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Pacific oyster condition and mortality in a U.S. Pacific coast estuary: Can relationships with environment and reproductive state be utilized to sustain future production ?

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Abstract: Pacific oysters (*Magallana* [*Crassostrea*] *gigas*) were introduced to the US Pacific coast beginning in the early 1900’s and have become the predominant cultivated shellfish species contributing substantially to US domestic production. While they were widely transported amongst locations, they only regularly spawned and became “naturalized” in several discrete estuarine locations like Willapa Bay, WA. Though culture methods differ, the US industry, like that in Japan, relied on “natural” set at these locations until the large-scale adoption of shellfish hatcheries in the late 1970’s. A monitoring program was therefore established to examine both larval set and the condition of adult oysters in Willapa Bay during the mid 1950’s and has been maintained since that time. The gametogenic cycle for oysters is relatively well studied and has been previously correlated with environmental triggers like temperature, salinity, and food which influence oyster growth but can also act as stressors and are linked to gametogenesis and summer mortality events. We summarize the results of an investigation into broad decadal temporal scale and Pacific Ocean basin spatial scale environmental forcing factors that influence oyster condition in Willapa Bay. We then, link these to seasonal shifts in oyster condition and reported summer mortality events that have occurred on an annual temporal scale within this estuary, including one such event in 2019 when a joint US-Japan study was being conducted. A comparison with similar observations and environmental data from the Seto Inland Sea in Japan that year suggests that multiple stressors are likely involved and differ by location but the response of oysters to local growing conditions (seagrass presence, on-off bottom culture) was similar. We provide a brief proposal and framework to further examine metabolic or energetic characteristics (glycogen content or anaerobic capacity) that could be used to either breed oysters for resilience to such stressors and/or provide the shellfish industry the ability to adapt to and mitigate for the effects of an uncertain future climate.

Key words: Pacific oysters, condition, reproductive state, mortality

Introduction

Pacific oysters (*Magallana* [*Crassostrea*] *gigas*) were introduced to the US Pacific coast beginning in the early 1900’s and have become the predominant cultivated shellfish species along this coast. Pacific oysters are currently produced by about 175 farms that employ about 2,500 people in often economically depressed coastal communities with harvest valued at more than $149 million annually (United States Department of Agriculture 2024). While these oysters have been widely transported amongst locations, until recently they only regularly spawned and therefore became “naturalized”

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populations at several discrete estuarine locations like Willapa Bay, WA (Lindsay and Simons 1997; McAfee and Connell 2021; Quayle 1988; Ruesink *et al*. 2005; Steele 1964). Though culture methods differ, the US industry relied on imports of seed from Japan or "natural" set at these locations until the large-scale adoption of shellfish hatcheries in the late 1970's (Chapman and Esveldt 1943; Chew 1984; Lindsay *et al*. 1959). A monitoring program was established to examine both larval set and the condition of adult oysters in Willapa Bay beginning in the mid 1950's and has been maintained since that time (Schoener and Tufts 1987; Schumacker 1999; Westley 1961). The gametogenic cycle for oysters is relatively well studied and has been previously correlated with environmental triggers like temperature, salinity, and food which influence oyster growth but can also act as stressors and are linked to gametogenesis and summer mortality events (Cheney *et al*. 2000; Garcia *et al*. 2011; King *et al*. 2021; Perdue *et al*. 1981; Solomieu *et al*. 2015).

We briefly summarize the results of an investigation into broad decadal temporal scale and Pacific Ocean basin spatial scale environmental forcing factors that influence oyster condition in Willapa Bay (Dumbauld *et al*. 2023). We then link these to seasonal shifts in oyster condition and summer mortality events that have occurred on an annual temporal scale within this estuary. This includes a brief summary and some additional results from a study conducted for joint UJNR research in 2019 and comparison with similar observations and environmental data from the Seto Inland Sea in Japan (Hasegawa *et al*. 2021) which suggest that multiple stressors are likely involved and could differ by location. Finally, we provide a brief proposal and framework to further examine metabolic or energetic characteristics (glycogen content or anaerobic capacity) that could be used to either breed oysters for resilience to such stressors and/or provide the shellfish industry the ability to adapt to and mitigate for the effects of an uncertain future marine environment.

Methods

Several different methods have been used to calculate bivalve condition that relate a measure of meat weight (wt) to that of the shell or the volume of the shell cavity. The condition index (CI) of oysters in Willapa Bay was historically measured using the Westley method calculated as: CI = dry body wt x 100 / [(whole wt in air − whole wt in water) – (shell wt in air − shell wt in water)] (all wts recorded in g) from 1954-1998 (Westley 1961). Biologists collected 20 individual adult oysters of similar size (generally about 2 years old, volume = 125 cc.) at each of 4 locations in Willapa Bay on a monthly basis. After a detailed comparison with other methods, it was determined that a less error prone and more widely used gravimetric method where CI = dry meat wt *100 / (whole wet wt – dry shell wt), produced similar and directly related estimates (Lawrence and Scott 1982; Schumacker 1999). This standardized procedure that used individual instead of pooled oyster samples and thus allowed for error estimates about monthly means was adopted in 1998. We present a brief summary of a recent analysis of this long-term data record (1960-2021) which relates CI to basin wide ocean conditions (Dumbauld *et al*. 2023), and evaluate the seasonal pattern of CI comparing the average long-term record with that for years when mass mortality events were documented.

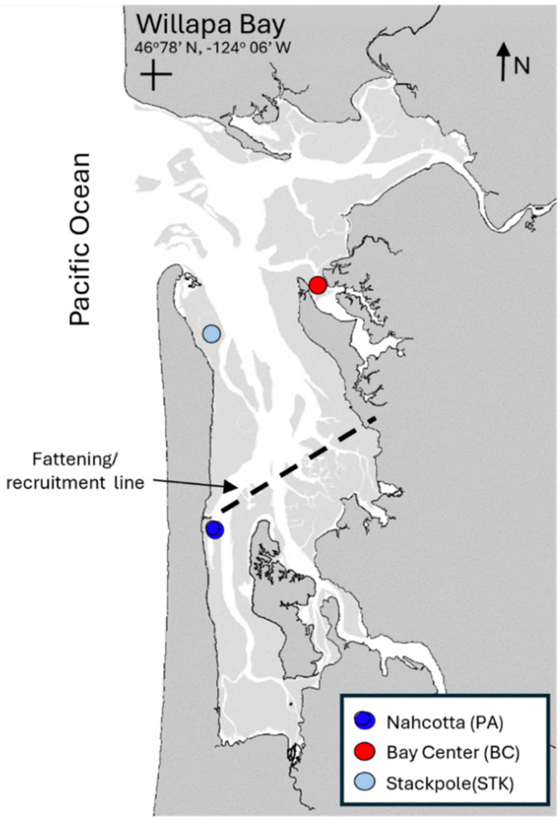

Fig.1 Map of Willapa Bay,Washington, USA showing 2019 transplant experiment sites (Nahcotta and Bay Center)

Nahcotta site (Parcel A, PA) is also a long-term oyster condition index monitoring location as is Stackpole (STK), a site closer to the estuary mouth. Also shown is a dashed line separating high quality oyster fattening beds in the northern portion of the estuary from southern portion of the estuary where growers usually plant oyster seed.

We analyzed experimental data collected as part of a UJNR study conducted in 2019 where adult oysters were collected from one of these long term sampling locations in Willapa Bay (Nahcotta = Parcel A, PA) near the south end of the estuary and then transplanted back to this same location and to a second location (Bay Center, BC) closer to the estuary mouth (Fig.1) to evaluate the seasonal pattern of condition and gametogenesis (Hasegawa *et al*. 2021). Oysters were placed in bags on poles in two habitats (eelgrass, open mudflat), in two configurations (directly on sediment surface and 25cm above the surface) and a second set deployed from a nearby pier where they would be continuously submerged. This submerged treatment was designed to be similar to the typical method for hanging culture in Japan (Fujiya 1970; Hirata and Akashige 2004). Six sets of bags were deployed at each location in February and 3 sets replicate bags with individually labeled oysters retrieved in July. The other 3 sets of bags were retrieved and survival and condition index measured in May, June and August to capture a seasonal trend and compare condition with that measured at the Nahcotta and Stackpole (STK) long term monitoring sites in this estuary. Similar experimental data were collected at Hatsukaichi in Hiroshima Bay, a part of the Seto Inland Sea, Japan in 2019 (see Hasegawa *et al*. 2021 for description).

Results and Discussion

An analysis of the long-term data set for oyster condition index collected at four locations in Willapa Bay indicated consistent trends amongst locations. A single component of the variability in CI was most closely related to similar variability in the upwelling index for the nearshore coastal ocean which was positively correlated with condition index during the summer upwelling period (Dumbauld *et al*. 2023). Two large scale shifts in oyster condition occurred in 1977/1978 and 1999/2000 (Fig.2). The first shift corresponded with a previously well documented change from a cool to warm phase of the basin scale Pacific Decadal Oscillation (PDO), but the more recent shift instead correlated with local fluctuations in temperature and upwelling intensity. Differences in the average condition index measured at Nahcotta and Stackpole (closer to the estuary mouth, Fig.1) were evident and shifts in seasonal timing of peak condition also appeared to be linked to basin wide indices with higher condition and earlier peaks occurring after the most recent shift.

Oyster condition index followed similar seasonal trends at

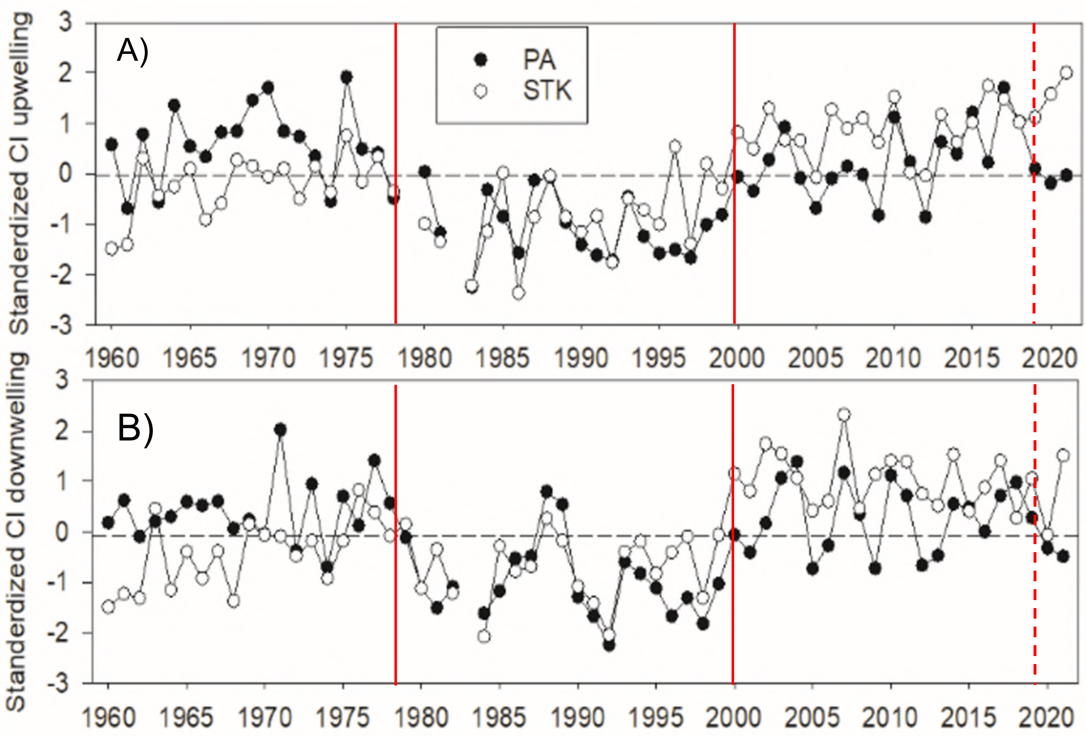

Fig.2 Long term record (1960-2022) of oyster condition index at Nahcotta (PA) and Stackpole (STK) locations averaged over A) the upwelling period (May-September) and B) the downwelling period (November-April) and standardized to the long term mean for those periods

Solid vertical lines represent years (1978/1979 and 1999/2000) when the index shifted and dashed line for 2019 when experimental transplant study was made (modified from Dumbauld *et al*. 2023).

both sites in Willapa Bay in the 2019 experiment, but condition was already higher at Bay Center than at Nahcotta when first measured in May and dropped significantly in August due to an apparent spawning event (Fig.3). By July condition was slightly higher for oysters suspended off bottom and trends differed for those continuously suspended at the pier with oysters in Bay Center having apparently spawned by July. Mortality was higher at Bay Center where it began in July but increased substantially in August with only 40% survival. Survival was higher at Nahcotta and generally higher for oysters deployed at the pier. Though slightly higher in eelgrass than open mud, neither oyster condition nor mortality were significantly influenced by habitat. (Fig.4).

The seasonal pattern of oyster condition index at the Nahcotta long-term monitoring site mirrored that recorded for the experimental oyster deployments and differed from the long-term average (1955-2019), with a large increase in condition occurring from April to June and then a sharp decline and apparent spawning event occurring by August followed by an extended period of recovery (Fig.5). Though condition was higher at the Stackpole long-term monitoring site closer to the estuary mouth, the seasonal pattern at that location was similar. Shellfish growers operating in Willapa Bay reported a significant summer mortality event in 2019, so we compared condition index with other years when mortality was similarly reported (Fig.5). Though not as dramatic, a similar pattern of higher-than-average condition in winter and a slightly earlier and larger increase in average condition with a significant drop (likely due to spawning events) occurred in these years as well.

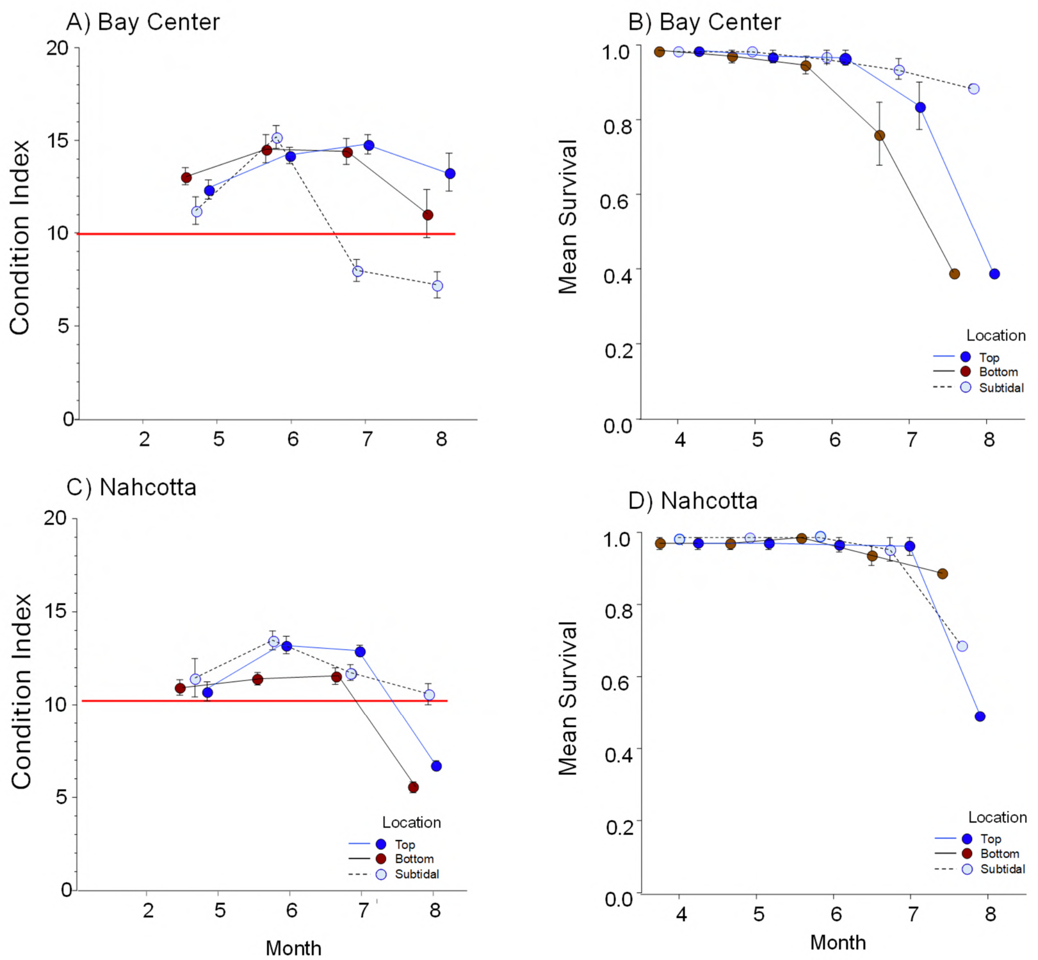

Fig.3 Results of transplant experiment conducted in Willapa Bay in 2019. Condition index and survival of oysters transplanted to Bay Center (A and B, respectively) and condition index and survival for those transplanted to Nahcotta (C and D, respectively)

Shown are oysters planted in bags deployed just above the sediment (Bottom), about 25 cm above the sediment (Top), and those deployed at a nearby pier (Subtidal). Red line at condition index = 10 added for visual reference.

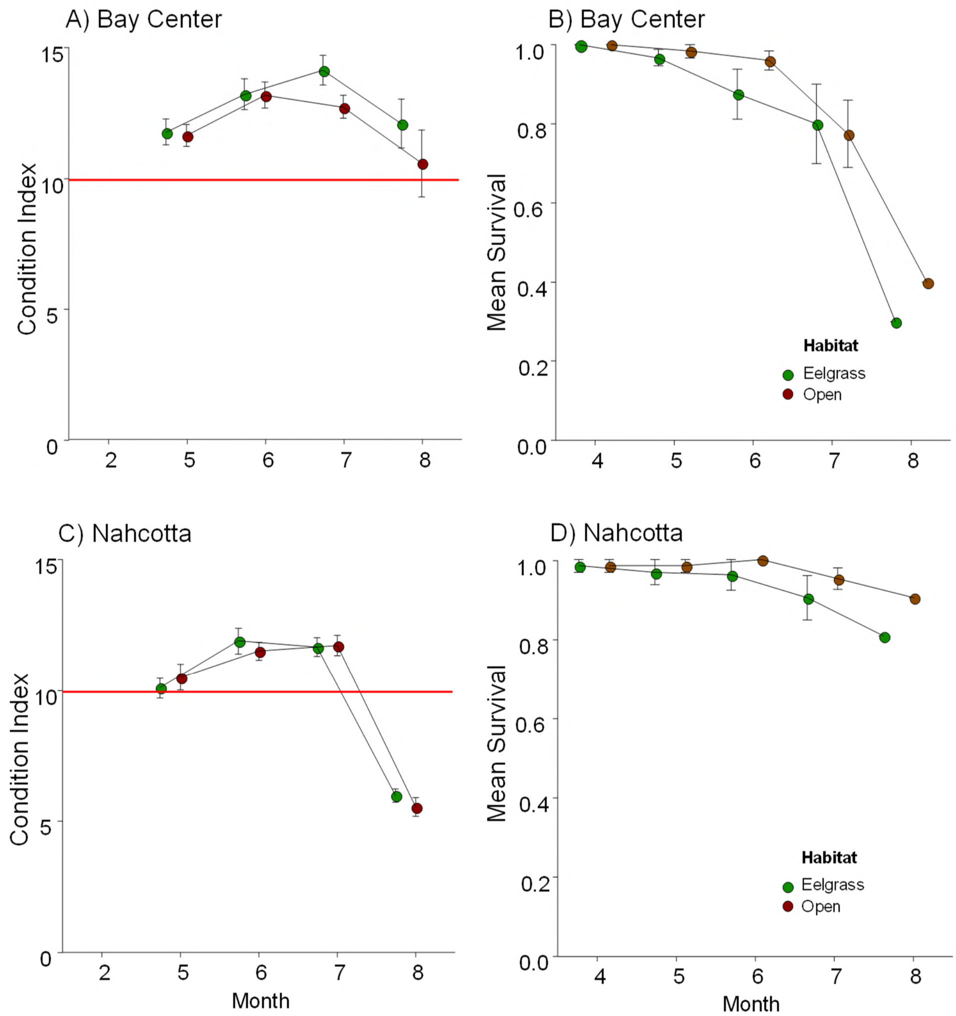

Fig.4 Results of transplant experiment conducted in Willapa Bay in 2019

Condition index and survival of oysters transplanted to Bay Center (A and B, respectively) and condition index and survival for those transplanted to Nahcotta (C and D, respectively). Shown are oysters planted in bags located within eelgrass and those planted in open habitat. Line at a condition index of 10 is added for visual reference.

We evaluated temperature and environmental records collected alongside the oysters in Willapa Bay during the 2019 experiment to compare with long-term records, but this year has since been shown to represent a significant warming event in the Northeast Pacific now recognized as marine heatwaves. These heatwaves are anomalously warm water events that extend over thousands of square kilometers in ocean basins and can be modulated by other climatic patterns like the PDO and El Niño-Southern Oscillation (ENSO) (Hobday *et al*. 2018; Ren *et al*. 2023). Though the scale of warming, distribution relative to the coast, and seasonal progression differed from a very large previous 2014-2016 event described as Blob 1.0, the 2019 heatwave became known as Blob 2.0 (Amaya *et al*. 2020; Chen *et al*. 2021). The effect of these events on nearshore coastal ocean conditions includes warmer seawater temperatures, potentially concentrated nearshore phytoplankton production and altered phytoplankton species composition that must also influence conditions for oysters in coastal estuaries (Stone *et al*. 2018, 2020).

Seasonal patterns of wind stress affect the transport of water and phytoplankton into coastal estuaries (Banas *et al*. 2007; Brasseale and Maccready 2025; Roegner *et al*. 2002). Phytoplankton distribution is subsequently influenced by water residence time both at the estuary scale, e.g. higher flushing and shorter residence = more frequent replenishing near the estuary mouth, but also across broad tide flats like those in Willapa Bay (Wheat *et al*. 2019). This estuary scale pattern is reflected in generally higher condition at the

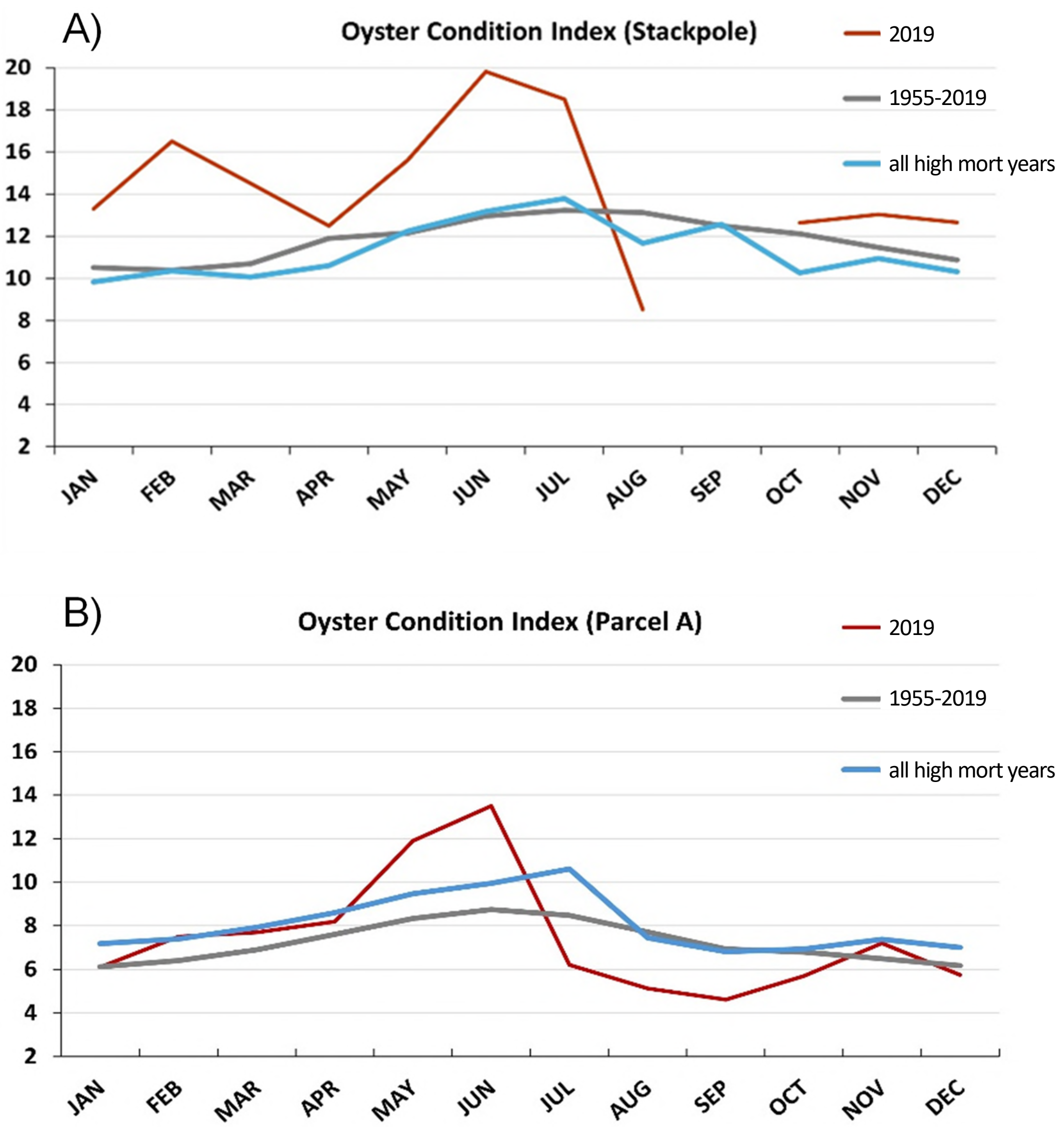

Fig.5 Seasonal trend of oyster condition index at A) Stackpole (STK) long term monitoring location and B) Nahcotta (PA) monitoring location in Willapa Bay

Shown are lines for 2019, the average condition index for 1955-2019, and a line representing the average condition index for years when shellfish growers reported significant mortality events in Willapa Bay.

Stackpole versus Nahcotta long-term monitoring sites across all years (Dumbauld *et al*. 2023) and at the Bay Center versus Nahcotta location in our 2019 experimental deployments. Shellfish growers have long taken advantage of this by planting and/or harvesting naturally caught seed near the south end of the estuary where larvae are retained and transplanting these oysters to fattening beds closer to the estuary mouth for harvest (fattening/recruitment line, Fig.1). Generally higher condition for oysters raised off the bottom observed at both locations in 2019 has also been previously documented, but most studies have been conducted on young oysters which devote less energy to reproduction. Results are site dependent and influenced by water flow, sediment conditions, distance to channel and even density of nearby oysters as competitors even when tidal elevation is held constant (Ruesink *et al*. 2003; Wheat and Ruesink 2013; Wheat *et al*. 2019). Nonetheless a recent study at numerous sites in Washington State, USA including several sites in Willapa Bay was consistent with our 2019 results with the condition of oysters positively influenced by raising them above the sediment surface but not influenced by the presence of eelgrass (Ruesink *et al*. 2023). Oyster survival was site dependent but also higher for oysters reared off-bottom and only marginally negatively influenced by eelgrass.

Multiple investigations into factors leading to summer mortality events for Pacific oysters observed in the field have been conducted including initial work by researchers in Japan (Imai *et al*. 1968) and the US (Beattie *et al*. 1980; Cheney *et al*. 2000; Perdue *et al*. 1981), leading to perhaps the most substantial investigation by researchers in France (The MOREST project, Samain 2011). This and subsequent research suggest that when opportunistic pathogens (like the ostreid herpes virus OsHV-1 and several species of *Vibrio*) were present, they were important, but multiple environmental stressors otherwise contribute by influencing oyster metabolism, growth, and gametogenesis and thus ultimately resistance/tolerance and gene response (de Lorgeril *et al*. 2020; Fleury *et al*. 2020; Pernet *et al*. 2019). Thus breeding programs have been developed and are advancing new genomic selection tools to identify traits and create disease resistant oyster broodstock that enable the shellfish aquaculture industry to avoid catastrophic losses due to OsHV-1 (Degremont *et al*. 2015; Delomas *et al*. 2023; Divilov *et al*. 2023; Gutierrez *et al*. 2020; Thompson *et al*. 2024), but pathogens are not the single cause of all mortality events. Recent evidence from laboratory stressor experiments suggests that food availability is an underlying and most significant factor affecting physiological response of juvenile seed oysters to disease, ocean warming, and acidity such that the lack of sufficient food limited growth, reproduction and energy reserves and thereby increased oxygen consumption and disease susceptibility (Caillon *et al*. 2023). Mortality of older oysters in the second summer has been previously linked to the gametogenic cycle and correlated with environmental triggers like temperature, salinity, and food which influence oyster metabolism and growth (Cheney *et al*. 2000; Garcia *et al*. 2011; King *et al*. 2021; Perdue *et al*. 1981; Solomieu *et al*. 2015). Long-term monitoring efforts of oyster condition and mortality in France point to the importance of feeding conditions during the winter/spring conditioning period where enhanced food and trophic conditions combined with warm temperatures lead to rapid gametogenesis and higher mortality risk in the presence of other metabolic stressors like low dissolved oxygen (Ernande *et al*. 2004; Gourault *et al*. 2019; Thomas *et al*. 2018).

Oysters were also investigated at Hatsukaichi in Hiroshima Bay in 2019 (Hasegawa *et al*. 2021), a part of the Seto Inland Sea in Japan, where oyster production has recently fluctuated markedly and mortality rates have increased (Hirata and Akashige 2004). Initial results indicated that the seasonal cycle of gametogenesis differed between the US and Japan. While the peak in sexual maturation occurred one month earlier in Japan (June versus July), oysters reached spawning stage over a similar period (600 cumulative temperature °C days) at locations in both countries. Spawning resulted in low condition and gonadosomatic indices and was more prevalent at Hatsukaichi when oysters were measured in June than in Willapa Bay in July, but mortality also increased in Willapa Bay in August. Relationships between environmental factors and growth in the Seto Inland Sea have also been recently investigated by Pang *et al*. (2024) who documented higher mortality in 2015-2021 than was observed in 1990. They found little difference in the temperature regime and attributed this to lower salinity and higher rainfall which has been previously shown to trigger mass spawning events in Matsushima Bay, Japan (Yokouchi *et al*. 2022). The Seto Inland Sea is much larger and less influenced by the nearshore coastal ocean than Willapa Bay with higher precipitation and lower salinities occurring during the summer months. Nonetheless, marine heatwaves of different origin are increasing in frequency (Sato *et al*. 2024), and what were once eutrophic conditions due to nutrient additions are now becoming more oligotrophic conditions with corresponding changes in the phytoplankton composition and abundance (Nishikawa *et al*. 2010). Despite these differences oysters displayed similar patterns with respect to deployment and habitat to those in Willapa Bay in 2019 with those grown off bottom having higher condition than those grown on bottom with a less obvious effect of seagrass presence.

Given significant increases in summer mortality events in both the US and Japan and recent advances in technology that might help resolve the mechanisms responsible and potentially allow shellfish industry participants to at least mitigate for losses, it seemed useful to briefly outline a new collaborative approach that we have proposed on the U.S. west coast. This proposed work involves addressing three research priorities outlined in a recent workshop on summer mortality (Virginia Institute of Marine Science 2024): 1) Develop a mechanistic understanding of mortality events, including energy budgets, pathobiology, etc., 2) Prepare oysters to withstand stress in all phases, for example through hardening or priming against future challenges, and 3) Breeding for increased, general resilience. The currently proposed work addresses priorities 1 and 3, but indirectly provides a foundation for addressing priority 2. The primary objective is to develop a generalized but quantitative resilience trait index that can be used by breeding programs to increase field survival and at the same time enable participating farmers to assess the level of stress experienced by their oysters. The first step involves employing a suite of cost effective assays based on physiological and metabolic stress that can be determined in field reared oysters. An example is measuring NA^+/K^+ ATPase activity which evaluates cellular stress and has been shown to decrease in oysters that are susceptible to mortality (George *et al*. 2023), but separate evaluations will also be made for organismal metabolic rate, energy storage, and capacities for aerobic and anaerobic metabolism. Since it is difficult to attribute mortality to a single stressor measured in the field, the strength of this approach is then to also apply these tests to bi-parental families from an oyster breeding program as part of the Pacific Oyster Genomic Selection (POGS) project which is developing oysters that are resistant/tolerant to OsHV-1 and deploying these at multiple farmed sites in collaboration with growers.

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Annotated Bibliography of Key Works

(1) Cheney D, MacDonald BF, Elston RA (2000) Summer mortality of Pacific oysters, *Crassostrea gigas* (Thunberg): Initial findings on multiple environmental stressors in Puget Sound, Washington, 1998. *J. Shellfish Res.*, **18**, 456-473.

This manuscript presents the results of a study conducted to investigate Pacific oyster summer mortality events in Puget Sound, Washington, USA where no specific disease factors appeared responsible but instead mortality events linked to multiple environmental stressors including temperature extremes, low oxygen conditions and phytoplanton as food. An initial comparison of mortality amongst diploid and triploid oysters was also made.

(2) Dumbauld BR, Du XN, Hunsicker M, Forster Z (2023) Multi-decade changes in the condition index of adult Pacific oysters (*Crassostrea gigas*) in response to climate in a US west coast estuary. *J. Sea Res.*, **193**, 102383.

The authors present an analysis of almost seven decades of oyster condition data collected in Willapa Bay, Washington, USA. They identified two important and coherent shifts in oyster condition that can be associated with changes in ocean climate at basin wide and more local scales. They also charactrized patterns in oyster condition within Willapa Bay that had long been recognized by industry participants and associated with oyster gametogenesis and spawning.

(3) George MN, Cattau O, Middleton MA, Lawson D, Vadopalas B, Gavery M, Roberts SB (2023) Triploid Pacific oysters exhibit stress response dysregulation and elevated mortality following heatwaves. *Glob. Change Biol.*, **29**, 6969-6987.

These authors examined the physiological response of Pacific oysters to environmental conditions that are potentially responsible for summer mortality. Physiological assays included metabolic depression due to a reduction in sodium pump activity and dysregulated expression of genes associated with glucose metabolism and mitiochondrial function.

(4) Hasegawa N, Dumbauld B, Hori M, Watanabe S, Rust M, Forster Z (2021) Comparative study of the impact of environmental change on oyster culture between USA and Japan, as collaborative research under UJNR. *Bull. Jap. Fish. Res. Edu. Agen.*, **50**, 115-121.

This is an introduction to the collaborative study initiated between the USA and Japan. Data was collected, but some analyses partially reported on at this time were delayed primarily due to the global pandemic.

(5) Samain JF (2011) Review and perspectives of physiological mechanisms underlying genetically-based resistance of the Pacific oyster to summer mortality. *Aquat. Living Resour.*, **24**, 227-236.

This review of multiple years of data collected for the “MOREST” project in France remains one of the important references that suggests a link between summer mortality events, physiological mechanisms like reproductive effort and stressors like temperature. The authors also suggest avenues for investigating genetically-based resistance to stress.