shown to be influenced by the tidal gradient and local estuarine hydrography which can move the same parcel of water over adjacent oysters and other benthic filter feeders repeatedly and thus deplete the concentration of phytoplankton on shorter temporal scales (Wheat and Ruesink, 2013; Wheat et al., 2019).

4.3. Interannual variation and relationships with ocean climate

Despite the consistent difference in average CI by location, our results also confirm a coherent long-term pattern in oyster CI at all of the sampling locations in Willapa Bay with the majority of this interannual variation explained by a single component. The best fitting DFA models also resulted in a single trend using data from all four locations. The results of both analyses were generally the same when data was separated by either calendar or upwelling/downwelling seasons yet the principal component of variation was only weakly related to the basin scale PDO or the more local upwelling index that we chose to represent ocean climate (positive with upwelling in summer and negative with PDO in autumn). Only weak correlations between this principal component and these ocean climate indices were found in a subsequent regression model, but the positive relationship with UI was most consistent. The DFA also suggests that correlations between CI and the climate indices are weak; models without climate covariates outperformed models that included PDO or UI. Previous researchers investigating this long-term record for CI have also documented significant but weak relationships with ocean climate. Schoener and Tufts (1987) examined the first 30 years of this data (1955–1985) and found a significant inverse relationship between sea level height, and CI with a phase lag and changes in sea level height preceding those in CI by several months. While they documented the lowest condition index on record to that point in time corresponding with a warm 1982–1983 El Niño and a break in the CI record in 1978 with lower CI values corresponding with generally warmer ocean temperatures thereafter, they did not find a direct relationship between CI and sea surface temperature. Instead, they speculated that extreme temperatures experienced during this ENSO event and the changes in sea level height resulted in lower CI because the water and therefore phytoplankton present along the coast were affected by these conditions. Hare and Mantua (2000) assembled a diverse set of climate and biological time series including CI from 1965 to 1997 to explore empirical evidence for common regime shifts after the 1989 climate event in the broader North Pacific ecosystem. They found that several of the biological variables including CI had large loadings on a single variance component consistent with that for sea surface temperature in the eastern North Pacific and a break in the CI record post-1977 which was consistent with the large basin scale regime shift and summertime west coast warming that they and others had previously documented. Oyster condition was the only non-salmon biological record of change for the northern California Current ecosystem examined in an evaluation of relationships between regional ecological processes and the PDO and North Pacific Gyre Oscillation (Litzow et al., 2020). These authors found a recent widespread weakening of these relationship including that for CI after 1988/89 suggesting that these correlative relationships to indices with fixed statistical values are not stable and that more mechanistic models are necessary to make predictions.

The 1978 shift in CI that corresponds with and has been previously linked most closely to the basin-scale ocean climate (PDO) index was

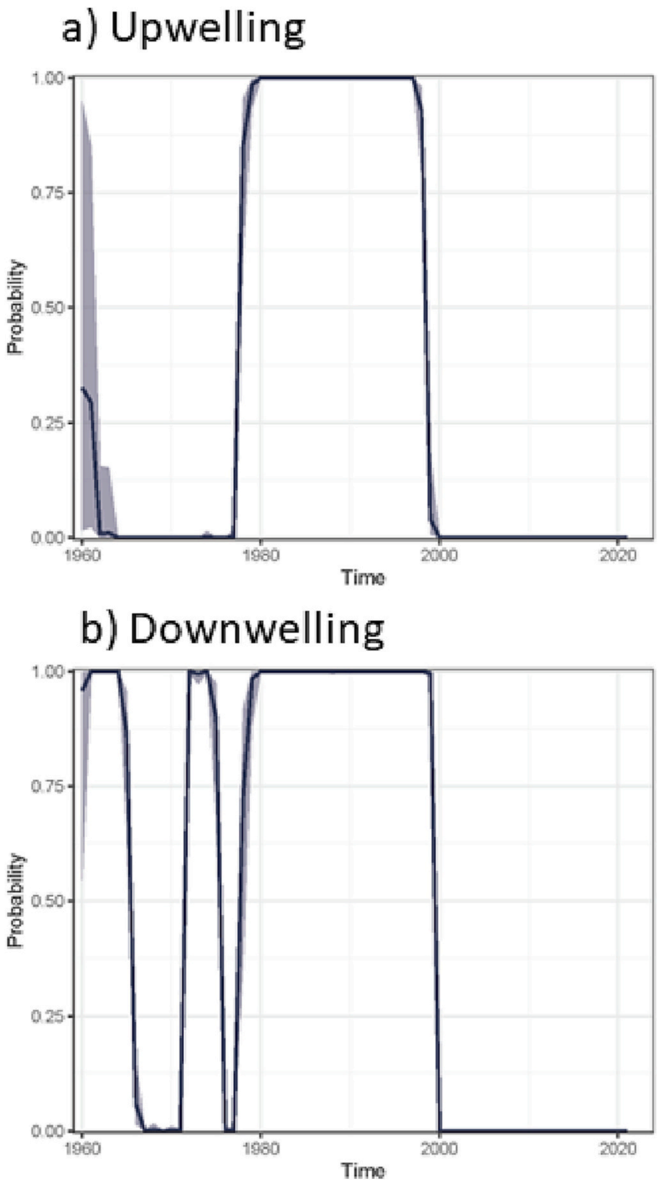


Fig. 8. Results of Hidden Markov Models (HMM) showing state probability for latent trends in the oyster condition indices during the A) upwelling season (May–September) and B) downwelling season (October–April) between 1960 and 2021. The best model invoked two states or regimes, and the median probability (and 95% credible intervals) of being in one state versus the other is shown.

again evident in our analyses. While we also observed a shift in average CI and an anomalous positive CI anomaly in 1989, we document a second more dramatic shift in the standardized CI anomaly in 1999 with greater CI and similar trends occurring at all locations thereafter. Association of values after this shift with the PDO are less certain and perhaps related to the weak but variable relationship we observed with local nearshore oceanography (UI). The PDO has recently also been correlated to phytoplankton community structure in the nearshore coastal ocean (Du et al., 2015) and in San Francisco Bay (Cloern et al., 2007) with cool PDO phases associated with a diatom rich community and warm phase communities with increased diversity and abundance of dinoflagellates. These authors have shown apparent phytoplankton community and species level responses to the local physical environment during recent marine heatwaves, and yet also found that the Chla signature and overall phytoplankton biomass remained high despite this temperature shift (Bond et al., 2015; Du and Peterson, 2018; Peterson et al., 2017). The heatwaves have also been linked to harmful algal blooms coastwide (McCabe et al., 2016). This enhanced food supply could at least in part explain the recent increase in CI values beginning in 2000 and the breakdown we observed in the relationship between the PDO anomaly and oyster condition at this point in time.

These shifts in CI could also represent similar shifts in the seasonal gametogenic cycle and spawning events, since multiple triggers including temperature, but also food and even disturbance events, can be associated with the latter (Dutertre et al., 2009; Ubertini et al., 2017). A preliminary re-examination of the seasonal CI record during the three periods identified in our analyses, suggests that peak condition occurred in July at both STK and PA during cool PDO years prior to 1978 (Fig. S10). The seasonal cycle and peak in condition became less defined but occurred later at STK closer to the estuary mouth thereafter, with distinctly higher average CI values occurring across seasons at this location, especially after 1998. The lack of a distinct peak could reflect the recent use of triploid oysters on beds where they were sampled at STK which may still develop gonads, but generally do not spawn and devote more energy to somatic tissues (Allen and Downing, 1986; Normand et al., 2008). Peak CI was instead progressively earlier occurring in June from 1978 to 1997 and in May after 1998 at PA where only diploid oysters would have been sampled. While the seasonal pattern in UI was consistent across time periods, the seasonal pattern in PDO differed dramatically, especially after 1998 (Fig. S10). A 1999 shift in climate has been previously associated with seasonal changes in biological communities in San Francisco Bay (Cloern et al., 2010; Cloern and Jassby, 2012) and could be linked to the oyster gametogenic cycle with cooler temperatures promoting autumn phytoplankton blooms when oysters would be expected to recover from spawning and/or resorb gametes. Similar long-term records collected along the coast of Europe showed that Pacific oyster spawning and mortality were more closely linked to Chla and phytoplankton abundance than to seawater temperature, yet timing of seasonal spikes in temperature could trigger gametogenesis (Gourault et al., 2019; Thomas et al., 2016). Researchers there documented a significant but lagged relationship between values of the North Atlantic Oscillation and oyster mortality two months thereafter. A closer evaluation of these seasonal shifts in timing of the gametogenic cycle with a focus on temperature and available phytoplankton may lead to a more mechanistic explanation for these multidecade shifts in CI along the US west coast. While the shellfish growers have long been aware of and adapted their practices to take advantage of within estuary spatial gradients and seasonal patterns in oyster growth and condition, understanding the factors driving these larger scale shifts will continue to be useful especially in the face of ongoing climate change. This could allow for adaptation and strategies to mitigate the effects of more frequent marine climate anomalies and potential shifts in condition which have also been linked to stressful conditions and summer mortality events.

5. Conclusion

Two important shifts were identified in the multi-decade record of Pacific oyster (*Crassostrea gigas*) condition index (CI) measured at four locations in Willapa Bay, an estuary that contributes a substantial portion of US West Coast oyster aquaculture production. The first shift from higher to lower condition occurred in 1977–1978 and had been previously correlated with the Pacific Decadal Oscillation, a basin scale change in ocean temperature and climate. A second shift from lower to higher condition in 1999–2000 appears to be correlated with fluctuations in ocean climate as well, since 50–70% of the interannual variability in CI could be explained by a single component that was related most strongly to variability in the local upwelling index. Oyster condition was highest at locations closest to the estuary mouth, a pattern long recognized by oyster growers and recently tied to estuarine hydrodynamics and water residence time. The multidecade scale shifts in CI may also be linked to changes in the seasonal seawater temperature cycle and

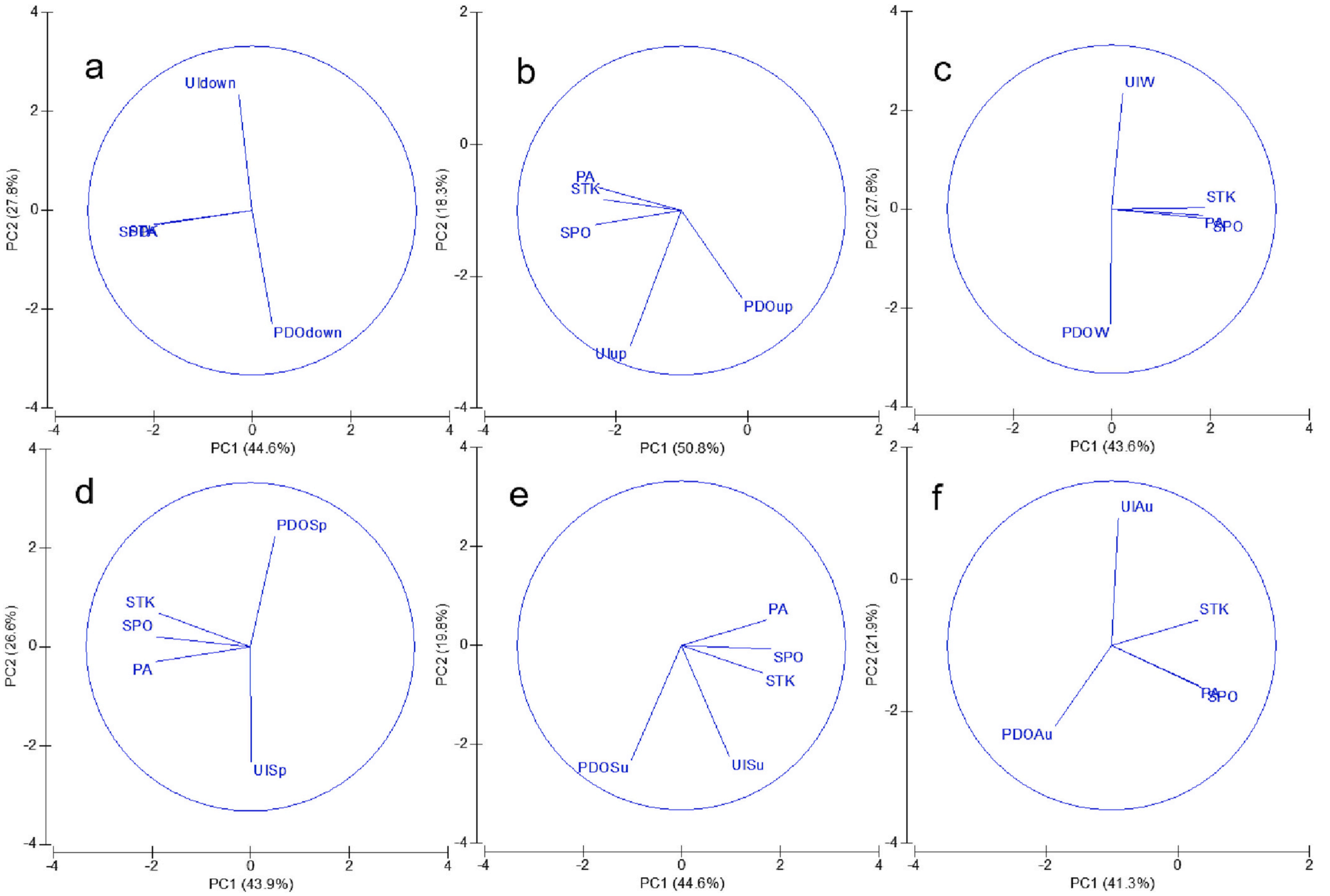


Fig. 9. Eigenvector patterns derived from Principal Component Analysis (PCA) of the CI time series showing relations between CI time series at PA, STK and SP and covariates PDO and UI in (a) upwelling (up), (b) downwelling (down), (c) winter (W), (d) spring (Sp), (e) summer (Su) and (f) autumn (Au).

timing/composition of phytoplankton blooms, both variables that are widely recognized to control the oyster gametogenic cycle and should be further examined.

Table 2
Results of linear regression models correlating PC score1 time series of CI temporal variability with environmental variables (PDO and UI). Interaction terms were removed in all models because they were insignificant so only additive terms are reported.

Data	Response	Effects	Rsqr	pValue	DF
All-season	PCscore1	PDO	0.02	0.048	234
		UI	0.22	**<0.0001**	234
		PDO,UI	0.23	**<0.0001**	234
Up/down	PCscore1	PDO	0.02	0.09	118
		UI	0.22	**<0.0001**	118
		PDO,UI	0.24	**<0.0001**	118
Winter	PCscore1	PDO	0	0.9	58
		UI	0.01	0.6	58
		PDO,UI	0.01	0.8	58
Spring	PCscore1	PDO	0.01	0.4	57
		UI	0	0.7	57
		PDO + UI	0.02	0.6	57
Summer	PCscore1	PDO	0.07	0.06	52
		UI	0.09	**0.03**	52
		PDO + UI	0.16	**0.01**	52
Autumn	PCscore1	PDO	0.08	**0.03**	59
		UI	0	0.8	59
		PDO + UI	0.08	0.08	59
Upwelling	PCscore1	PDO	0.13	**0.005**	58
		UI	0.08	**0.029**	58
		PDO + UI	0.18	**0.004**	58
Downwelling	PCscore1	PDO	0	0.8	59
		UI	0	0.9	59
		PDO + UI	0	0.9	59

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2023.102383.

References

Abbe, G.R., Albright, B.W., 2003. An improvement to the determination of meat condition index for the eastern oyster, *Crassostrea virginica* (Gmelin 1791). J. Shellfish Res. 22, 747–752.

Allen, S.K., Downing, S.L., 1986. Performance of triploid Pacific oysters, *Crassostrea gigas* (Thunberg).1. Survival, growth, glycogen-content, and sexual-maturation in yearlings. J. Exp. Mar. Biol. Ecol. 102, 197–208.

Austin, H., Haven, D.S., Moustafa, M.S., 1993. The relationship between trends in a condition index of the American oyster, *Crassostrea virginica*, and environmental parameters in three Virginia estuaries. Estuaries 16, 362–374.

Banas, N.S., Hickey, B.M., MacCready, P., Newton, J.A., 2004. Dynamics of Willapa Bay, Washington: a highly unsteady, partially mixed estuary. J. Phys. Oceanogr. 34, 2413–2427.

Banas, N.S., Hickey, B.M., Newton, J.A., Ruesink, J.L., 2007. Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. Mar. Ecol. Prog. Ser. 341, 123–139.

Bayne, B.L., Ahrens, M., Allen, S.K., D'auriac, M.A., Backeljau, T., Beninger, P., Bohn, R., Boudry, P., Davis, J., Green, T., Guo, X., Hedgecock, D., Ibarra, A., Kingsley-Smith, P., Krause, M., Langdon, C., Lapègue, S., Li, C., Manahan, D., Mann, R., Perez-Paralle, L., Powell, E.N., Rawson, P.D., Speiser, D., Sanchez, J.-L., Shumway, S., Wang, H., 2017. The proposed dropping of the genus *Crassostrea* for all pacific cupped oysters and its replacement by a new genus, *Magallana*, a dissenting view. J. Shellfish Res. 36, 545–547.

Bayne, B., Anglès d'Auriac, M., Backeljau, T., Beninger, P., Boudry, P., Carnegie, R., Davis, J., Guo, X., Hedgecock, D., Krause, M., Langdon, C., Lapègue, S., Manahan, D., Mann, R., Powell, E., Shumway, S., 2019. A scientific name for Pacific oysters. Aquaculture 499, 373.

Bernard, I., de Kermoysan, G., Pouvreau, S., 2011. Effect of phytoplankton and temperature on the reproduction of the Pacific oyster *Crassostrea gigas:* investigation through DEB theory. J. Sea Res. 66, 349–360.

Bond, N.A., Cronin, M.F., Freeland, H., Mantua, N., 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett. 42, 3414–3420.

Brown, J.R., 1988. Multivariate analyses of the role of environmental factors in seasonal and site-related growth variation in the Pacific oyster *Crassostrea gigas*. Mar. Ecol. Prog. Ser. 454, 225–236.

Brown, J.R., Hartwick, E.B., 1988. Influences of temperature, salinity and available food upon suspended culture of the Pacific oyster, *Crassostrea-gigas*. 2. Condition index and survival. Aquaculture 70, 253–267.

Burkner, P.C., Gabry, J., Vehtari, A., 2020. Approximate leave-future-out cross-validation for Bayesian time series models. J. Stat. Comput. Simul. 90, 2499–2523.

Chapman, W.M., Esveldt, G.D., 1943. The Spawning and Setting of the Pacific Oyster (*Ostrea Gigas* Thunberg) in the State of Washington in 1942. Washington Department Fisheries, Biological Report, Seattle, WA, pp. 1–61.

Chavez-Villalba, J., Cochard, J.-C., le Pennece, M., Barret, J., Enriquez-Diaz, M., Caceres-Martinez, C., 2003. Effects of temperature and feeding regimes on gametogenesis and larval production in the oyster, *Crassostrea gigas*. J. Shellfish Res. 22, 721–732.

Chew, K.K., 1984. Recent advances in the cultivation of molluscs in the Pacific United States and Canada. Aquaculture 39, 69–81.

Clark, J.E., Langmo, R.D., 1979. Oyster seed hatcheries on the United-States west-coast - an overview. Mar. Fish. Rev. 41, 10–16.

Clarke, K.R., Gorley, R.N., 2006. Primer v.6 :User Manual/Tutorial. PRIMER-E Ltd., Plymouth, England.

Cloern, J.E., Jassby, A.D., 2012. Drivers of change in estuarine-coastal ecosystems: discoveries from four decades of study in San Francisco Bay. Rev. Geophys. 50, 1–30.

Cloern, J.E., Jassby, A.D., Thompson, J.K., Hieb, K.A., 2007. A cold phase of the East Pacific triggers new phytoplankton blooms in San Francisco Bay. Proc. Natl. Acad. Sci. U. S. A. 104, 18561–18565.

Cloern, J.E., Hieb, K.A., Jacobson, T., Sanso, B., Di Lorenzo, E., Stacey, M.T., Largier, J.L., Meiring, W., Peterson, W.T., Powell, T.M., Winder, M., Jassby, A.D., 2010. Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific. Geophys. Res. Lett. 37, L21602.

Costil, K., Royer, J., Ropert, M., Soletchnik, P., Mathieu, M., 2005. Spatio-temporal variations in biological performances and summer mortality of the Pacific oyster *Crassostrea gigas* in Normandy (France). Helgol. Mar. Res. 59, 286–300.

Crosby, M.P., Gale, L.D., 1990. A review and evaluation of bivalve condition index methodologies with a suggested standard method. J. Shellfish Res. 9, 233–237.

Du, X., Peterson, W.T., 2018. Phytoplankton community structure in 2011-2013 compared to the extratropical warming event of 2014-2015. Geophys. Res. Lett. 45, 1534–1540.

Du, X.N., Peterson, W., O'Higgins, L., 2015. Interannual variations in phytoplankton community structure in the northern California current during the upwelling seasons of 2001-2010. Mar. Ecol. Prog. Ser. 519, 75–87.

Dumbauld, B.R., McCoy, L.M., 2015. The effect of oyster aquaculture on seagrass (*Zostera marina*) at the estuarine landscape scale in Willapa Bay, Washington (USA). Aquacult. Environ. Interact. 7, 29–47.

Dumbauld, B.R., Ruesink, J.L., Trimble, A.C., Kauffman, B.E., 2011. The Willapa Bay oyster reserves in Washington state: fishery collapse, creating a sustainable replacement, and the potential for habitat conservation and restoration. J. Shellfish Res. 30, 71–83.

Dumbauld, B.R., Ruesink, J.L., Trimble, A.C., Forster, Z., 2021. The Influence of climate and environment on the spawning, condition, and larval set of naturalized Pacific Oysters *Crassostrea gigas* in a U.S. West Coast estuary. In: Jabanoski, C.O.K., Sturm, E., Rust, M. (Eds.), Marine Aquaculture in a Changing Environment: Proceedings of the 46th U.S.-Japan Aquaculture Panel Symposium, Mystic, CT, November 14–15, 2018. National Oceanic and Atmospheric Administration, Washington, D.C, pp. 34–48.

Dutertre, M., Beninger, P.G., Barille, L., Papin, M., Rosa, P., Barille, A.L., Haure, J., 2009. Temperature and seston quantity and quality effects on field reproduction of farmed oysters, *Crassostrea gigas,* in Bourgneuf Bay, France. Aquat. Living Resour. 22, 319–329.

Ebbesmeyer, C.C., Strickland, R.M., 1995. Oyster condition and climate: Evidence from Willapa Bay. In: 5th Conference for Shellfish Growers, Washington Sea Grant, p. 10.

Edwards, M., Beaugrand, G., Hays, G.C., Koslow, J.A., Richardson, A.J., 2010. Multi-decadal oceanic ecological datasets and their application in marine policy and management. Trends Ecol. Evol. 25, 602–610.

Enriquez-Diaz, M., Pouvreau, S., Chavez-Villalba, J., Le Pennec, M., 2009. Gametogenesis, reproductive investment, and spawning behavior of the Pacific giant oyster *Crassostrea gigas*: evidence of an environment-dependent strategy. Aquac. Int. 17, 491–506.

Galtsoff, P.S., 1964. The American oyster *Crassostrea virginica* Gmelin. Fish. Bull. 64, 1–480.

Gasmi, S., Bernard, I., Pouvreau, S., Maurer, D., Schaal, G., Ganthy, F., Cominassi, L., Allain, G., Sautour, B., David, V., 2017. Spatial patterns in the condition index of the wild Pacific oyster *Crassostrea gigas* in a macrotidal coastal ecosystem: influence of tidal processes and beyond. J. Sea Res. 119, 28–36.

Gourault, M., Petton, S., Thomas, Y., Pecquerie, L., Marques, G.M., Cassou, C., Fleury, E., Paulet, Y.-M., Pouvreau, S., 2019. Modeling reproductive traits of an invasive bivalve species under contrasting climate scenarios from 1960 to 2100. J. Sea Res. 143, 128–139.

Grant, J., 1996. The relationship of bioenergetics and the environment to the field growth of cultured bivalves. J. Exp. Mar. Biol. Ecol. 200, 239–256.

Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47, 103–145.

Hedgepeth, J., Obrebski, S., 1981. Willapa Bay: A Historical Perspective and a Rationale for Research, U.S. Fish and Wildlife Service. Office of Biological Services, Washington, D.C, p. 52.

Helmuth, B., Broitman, B.R., Blanchette, C.A., Gilman, S., Halpin, P., Harley, C.D.G., O'Donnell, M.J., Hofmann, G.E., Menge, B., Strickland, D., 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. Ecol. Monogr. 76, 461–479.

Hickey, B.M., Banas, N.S., 2003. Oceanography of the US Pacific northwest coastal ocean and estuaries with application to coastal ecology. Estuaries 26, 1010–1031.

Hickey, B.M., Zhang, X., Banas, N., 2002. Coupling between the California current system and a coastal plain estuary in low riverflow conditions. J. Geophys. Res. Oceans 107.

Holmes, F.F., Ward, E.J., Scheuerell, M.D., 2018. Analysis of Multivariate Time Series Using the MARSS Package. NOAA Northwest Fisheries Science Center, Seattle.

Hunsicker, M.E., Ward, E.J., Litzow, M.A., Anderson, S.C., Harvey, C.J., Field, J.C., Gao, J., Jacox, M.G., Melin, S.R., Thompson, A.R., Warzybok, P., 2022. Tracking and forecasting community responses to climate perturbations in the California current ecosystem. PLOS Climate 1 (3), e0000014.

Im, K.H., Johnston, R.S., Langmo, R.D., 1976. The economics of hatchery production of Pacific oyster seed: a research progress report. In: Proceedings of the National Shellfisheries Association, 66, pp. 81–94.

Jones, P.D., Hulme, M., 1996. Calculating regional climatic time series for temperature and precipitation: methods and illustrations. Int. J. Climatol. 16, 361–377.

Kang, C.-K., Park, M.S., Lee, P.-Y., Choi, W.-J., Lee, W.-C., 2000. Seasonal variations in condition, reproductive activity, and biochemical composition of the Pacific oyster, *Crassostrea gigas* (Thunberg), in suspended culture in two coastal bays of Korea. J. Shellfish Res. 19, 771–778.

King, N.G., Wilmes, S.B., Smyth, D., Tinker, J., Robins, P.E., Thorpe, J., Jones, L., Malham, S.K., 2021. Climate change accelerates range expansion of the invasive non-native species, the Pacific oyster, *Crassostrea gigas*. ICES J. Mar. Sci. 78, 70–81.

Lawrence, D.R., Scott, G.I., 1982. The determination and use of condition index of oysters. Estuaries 5, 23–27.

Lindsay, C.E., Simons, D., 1997. The fisheries for Olympia oysters, Ostreola conchaphila; Pacific oysters, Crassostrea gigas; and Pacific razor clams, Siliqua patula, in the State of Washington. In: Mackenzie, C.L.J., Burrell, V.G.J., Rosenfield, A., Hobart, W.L. (Eds.), The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe. Vol. 2, Pacific Coast and Supplemental Topics. NOAA, U.S. Dept. Commerce, Seattle, WA, pp. 89–113.

Lindsay, C., Westley, R.E., Sayce, C.S., 1959. Prediction of oyster setting in the state of Washington. In: Proceedings of the National Shellfisheries Association, 49, pp. 59–70.

Litzow, M.A., Hunsicker, M.E., Bond, N.A., Burke, B.J., Cunningham, C.J., Gosselin, J.L., Norton, E.L., Ward, E.J., Zador, S.G., 2020. The changing physical and ecological meanings of North Pacific Ocean climate indices. Proc. Natl. Acad. Sci. 117, 7665–7671.

Macias, D., Landry, M.R., Gershunov, A., Miller, A.J., Franks, P.J.S., 2012. Climatic control of upwelling variability along the Western north-American coast. PLoS One 7.

Mason, C.J., Nell, J.A., 1995. Condition index and chemical-composition of meats of Sydney rock oysters (*Saccostrea-commercialis*) and Pacific oysters (*Crassostrea-gigas*) at 4 sites in port-Stephens, NSW. Mar. Freshw. Res. 46, 873–881.

McCabe, R.M., Hickey, B.M., Kudela, R.M., Lefebvre, K.A., Adams, N.G., Bill, B.D., Gulland, F.M.D., Thomson, R.E., Cochlan, W.P., Trainer, V.L., 2016. An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. Geophys. Res. Lett. 43, 10,366-310,376.

Medcof, J.C., Needler, A.W.H., 1941. The influence of temperature and salinity on the condition of oysters (*O. virginica*). J. Fish. Res. Board Can. 5, 253–257.

Menge, B.A., Gouhier, T.C., Freidenburg, T., Lubchenco, J., 2011. Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: toward explaining “unexplained” variation. J. Exp. Mar. Biol. Ecol. 400, 236–249.

Minchin, D., 2007. Aquaculture and transport in a changing environment: overlap and links in the spread of alien biota. Mar. Pollut. Bull. 55, 302–313.

Moore, P.J., Thompson, R.C., Hawkins, S.J., 2011. Phenological changes in intertidal con-specific gastropods in response to climate warming. Glob. Chang. Biol. 17, 709–719.

Newman, M., Compo, G.P., Alexander, M.A., 2003. ENSO-forced variability of the Pacific decadal oscillation. J. Clim. 16, 3853–3857.

Newton, J.A., Horner, R.A., 2003. Use of phytoplankton species indicators to track the origin of phytoplankton blooms in Willapa Bay, Washington. Estuaries 26, 1071–1078.

Normand, J., Le Pennec, M., Boudry, P., 2008. Comparative histological study of gametogenesis in diploid and triploid Pacific oysters (*Crassostrea gigas*) reared in an estuarine farming site in France during the 2003 heatwave. Aquaculture 282, 124–129.

Nosho, T.Y., Chew, K.K., 1991. Remote Setting and Nursery Culture for Shellfish Growers. Washington Sea Grant, Seattle, Washington, p. 68.

Packer, J.F., Mathews, S.B., 1980. Vertical Movement Behavior, Growth, and Prediction of Spatfall for Pacific Oyster Larvae in Dabob Bay. State of Washington Department of Fisheries, Olympia, Washington, p. 80.

Peterson, W.T., Fisher, J.L., Strub, P.T., Du, X.N., Risien, C., Peterson, J., Shaw, C.T., 2017. The pelagic ecosystem in the northern California current off Oregon during the 2014-2016 warm anomalies within the context of the past 20 years. J. Geophys. Res. Oceans 122, 7267–7290.

Quayle, D.B., 1988. Pacific oyster culture in British Columbia. Can. J. Fish. Aquat. Sci. 218, 1–241.

Rainer, J.S., Mann, R., 1992. A comparison of methods for calculating condition index in eastern oysters, *Crassostrea virginica* (Gmelin, 1791). J. Shellfish Res. 11, 55–58.

Rheault, R.B., Rice, M.A., 1996. Food-limited growth and condition index in the eastern oyster, *Crassostrea virginica* (Gmelin 1791), and the bay scallop, *Argopecten irradians irradians* (Lamarck 1819). J. Shellfish Res. 15, 271–283.

Roegner, C.G., Hickey, B.M., Newton, J.A., Shanks, A.L., Armstrong, D.A., 2002. Wind-induced plume and bloom intrusions into Willapa Bay, Washington. Limnol. Oceanogr. 47, 1033–1042.

Royer, J., Seguineau, C., Park, K.-I., Pouvreau, S., Choi, K.-S., Costil, K., 2008. Gametogenetic cycle and reproductive effort assessed by two methods in 3 age classes of Pacific oysters, *Crassostrea gigas,* reared in Normandy. Aquaculture 277, 313–320.

Ruesink, J.L., Roegner, G.C., Dumbauld, B.R., Newton, J.A., Armstrong, D.A., 2003. Contributions of coastal and watershed energy sources to secondary production in a northeastern Pacific estuary. Estuaries 26, 1079–1093.

Ruesink, J.L., Lenihan, H.S., Trimble, A.C., Heiman, K.W., Micheli, F., Byers, J.E., Kay, M.C., 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. Annu. Rev. Ecol. Syst. 36, 643–689.

Ruesink, J.L., Sarich, A., Trimble, A.C., 2018. Similar oyster reproduction across estuarine regions differing in carbonate chemistry. ICES J. Mar. Sci. 75, 340–350.

Sainz, J.F., Di Lorenzo, E., Bell, T.W., Gaines, S., Lenihan, H., Miller, R.J., 2019. Spatial planning of marine aquaculture under climate decadal variability: a case study for mussel farms in Southern California. Front. Mar. Sci. 6.

Schoener, A., Tufts, D.F., 1987. Changes in oyster condition index with El Niño southern oscillation events at 46 degrees north in an eastern Pacific bay. J. Geophys. Res. 92, 429–435.

Schumacker, E.J., 1999. Oyster Condition Index Studies in Willapa Bay, Washington: Methodologies and Relationships with Environmental Variables.. MS thesis, University of Washington, Seattle, WA.

Soniat, T.M., Smith, L.E., Brody, M.S., 1989. Mortality and condition of the American oyster in Galveston Bay, Texas. Contrib. Mar. Sci. 313460, 77–94.

Steele, E.N., 1964. The Immigrant Oyster (Ostrea Gigas) Now Known as the Pacific Oyster. Warren’s Quick Print, Olympia, Washington.

Steele, S., Mulcahy, M.F., 1999. Gametogenesis of the oyster *Crassostrea gigas* in southern Ireland. J. Mar. Biol. Assoc. U. K. 79, 673–686.

Thomas, Y., Pouvreau, S., Alunno-Bruscia, M., Barille, L., Gohin, F., Bryere, P., Gernez, P., 2016. Global change and climate-driven invasion of the Pacific oyster (*Crassostrea gigas*) along European coasts: a bioenergetics modelling approach. J. Biogeogr. 43, 568–579.

Thomas, Y., Cassou, C., Gernez, P., Pouvreau, S., 2018. Oysters as sentinels of climate variability and climate change in coastal ecosystems. Environ. Res. Lett. 13, 104009.

Ubertini, M., Lagarde, F., Mortreux, S., Le Gall, P., Chiantella, C., Fiandrino, A., Bernard, I., Pouvreau, S., d`Orbcastel, E.R., 2017. Gametogenesis, spawning behavior and larval abundance of the Pacific oyster *Crassostrea gigas* in the Thau lagoon: evidence of an environment-dependent strategy. Aquaculture 473, 51–61.

Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. 27, 1413–1432.

Ward, E.J., Anderson, S.C., Damiano, L.A., Hunsicker, M.E., Litzow, M.A., 2019. Modeling regimes with extremes: the bayesdfa package for identifying and forecasting common trends and anomalies in multivariate time-series data. R J. 11, 46–55.

Ward, E.J., Anderson, S.C., Hunsicker, M.E., Litzow, M.A., 2022. Smoothed dynamic factor analysis for identifying trends in multivariate time series. Methods Ecol. Evol. 13, 908–918.

Westley, R.E., 1959. Olympia and Pacific Oyster Condition Factor Data: State of Washington (1954–1958). Washington State Dept. Fisheries State Shellfish Laboratory, Olympia, Washington, p. 9p.

Westley, R.E., 1961. Selection and evaluation of a method for quantitative measurement of oyster condition. In: Proceedings of the National Shellfisheries Association, 50, pp. 145–149.

Westley, R.E., 1964. Some relationships between Pacific oyster (*Crassostrea gigas*) condition and the environment. In: Proceedings of the National Shellfisheries Association, 55, pp. 19–33.

Wheat, E., Ruesink, J.L., 2013. Commercially-cultured oysters (*Crassostrea gigas*) exert top-down control on intertidal pelagic resources in Willapa Bay, Washington, USA. J. Sea Res. 81, 33–39.

Wheat, E.E., Banas, N.S., Ruesink, J.L., 2019. Multi-day water residence time as a mechanism for physical and biological gradients across intertidal flats. Estuar. Coast. Shelf Sci. 227, 106303.

White, J., Ruesink, J.L., Trimble, A.C., 2009. The nearly forgotten oyster: *Ostrea lurida* Carpenter 1864 (Olympia oyster) history and management in Washington state. J. Shellfish Res. 28, 43–49.

Zeng, Y., Yang, H., 2021. Review of molluscan bivalve condition index calculations and application in northern quahogs *Mercenaria mercenaria*. Aquac. Res. 52, 23–36.

Zuur, A.F., Fryer, R.J., Jolliffe, I.T., Dekker, R., Beukema, J.J., 2003. Estimating common trends in multivariate time series using dynamic factor analysis. Environmetrics 14, 665–685.