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Predicting restoration and aquaculture potential of eastern oysters through an eco-physiological mechanistic model

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ABSTRACT

A simple, non-negotiable truth of ensuring success in the restoration of ecological engineers (EE) and the functions they support is the need for the focal species to survive, grow and reproduce. Using mechanistic modeling, such as a dynamic energy budget (DEB), to map an EE's fundamental niche supports restoration and management predictive of EE resilience under current and future conditions. One EE, the eastern oyster, *Crassostrea virginica*, provides critical estuarine habitat and supports a valuable fishery across the northern Gulf of Mexico. Recent declines in oyster populations in this region from anthropogenic activities and extreme events have led to significant efforts to restore wild, self-sustaining broodstock reefs, and develop off-bottom aquaculture. To explore potential outcomes for oyster restoration and aquaculture development, we used an individual bioenergetic model based on DEB theory to derive an aquaculture index, based on survival and time to market size, and a restoration index, based on survival and reproductive output. The model was run across six major Texas and Louisiana estuaries under current (2014–2020) and future (2041–2050) projected environmental conditions. Aquaculture scores using daily averaged current conditions reproduce an observed gradient of oyster growth success increasing from the upper estuary to lower estuary (Texas) or offshore areas (Louisiana), with lower variation occurring in Texas estuaries. Restoration scores under daily averaged current conditions showed similar trends with more variability than the aquaculture index due to spawning potential, which is important for reef sustainability. In general, Louisiana estuaries showed higher growth rates and reproduction than Texas estuaries, but due to the higher variability and more frequent extremes in salinity and temperature, Louisiana estuaries were more likely to experience mortal conditions in any given year, as compared to Texas estuaries. Comparison between current and future conditions indicated that oyster aquaculture and restoration potential in presently occupied areas might decrease in the future; however, the spatial resolution of currently available climate model outputs within coastal and estuarine areas limits planning information. Addressing this gap represents a necessary improvement to better evaluate the physiological response of EE to future conditions, especially since most aquaculture and restoration developments are likely to occur close to the coastline. Finally, this work demonstrates the potential of mechanistic modeling to inform future planning under environmental conditions not currently within the realized niche of EE.

1. Introduction

Tools that predict a species' fundamental niche provide critical information to support the restoration of ecologically and economically important organisms (Wiens et al., 2009; Tomlinson, 2020; Lavaud et al., 2021a; Marn et al., 2022). This is because the likelihood of successful, sustainable and resilient ecological restoration depends at the most basic level on the organisms' physiological performance and

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fitness, including sub-lethal responses such as reproductive and recruitment success under current and future environmental conditions (Sangare et al., 2019; Briscoe et al., 2023). Yet, most restoration decision-making relies on data derived from approaches dependent on exploring an organisms' realized niche (i.e., using data from current distributions of species) determined using correlative models and indices based on statistical regressions between species observations and environmental conditions (Kearney et al., 2010a; Beseres Pollack et al., 2012; Sarà et al., 2013). As climate change modifies environmental conditions, the use of realized niche-based models, including suitability indices to predict species' persistence, can be problematic as (1) the novel conditions may be beyond the realized niche but still within the species' fundamental niche or (2) the experienced changes may trigger niche shifts (Bates and Bertelsmeier, 2021). Moreover, novel acute variations or extremes, often not captured in correlative models, may trigger unknown physiological responses (Briscoe et al., 2023). These issues have been identified as potential barriers to predicting species' ranges or range shifts and, along the same lines, impose a limitation on restoration decision-making by restricting restoration options.

The emergence of mechanistic models built on knowledge of the physiological or phenological response processes (energy and matter uptake and use to grow and reproduce) of organisms to environmental variables provides a robust framework to map species' fundamental niches (Sarà et al., 2013; Kearney et al., 2010b, 2021; Lavaud et al., 2021a). Dynamic Energy Budget (DEB) models are mechanistic, implementing physiological and metabolic processes common to all living species. They provide a potentially powerful tool enabling comparisons between species and sites while using a common set of parameters. The use of DEB models, particularly in combination with studies exploring organisms' physiological responses to environmental conditions (e.g., temperature, food availability) outside their current realized niche, enables predictions of potential changes in growth, survival and reproduction under novel conditions (Thomas and Bacher, 2018; Mangano et al., 2020). This ability to predict individual and population-level responses to novel conditions is particularly valuable as climate models predict, among other things, global warming (IPCC, 2023), which will have different effects across regions, and across annual cycles (Alexander et al., 2018); organisms may thus be exposed to different and sometimes new conditions across their current ranges (Strubbe et al., 2023). Using mechanistic-based models provides flexibility to understand and predict how an organism may respond to future scenarios and provides input into management for species where restoration, conservation and production (i.e., commercial operations including aquaculture) are of concern, including some ecological engineers (EE).

Within the estuarine environment, reef-building organisms function as EE, providing habitat to support diversity and an important food source for the global population (FAO, 2022). In many places, reefs have declined in area and function and are considered highly vulnerable to future conditions, namely temperature, salinity, oxygen and pH (Beck et al., 2011; Reece et al., 2018). As such, restoration of these EEs is a high priority in many regions. In particular, the eastern oyster, *Crassostrea virginica*, is an important EE within the U.S. northern Gulf of Mexico (nGoM) supporting some of the most productive fisheries in the United States, accounting for one-fifth of domestic seafood landings, and one-half of *C. virginica* production (NMFS, 2021). After the *Deepwater Horizon* oil spill in 2010, assessments estimated the loss of billions of inter- and sub-tidal oysters across the nGoM (DWH NRDA, 2017). Not surprisingly, eastern oysters have been prioritized for restoration in this region. Efforts have focused on developing protected reefs for broodstock spawning and oyster aquaculture to ensure consistent production to support the industry without detriment to the native population. A key gap identified for regional oyster restoration in recent multi-agency efforts is the ability to identify suitable site locations for ensuring future production, aquaculture success and resilient and sustainable wild populations of oysters given changing climate, human activities and the increased frequency of extreme events (e.g., hurricanes, storm surge, heat waves; DWH NRDA 2017).

Recent efforts across the nGoM have documented > 60 projects and $200 M invested in oyster restoration to support aquaculture and wild populations (Brooke and Alfasso, 2022). A review of completed projects (as of 2020) identified the restoration of 62 individual reef footprints across 11 different nGoM estuaries and found some positive outcomes immediately post-restoration, but a 75 % decline in oyster abundances within six years of restoration completion and multiple failed sites (La Peyre et al., 2022). While reefs were located on historic footprints and fell within areas of suitability of correlative models based largely on environmental means (i.e., Soniat et al. 2022), many sites experienced both acute and sustained forays outside of the mean conditions after restoration (La Peyre et al., 2022). Zabin et al. (2022) suggest restoration often fails because of a failure to plan for extreme climatic or acute events. For instance, the deployment of settlement substrate for natural oyster recruitment in San Francisco Bay saw mass mortality during floods, despite planning for wet and dry years, identifying the need to include more high salinity refuges in the spatial planning to cope with such extreme events (Zabin et al., 2022). Using environmental data on a daily scale to evaluate the physiological response of organisms allows for the incorporation of short-term events whose effects often override the effects of observed monthly or annual mean conditions (Briscoe et al., 2023). Many experimental studies have demonstrated that conditions persisting for less than seven days can lead to 100 % mortality (e.g., Marshall et al. 2021a, Coxe et al. 2023), which are often not captured in models using means to define suitability indices (Swannack et al., 2014; La Peyre et al., 2021; Sable et al., 2023). Spatial planning zones for broodstock restoration and aquaculture, as developed and suggested by Swam et al. (2022) for the state of Louisiana, provide one approach to reduce risks from extreme and acute events, but the development and use of mechanistic model outputs, with daily environmental data would strengthen our mapping of the fundamental niche of the eastern oyster targeting specifically aquaculture (growth, survival) and broodstock reef restoration (survival, reproduction).

Lavaud et al. (2017) developed a DEB model for nGoM oysters to simulate the individual bioenergetics in highly variable salinity conditions common to nGoM estuaries (Orlando et al., 1993; Swam et al., 2022). Critical to the survival, growth and reproduction of oysters in the nGoM, including salinity as a forcing variable in the oyster DEB model allowed improved prediction of observed patterns in growth and reproduction (Lavaud et al., 2017). The model was later used to explore the effects of river management and climate change on oysters within one estuary in Louisiana (Lavaud et al., 2021b). These applications were spatially limited by the availability of environmental data (namely temperature, chlorophyll and salinity) to force the model, restricting predictions to discrete locations equipped with environmental monitoring sensors. Model outputs for future temperature conditions are becoming increasingly available (Liu et al., 2015; Gabler et al., 2017); however, projections of future salinity and chlorophyll concentration are still limited, particularly in coastal and estuarine systems. Ongoing work on modeling salinity consists of hindcast studies (Xue et al., 2018; Ou et al., 2020) while chlorophyll projections generally focus on the open ocean (Elshall et al., 2022). Previous efforts to provide spatial outputs also lack the spatial resolution necessary to identify suitable restoration, or aquaculture locations (La Peyre et al., 2021). Restoration and aquaculture sites are often in the range of 0.1 ha in size, while grid cells of many models exceed 500 m x 500 m, the equivalent of 25 ha (Sable et al., 2023). In estuaries defined by spatiotemporal variation, this mismatch of scales between management and predictions often means that site-specific predictions may be highly generalized and may fail to capture critical thresholds or site-specific variations affecting the organism. Recent work focusing on spatial planning zones for broodstock restoration (Swam et al., 2022) calls to consider meta-populations (i.e., Lipcius et al. 2015, La Peyre et al. 2021) and increased availability of high-resolution spatiotemporal data to provide opportunities for more spatially relevant predictions.

Evolving computational power allows for ever higher climate model resolutions, enabling models to better address the needed higher spatiotemporal resolution. Building upon an existing general circulation model (GCM; e.g., Williams et al. 2015), Williams et al. (2018) implemented the Hadley centre Global Environment Model version 3 (HadGEM3-GC3.1) for the High Resolution Model Intercomparison Project (HighResMIP v1.0 for the Coupled Model Intercomparison Project 6; Haarsma et al. 2016). The HighResMIP project presents a multi-model approach to the systematic investigation of the effect of GCM horizontal resolution and focuses on identifying biases and consequences of increased model resolution (Haarsma et al., 2016). Research has shown that enhancing horizontal model resolution can reduce some biases in climate models (Hewitt et al., 2016; Roberts et al., 2016, 2018) and improve the robustness of future projections (Roberts et al., 2019). Here, we use daily HadGEM3-GC3.1 sea surface temperature and salinity in the validated DEB model to explore the spatial and temporal effects of predicted environmental conditions on oyster aquaculture and restoration potential.

In this paper, we used the oyster DEB model from Lavaud et al. (2017) to simulate the growth, reproduction and survival potential of eastern oysters under current (2014–2020) and future conditions (2041–2050) in six oyster-growing estuarine regions along the Texas-Louisiana nGoM coast. We develop restoration and aquaculture indices based on reproduction and oyster production (restoration), and time to harvest and survival (aquaculture), and present spatial index maps of these outcomes under the mean (i.e., typical yearly dynamics of) current and future conditions. This research provides site and population-specific information on oyster production to inform restoration efforts and support oyster aquaculture, examines how the use of averaged environmental data versus annual variation may be used to inform decision-making, and explores the potential expansion or shift of an EE's realized niche under future conditions.

2. Materials and methods

2.1. Study area

Estuaries and nearshore waters of the nGoM present a broad range of spatiotemporal conditions resulting from differing riverine inputs, basin morphology and management (Orlando et al., 1993; Solis and Powell, 1999; CPRA, 2017). Within Texas and Louisiana, estuaries display a salinity continuum that shifts from higher salinity levels in the southwest to comparatively lower salinity levels in the northeast (e.g., Montagna et al. 2018, Marshall et al. 2021b), yet most estuaries support eastern oyster reefs (La Peyre et al., 2021; Fig. 1). These differences in estuarine conditions are expected to be exacerbated by the effects of climate change on precipitation (both inland and offshore) and extreme events, varying across the region, with the southwestern portion of Texas predicted to become hotter and drier (Vose et al., 2017; Gutiérrez et al., 2021), and the northeastern portion, in Louisiana, experiencing increasing frequency and intensity of precipitation events (Easterling et al., 2017; Seneviratne et al., 2021) consistent with observations (Powell and Keim, 2015; Brown et al., 2019). The modeled study area extent differed for current and future conditions due to differences in available environmental data to inform the model (see Section 2.2), as described below.

2.1.1. Current conditions

Six estuarine study zones in Louisiana and Texas that support oyster resources and production were selected (Fig. 1) for current condition modeling. In Louisiana, three study zones defined by estuarine basin boundaries (CPRA, 2017) were selected and included Breton Sound (BRE), Barataria Bay (BAR) and Chenier Basin (CHE). The inshore boundary included all zones of each basin that showed > 80 % water coverage in a given year, while the offshore boundary extended 5 km from the estuarine basin boundary (CPRA, 2017). The three Louisiana estuarine study zones represent important oyster grounds across the state, with CHE supporting more than 50 % of the estimated oyster stock in Louisiana's public oyster areas (LDWF, 2022), split between two

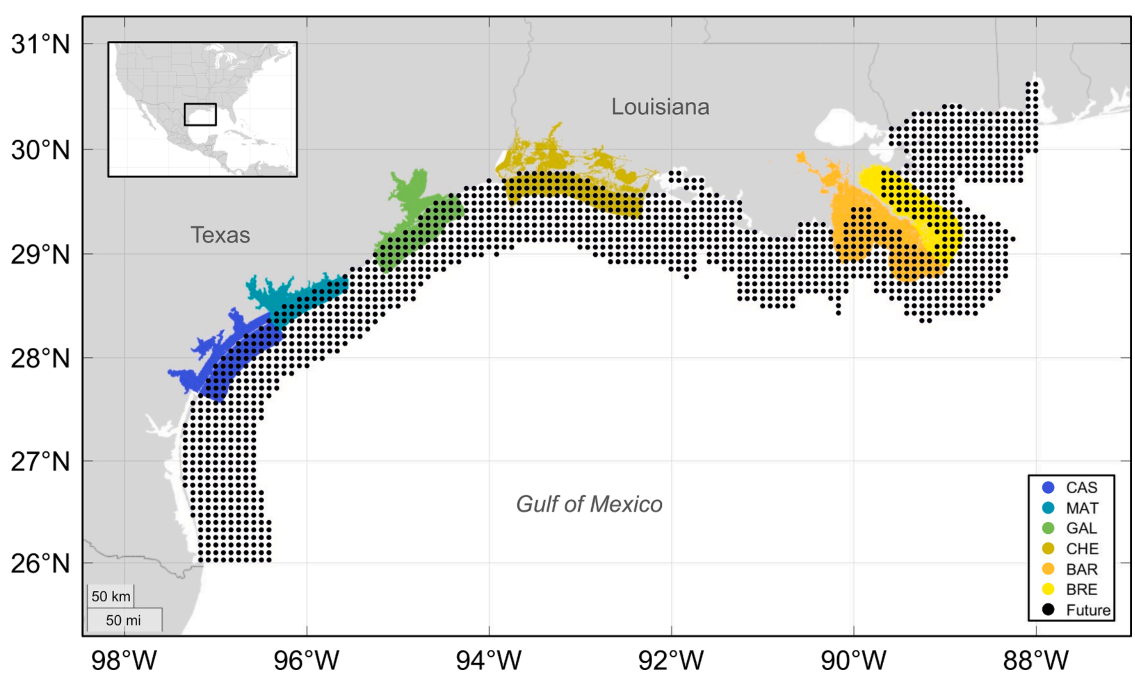

Fig. 1. Location of the six estuarine study zones (colors): CAS (Corpus Christi Bay/Aransas Bay/San Antonio Bay; blue), MAT (Matagorda Bay; teal), GAL (Galveston Bay; green), CHE (Chenier Basin; tan), BAR (Barataria Bay; orange) and BRE (Breton Sound; yellow), used to run the model under current conditions and the coast-wide area (black dots) used to run the model under future conditions. Map background is from Matlab, created using Natural Earth (2023) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

semi-enclosed estuarine lakes, Sabine and Calcasieu. Sabine represents a unique area due to a 50-year harvest ban, while Calcasieu is the focus of ongoing state efforts to expand off-bottom oyster aquaculture (LDWF, 2022). In contrast, BRE and BAR, located in the Mississippi River delta, were historically high-producing areas, but have experienced significant declines in oyster production (LDWF, 2022). These two estuarine zones support significant oyster production in coastal Louisiana with ~680, 000 ha of public areas (representing an estimated 6,4 10^6 kg of oysters) and ~450,000 ha of private leases (no stock assessment available but landings amount to about 3.5 10^6 kg; LDWF, 2022). Most of the current and planned restoration investment by the state of Louisiana (~$120 M) target areas within the BRE and BAR estuarine zones, and involves the creation of broodstock spawning reefs, and investment in off-bottom aquaculture (LDWF, 2022).

In Texas, three estuarine study zones were selected (Fig. 1), representing a range of salinity and temperature conditions (Montagna et al., 2012) and supporting extensive oyster reef areas. Estuaries in this region are geomorphologically similar but hydrologically distinct due to a strong climatic gradient, with decreasing precipitation and increasing salinity from northeast to southwest (Montagna et al., 2012, 2018). The most southwest estuarine zone in this study, encompassing a complex of bays including Corpus Christi Bay, Aransas Bay and San Antonio Bay (CAS), is the most saline site; freshwater inflow typically occurs in isolated pulses and the system routinely experiences extended droughts (Orlando et al., 1993). Higher freshwater inflows in Matagorda Bay (MAT) and Galveston Bay (GAL) drive lower average annual salinities (Longley, 1994). Over 90 % of commercial oyster landings from public reefs in Texas are harvested from these areas (Bohannon et al., 2015). Over 500 acres of oyster reef have been restored in these systems *via* cultch placement, principally by the Texas Parks and Wildlife Department.

2.1.2. Future conditions

The geographical extent of the GCM used to provide inputs for the oyster DEB model (see Section 2.3) did not permit the same coverage of the study zones described above, except in the case of BRE and BAR in Louisiana. Future conditions were run within these two estuarine zones, and in more offshore areas across the entire coast of Texas and Louisiana. To facilitate visualization of the results, the area extended 75 km offshore, beyond known and mapped areas of oysters but still includes shallow waters (< 20 m; https://www.ncei.noaa.gov/maps/gulf-data-atlas/atlas.htm), and covers area that could represent a shift in the realized niche of oysters, including potential areas for development of mariculture, as identified by the U.S. National Oceanographic and Atmospheric Administration (Riley et al., 2021).

2.2. Environmental data sources and interpolation

2.2.1. Current conditions

Daily temperature and salinity data from 2014 to 2020 for the Louisiana estuarine study zones were obtained from continuous recorders maintained by the Louisiana Coastwide Reference Monitoring System (CPRA, 2021) and the U.S. Geological Survey (USGS, 2021). Daily salinity data for the Texas estuarine study zones were comprised of observed data from the Texas Commission on Environmental Quality, Texas Parks and Wildlife Department and the U.S. Geological Survey as well as modeled data from the TxBLEND models obtained from the Texas Water Development Board (Schoenbaechler et al., 2011). Daily temperature data were not available from the TxBLEND models. Therefore, in addition to observed data from the previously mentioned sources in Texas, daily temperature data for portions of the Texas estuarine study zones was supplemented with remotely sensed products including the Modis SST (NASA/JPL, 2020) and Landsat 8 Thermal Infrared Sensor data. Offshore salinity and temperature data were obtained from the Hybrid Coordinate Ocean Model (HYCOM) for salinity (GODAE, 2021) and the National Oceanographic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature dataset for temperature (Huang et al., 2021). The methods followed to interpolate temporally and/or spatially patchy temperature and salinity data sets in Louisiana and salinity data sets in Texas are described in Swam et al. (2022). Temperature data sets in in-shore or near-shore portions of Texas estuarine study zones were interpolated temporally and spatially through harmonic analysis. All data were interpolated to a resolution of 200 m and restricted to water bodies with a frequency of inundation of at least 80 % during the 2014–2020 period, as determined by the Global Surface Water dataset (Pekel et al., 2016).

Both individual-year daily data and averaged 7-year daily data were used to calculate aquaculture and restoration indices (see Section 2.4) across the six estuarine zones. The 7-year averaged simulations enabled a long-term assessment of specific site outcomes, while individual-year simulations enabled the identification of the effects of extremes in environmental conditions that may affect oyster populations and aquaculture outcomes, which may be masked through the use of averages. Due to the scatter in data availability, single-year datasets do not necessarily contain a value for temperature or salinity at every time step for a given location (part of the initial rationale to interpolate data spatially and temporally over multiple years).

2.2.2. Future conditions

Daily sea surface temperature and sea surface salinity from 2041 to 2050 were obtained from the HadGEM3-GC3.1 (Williams et al., 2018), created by the Met Office Hadley centre as part of the CMIP6 HighResMip project (Haarsma et al., 2016), which focuses on assessing the effect of increased horizontal grid resolution on average model biases (Roberts et al., 2019). HadGEM3-GC3.1 was chosen to force the oyster DEB model because of its high spatial resolution (1/12° or 10 km nominal resolution). The model output is from the coupled future 2015–2050 experimental scenario that is as close to CMIP5 Representative Concentration Pathway 8.5 (RCP 8.5) as possible with CIMP6 (Shared Socioeconomic Pathway 5 or SSP5_8.5). The scenario represents the high end of plausible future conditions and is the only scenario with an emissions scenario high enough/on par with RCP 8.5 (see Riahi et al. 2011), which is 8.5 W/m^2 of forcing in 2100 (Kriegler et al., 2017). While this scenario has a low probability of realization due to its relatively extreme assumptions about population trends, technological advancements, energy improvements, land use and unmitigated greenhouse gas emission policy (see Riahi et al. 2011, Van Vuuren et al. 2011, Kriegler et al. 2017), it is useful in providing an upper bound on potential future outcomes. Use of multiple scenarios and models would be beneficial to determine a continuum of possible outcomes. However, only one other model at 10 km nominal resolution containing both sea surface temperature and sea surface salinity was available on the Earth System Grid Federation, World Climate Research Programme – CMIP6 (https://esgf-node.llnl.gov/search/cmip6/) at the time this study was conducted and it was the same experiment (i.e., CIMP5 8.5′s closest analogue in CIMP6) as the model selected. Future work that includes a diverse suite of models spanning different SSP's could help determine a range of potential future outcomes.

2.3. Oyster DEB model

We used the oyster DEB model developed by Lavaud et al. (2017, 2021b) to simulate individual oyster bioenergetics (Tables S1 and S2). Because this model only covered the adult part of the life cycle, maturity E_H was not originally included but had to be accounted for in the present study to simulate younger stages. With this addition and to ensure computation efficiency, the state variable for energy used to create gametes, E_{Go}, was removed. The release of energy fixed in gametes was thus simplified and directly deducted from the reproduction buffer E_R during spawning events. Spawning occurs in the model when temperatures are above 22.5 °C (Ingle, 1951) and the gonado-somatic index, calculated as the ratio between the mass of the reproduction buffer and the total tissue mass, reaches 0.06 (Lavaud et al., 2017). Salinity affects the uptake of energy through shell valve closure with feeding rates linearly decreasing between salinity of 10 to 3, at which point oysters remain closed (Lavaud et al., 2017).

Since the reproduction module of the DEB model was initially calibrated with data from Louisiana, and because oyster populations in Texas experience widely different conditions, particularly in salinity and food availability, we first tested and validated the DEB model on independent data from Lebreton et al. (2021) including shell and tissue growth in the Mission-Aransas estuary (Fig. S1). The only change necessary to validate the DEB model was a decrease in the gonado-somatic threshold for spawning from 0.06 to 0.04. We used an intermediate value of 0.05 for simulations under future conditions as the modeled area encompassed both Texas and Louisiana waters. Mortality is implemented both mechanistically (i.e., as a function of state variables) and empirically (i.e., based on knowledge from field and laboratory experiments). When energy in the reserve is not enough to pay daily somatic maintenance costs, oysters may divert energy allocated to reproduction and, if necessary, tap into structural volume to fuel this maintenance requirement. This reduction in structural volume is known as shrinking; death was set to occur when structural volume falls below one third of the value at the beginning of shrinking. Based on experimental and field monitoring data (La Peyre et al. 2013, Marshall et al. 2021a,2021b; more references in Lavaud et al. 2021a), death also occurs when oysters are exposed for 7 consecutive days to a salinity of 1 and a temperature of 20 °C or a salinity of 5 and a temperature of 32 °C (Lavaud et al., 2021a). We also implemented an additional cause of mortality linked to high salinity exposure, as Texas estuaries are typically more saline than Louisiana estuaries. Such mortality can be explained by increased predation (Shumway, 1996; Beseres Pollack et al., 2012), increased vulnerability to diseases (La Peyre et al., 2006, 2010) and the general metabolic failure of the species when exposed to concomitant salinity of 35 and temperature of 35 °C for more than a week (Marshall et al., 2021a).

2.4. Simulations and model outputs evaluation

Daily average temperature and salinity conditions for single years (2014 through 2020) and averaged across years for current (2014–2020) and future (2041–2050) conditions were used as forcing variables of the DEB model. Food was considered non-limiting in Louisiana based on evidence of consistently high eutrophic conditions (D'Sa, 2014; Turner et al., 2019) and the scaled functional response (f), a measure of food availability in the model varying between 0 and 1 (0 corresponding to no food, 1 to *ad libitum* conditions), was set to 1; a value that has been validated previously (Lavaud et al., 2017, 2021a). In Texas estuaries, however, while the warm waters support high microalgal growth, seasonality and spatial variability of food resources are more pronounced and indicate potential low food availability occurrences through time and space (Qian et al., 1996; Lebreton et al., 2021). In Texas, f was calibrated at 0.85, based on data used during the validation process (Fig. S1). For simulations under future conditions, we set the value of f at 0.9, based on projected phytoplankton production in the Louisiana shelf (Lehrter et al., 2017).

Simulations were initiated with a seed oyster individual (shell height = 6 mm) in each grid cell defined for current condition study zones and the future condition area. Simulations started on May 15th, when oyster managers and producers generally purchase young oysters from hatcheries for aquaculture and restoration. This corresponds to the beginning of the spawning season for natural populations. Model outputs consisted of final shell height (mm), final wet tissue weight (g), cumulated number of eggs spawned (#), average monthly shell growth rate (mm mo^{-1}), time to reach market size (d; 75 mm shell height) and survival were retrieved after one year of simulation. Model outputs were generated using (1) individual years inclusive of 2014 through 2020 for the six estuarine zones, (2) averaged outcomes across 2014–2020 years for the six estuarine zones, (3) averaged outcomes across 2041–2050 years for future conditions output zone.

Model outputs were standardized from 0 to 1 by the maximum value in each study zone. To obtain higher standardized values for shorter times to market size we used the formula: $-(x - t) / \max(x)$, with x the time to market size (d) and t the simulation duration (365 d). Using these standardized model outputs, we computed suitability indices, ranging from 0 to 1, for oyster aquaculture (SI_{Aqua}) and restoration (SI_{Resto}) according to the following equations:

$$SI_{Aqua} = (\text{Shell height} + \text{Time to market size})/2 \quad (1)$$

$$SI_{Resto} = (\text{Tissue wet weight} + \text{Cumulated eggs spawned})/2 \quad (2)$$

Grid cells in which oysters did not survive were assigned an index of 0. Indices values were considered low if they were below 0.33, medium if they were between 0.33 and 0.66, and high if they were above 0.66. The rationale behind using different outputs for aquaculture and restoration lies in the fact that (1) oyster farming relies on timely and consistent shell growth, and (2) egg production is almost exclusively important for restoration.

Using the individual year simulations, two added metrics were calculated. A score based solely on mortality was calculated to identify cells exposed to lethal events within a given year. This score ranged from 0 to 7 depending on the number of years survival was predicted to occur. Similarly, we computed a score that reflected how many years oysters in a given cell survived and reached market size each year. In this case, a score of seven indicates that oysters reached market size within 365 days every year, while a score of 0 shows that no oyster reached that mark during any of the years.

Model input and output data generated during this study are available as a USGS data release (Lavaud et al., 2023).

3. Results

3.1. Environmental conditions

Temperature and salinity annual mean, variation and extremes over the 2014–2020 period were calculated for each study zone and are summarized in Table 1. The general pattern is a gradient of temperature and salinity ranging from high values in the southwest to lower values in the northeast of the study zone. Over this period, the highest average temperature was observed in the CAS study zone (23.8 ± 6.3 °C) and the lowest in BRE (22.8 ± 6.0 °C). BRE also experienced the lowest average salinity (17.7 ± 11.7), and CAS had the highest average salinity (25.7 ± 8.7). Louisiana estuarine zones also had higher salinity variability (standard deviation of 11.7–12.8) than Texas estuarine zones (standard deviation of 6.3–8.7). Because these salinity values represent grid cells across an estuarine zone, the range of values was large, running from fresh to full seawater across all estuarine zones.

Comparison of current conditions to predicted future conditions was difficult because no direct geographical correspondence exists between the datasets for each period. Moreover, future projections inside estuaries were only available in BAR and BRE study zones, given the limited spatial extent of the future GCM in coastal zones. HadGEM3-GC3.1-derived output indicated warmer average temperatures and much higher salinities in BAR and BRE with very small variations within the part of these study zones covered by the GCM (Table 1; Fig. S2). Although no projections were available in Texas estuaries, general trends near barrier islands along these estuaries show similar trends with the same caveat of higher temperature and salinity.

3.2. Current conditions

3.2.1. Aquaculture potential

The SI_{Aqua} showed a consistent pattern of medium values (~0.5) in all three Texas estuarine study zones, with very low SI_{Aqua} values in the

Table 1
Mean temperature and salinity, their standard deviation (SD) and minimum (min) and maximum (max) values in each study zone over the 2014–2020 period. CAS: Corpus Christi Bay/Aransas Bay/San Antonio Bay, MAT: Matagorda Bay, GAL: Galveston Bay, CHE: Chenier Basin, BAR: Barataria Bay and BRE: Breton Sound. BAR-future and BRE-future represent modeled conditions for the 2041–2050 period (Williams et al., 2018).

Study zones	CAS	MAT	GAL	CHE	BAR	BRE	BAR-future	BRE-future
Temperature (°C)								
Mean	23.8	23.4	23.1	23.0	23.5	22.8	25.4	26.2
SD	6.3	6.6	6.7	5.8	5.5	6.0	0.4	0.8
Max	45.1	43.3	44.6	35.9	34.4	32.1	26.7	26.1
Min	0.2	10.5	4.2	8.1	6.9	6.6	24.5	23.5
Salinity								
Mean	25.7	25.1	23.5	21.5	22.1	17.7	35.4	35.6
SD	8.7	6.3	7.9	12.8	12.1	11.7	0.2	0.1
Max	36.4	31.3	32.8	37.4	36.2	36.3	35.6	35.8
Min	0.0	0.0	0.1	0.0	0.0	0.0	35.2	35.4

upper estuary and feeder creeks and rivers (Fig. 2). In the three Louisiana study zones SI_{Aqua} generally showed better outcomes moving down-estuary and offshore, with SI_{Aqua} ranging up to the maximum value, 1. However, the percentage surface area of Louisiana zones that obtained a low score (<0.33) was much higher (>18.1 %) than for Texas zones (< 5 %; Table 2). Across all six estuarine study zones, the results reflect a southwest-to-northeast gradient, with the saltier southwest estuaries showing only small areas of unsuitable SI_{Aqua} (Table 2), which in contrast dominates in the upper-estuarine areas of Louisiana study zones, with suitable (>0.66) areas occurring more in the lower-estuary and offshore. Maximum index values nearing 1 (on the 0–1 scale) were observed off the CHE and the BRE zones, while the Texas offshore zones remained below 0.66 (only a small patch south of CAS yielded scores just over 0.66). Under future conditions in BAR and BRE, low SI_{Aqua} were reduced (Table 2), although this likely reflects that this spatial grid failed to capture fewer up-estuary areas.

Included in the calculation of the index, time to market in the best scoring areas (represented by minimum values) varied between 259 and 291 within Louisiana estuarine zones, while oysters were consistently predicted not to reach the threshold within the first year across all Texas estuaries, apart from very small areas in CAS and GAL (Table 3). However, oysters from Texas zones were within a few mm of the 75 mm market size on average (Table 3), and if the model was run for more than 365 days, they would likely have reached time to market within a limited time (see Table S3).

3.2.2. *Restoration potential*

Oyster restoration potential across the six study zones showed high variability between the six studied estuarine zones. Like aquaculture, a general positive gradient from upper-estuary to offshore waters was observed, this time in all the study zones, with increasing areas predicting low SI_{Resto} inshore in the lower salinity Louisiana estuaries as compared to the Texas estuaries (Fig. 3). Texas estuary study zones, which did not score high (>0.66) SI_{Aqua} obtained much higher results for SI_{Resto}, with more than half of the study area obtaining high scores.

In the BRE study zone, a well-defined zone of low SI_{Resto} (0–0.2) along the west part of the BRE was predicted immediately next to much higher-ranking restoration scores moving offshore (>0.5; Fig. 3). This low score is likely due to a low gonado-somatic index, which did not necessarily affect tissue growth over the year but limited spawning and, thus SI_{Resto}. Oysters in the adjacent area, with higher predicted SI_{Resto}, spawned and briefly lost weight (due to the egg release), but as spawning events have little effect on tissue biomass at the end of the year, a high restoration score was predicted in these areas bordering the above-described low score area.

Overall, the model predicted higher reproductive outputs in

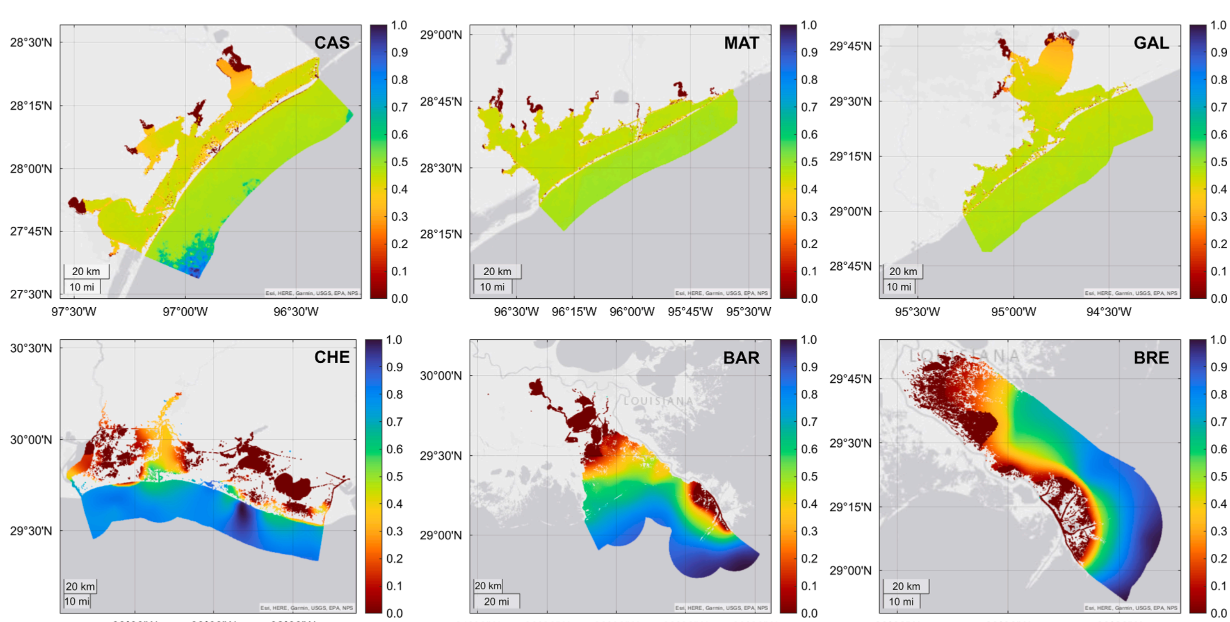

Fig. 2. Current aquaculture potential index (SI_{Aqua}) for oysters calculated using averaged environmental conditions over the 2014–2020 period in CAS (Corpus Christi-Aransas-San Antonio Bays; top left), MAT (Matagorda Bay; top center), GAL (Galveston Bay; top right), CHE (Chenier basin; bottom left), BAR (Barataria Bay; bottom center) and BRE (Breton Sound; bottom right). Color bars represent the SI_{Aqua} scale, with 0 indicating a low score and 1 a high score, calculated using Eq. (1). Map background is from Matlab, created using Esri (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

Table 2
Percentage of study zones grid cells with predicted high (> 0.66), medium (0.33–0.66), and low (< 0.33) suitability indices for aquaculture and restoration of oysters over the 2014–2020 period. CAS: Corpus Christi Bay/Aransas Bay/San Antonio Bay, MAT: Matagorda Bay, GAL: Galveston Bay, CHE: Chenier Basin, BAR: Barataria Bay and BRE: Breton Sound. BAR-future and BRE-future represent modeled conditions for the 2041–2050 period (Williams et al., 2018).

Study zones	CAS	MAT	GAL	CHE	BAR	BRE	BAR-future	BRE-future
SI_{Aqua} (% total area)								
High ($SI_{Aqua} > 0.66$)	2.7	0.0	0.0	65.4	49.4	41.1	25.4	50.9
Medium ($0.33 < SI_{Aqua} < 0.66$)	92.4	97.5	96.4	11.1	32.5	28.1	74.6	49.1
Low ($SI_{Aqua} < 0.33$)	4.9	2.5	3.6	23.5	18.1	30.8	0.0	0.0
SI_{Resto} (% total area)								
High ($SI_{Resto} > 0.66$)	54.8	69.8	68.3	70.3	59.2	53.8	11.3	14.5
Medium ($0.33 < SI_{Resto} < 0.66$)	37.2	27.5	26.3	5.0	17.2	9.3	88.7	85.5
Low ($SI_{Resto} < 0.33$)	8.0	2.7	5.4	24.7	23.6	36.9	0.0	0.0

Louisiana compared to Texas estuarine zones (Table 3). The highest spawning potential was predicted in the south of BAR, with close to 8 million eggs released during the first year of growth. Similarly, BAR was found to provide conditions for the highest tissue growth, with individual oysters weighing more than 9 g WW at the end of the one-year simulation.

3.2.3. Inter-annual variability in mortality

Oyster survival throughout seven individual years of simulations (2014–2020) was predicted across more than 72 % of each estuarine zone (Table 4; Fig. S3). MAT had the highest survival level, with 88 % of its area presenting no mortality in any year, while CHE had the lowest survival level, and BRE showed the highest annual variability in survival. However, all estuarine zones had areas that were predicted to experience mortality in at least one of the seven years examined, accounting for ~ 12–28 % of each estuarine zone.

3.3. Future conditions

SI_{Aqua} using GCM outputs along the coast of Texas and Louisiana were not comparable to current condition outputs due to the above-described differences in spatial extent and resolution. For the future conditions modeled, SI_{Aqua} predicts better suitability moving offshore along the whole coast and is most suitable in southwest Texas, followed by offshore from the Mississippi River outlet in Louisiana (Fig. 4). The restoration potential under future predicted conditions showed similar patterns with generally higher index values compared to SI_{Aqua} in all six estuarine study zones under current conditions (Fig. 4). The highest index values (>0.9) were also predicted off the coast in Southwest Texas and off the mouth of the Mississippi River.

In two Louisiana estuaries, BRE and BAR, where projections were obtained for current and future conditions, we only compared general trends since the spatial resolution under the two timelines (current vs. future) differed. SI_{Aqua} in BAR was projected to decline by ~0.15 overall under future conditions (Fig. 5). The decrease was especially important in down-estuary locations, which extended only 5 km offshore (Fig. 6). Meanwhile in BRE, SI_{Aqua} was projected to slightly increase by ~0.08 overall, with the SI_{Aqua} gradient pushing slightly inshore up-estuary compared to the current trends (Fig. 6); however, this change in the gradient may reflect as much the coarser spatial resolution under future conditions.

Comparing current and future conditions in BAR and BRE, where both time series can be superimposed, SI_{Resto} was generally lower under future conditions, except for offshore locations where little difference occurred (Fig. 6). Mean SI_{Resto} in BAR and BRE was projected to decline by ~0.18 and ~0.02, respectively, under future conditions (Fig. 5). As with SI_{Aqua}, the higher values of SI_{Resto} inside the BRE estuary result from much higher future salinity conditions originating from the GCM along the coastline.

Table 3
Mean, standard deviation (SD), max and min values for oysters averaged by estuarine zone for 2014–2020 for time to market (d; shell height = 75 mm), shell height (mm), wet tissue weight (g) and cumulated eggs (#) at the end of one year simulation (365 days). CAS: Corpus Christi Bay/Aransas Bay/San Antonio Bay, MAT: Matagorda Bay, GAL: Galveston Bay, CHE: Chenier Basin, BAR: Barataria Bay and BRE: Breton Sound. BAR-future and BRE-future represent modeled conditions for the 2041–2050 period (Williams et al., 2018).

Study zones	CAS	MAT	GAL	CHE	BAR	BRE	BAR-future	BRE-future
Time to market (d)								
Mean	365	—*	365	333	320	331	341	334
SD	2	—*	0	22	34	33	14	17
Max	—*	—*	—*	—*	—*	—*	—*	—*
Min	349	—*	363	291	259	265	318	310
Shell height (mm)								
Mean	6.88	6.78	6.65	6.74	7.32	6.58	7.80	7.85
SD	0.85	0.79	0.74	2.91	2.69	2.87	0.28	0.37
Max	7.77	7.48	7.53	8.97	9.56	9.33	8.30	8.37
Min	0.60	0.60	0.60	0.71	0.71	0.71	7.29	7.12
Weight (g)								
Mean	3.32	3.18	2.97	4.49	5.25	4.25	4.86	4.92
SD	0.83	0.62	0.69	2.54	2.63	2.82	0.63	0.67
Max	4.62	4.09	4.23	7.42	9.06	8.28	7.86	5.92
Min	0.00	0.00	0.00	0.00	0.00	0.00	3.90	3.64
Cumulated eggs (#)								
Mean	$2.8\ 10^6$	$2.6\ 10^6$	$2.4\ 10^6$	$4.0\ 10^6$	$4.5\ 10^6$	$3.8\ 10^6$	$2.5\ 10^6$	$2.6\ 10^6$
SD	$1.1\ 10^6$	$0.7\ 10^6$	$0.7\ 10^6$	$2.3\ 10^6$	$2.6\ 10^6$	$2.9\ 10^6$	$1.4\ 10^6$	$1.6\ 10^6$
Max	$4.8\ 10^6$	$3.8\ 10^6$	$3.6\ 10^6$	$6.1\ 10^6$	$7.8\ 10^6$	$7.7\ 10^6$	$6.5\ 10^6$	$6.7\ 10^6$
Min	0.0	0.0	0.0	0.0	0.0	0.0	$1.9\ 10^6$	$1.9\ 10^6$

[*] No value when market size threshold (75 mm) was not reached at the end of the simulation after 1 year.

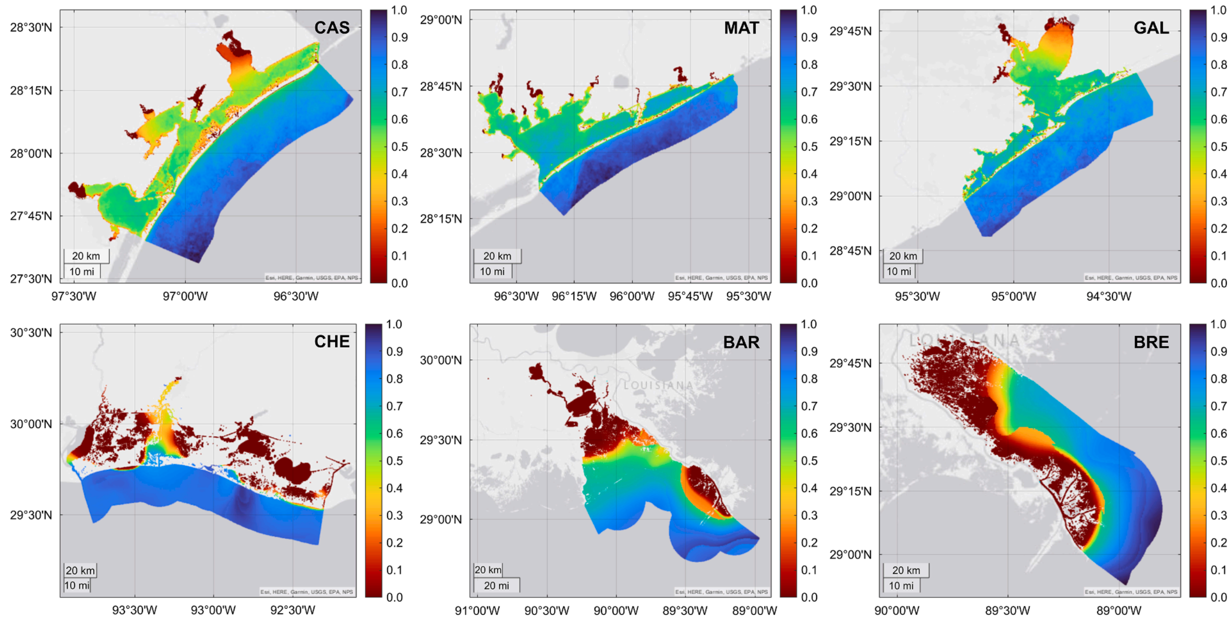

Fig. 3. Current restoration potential index (SI_{Resto}) for oysters calculated using averaged environmental conditions over the 2014–2020 period in CAS (Corpus Christi-Aransas-San Diego Bays; top left), MAT (Matagorda Bay; top center), GAL (Galveston Bay; top right), CHE (Chenier basin; bottom left), BAR (Barataria Bay; bottom center) and BRE (Breton Sound; bottom right). Color bars represent the SI_{Resto} scale, with 0 indicating a low score and 1 a high score, calculated using Eq. (2). Map background is from Matlab, created using Esri (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

Table 4
Percentage of estuarine study zones grid cells with predicted oyster survival across all seven years over the 2014–2020 period. CAS: Corpus Christi Bay/Aransas Bay/San Antonio Bay, MAT: Matagorda Bay, GAL: Galveston Bay, CHE: Chenier Basin, BAR: Barataria Bay and BRE: Breton Sound. BAR-future and BRE-future represent modeled conditions for the 2041–2050 period (Williams et al., 2018).

Study zones	CAS	MAT	GAL	CHE	BAR	BRE	BAR-future	BRE-future
Survival in all 7 years	74.8	88.1	77.6	72.6	83.4	73.5	100.0	100.0
Survival in 4 to 6 years	3.9	1.3	3.4	6.7	3.7	9.9	0.0	0.0
Survival in 1 to 3 years	5.4	3.6	6.5	4.7	3.5	8.2	0.0	0.0
No survival	15.9	7.0	12.5	13.0	9.4	8.4	0.0	0.0

4. Discussion

Mechanistic modeling of organisms' physiological responses to changes in environmental conditions provides valuable predictions to inform the conservation, restoration and management of farmed and natural resources. Here, using an oyster bioenergetics model based on DEB theory enables predictions of oyster growth, survival and reproduction across the fundamental niche of the eastern oyster, including environmental conditions not currently observed but predicted to occur with climate change. Future scenario scores were limited by a lack of estuarine and coastal future projections for salinity and temperature, presenting a key limitation of current GCMs. With over 80 % of commercial fisheries dependent on coastal areas, and over 27 % of the global population living in coastal areas, this highlights a priority to improve inshore GCM projections to assist decision makers in ensuring the future resilience of resources (Reimann et al., 2023). Regardless, the oyster DEB model identifies potential aquaculture and restoration potential at a spatial resolution matching decision-making; combined with information on competing uses, local regulations and accessibility information, this tool can support managers, restoration practitioners and producers in planning reef restoration and aquaculture projects.

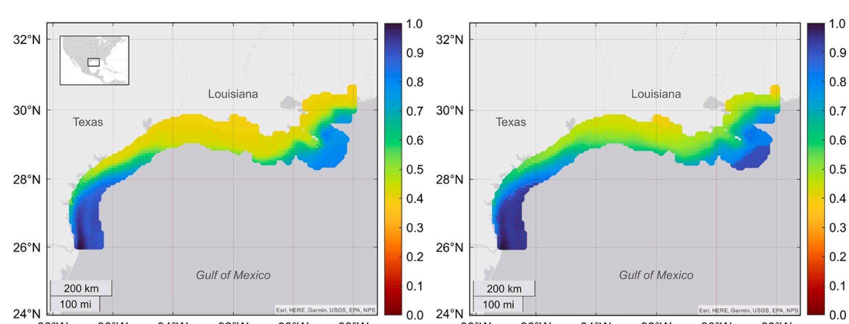

Fig. 4. Future aquaculture potential index (SI_{Aqua}; left) and restoration potential index (SI_{Resto}; right) for oysters calculated using averaged environmental conditions over the 2041–2050 period along the Texas-Louisiana coast. Color bar represents the SI_{Aqua} and SI_{Resto} scales, with 0 indicating a low score and 1 a high score, calculated using Eq. (1) and Eq. (2), respectively. Map background is from Matlab, created using Esri (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

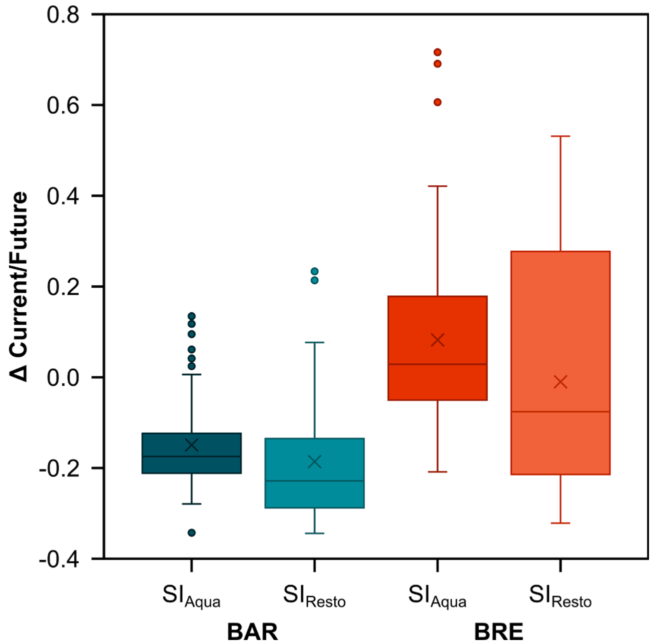

Fig. 5. Change in aquaculture potential index (SI_{Aqua}) and restoration potential index (SI_{Resto}) for oysters in Barataria Bay (BAR) and Breton Sound (BRE), between current (2014–2020) and future (2041–2050) periods. Box plots depict the minimum, first quartile, median, third quartile, and maximum, with outliers depicted as single points (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

4.1. Current conditions

Simulation outputs across the six estuarine study zones matched the general growth, reproduction and survival patterns observed in field monitoring studies; however, direct comparisons are difficult because of the discrete nature of field samplings in space and time. Lowe et al. (2017) provide an extensive comparison of seasonal size-structured oyster growth rates across Louisiana estuaries based on long-term (1988–2015) monitoring data, showing that spat oysters from Calcasieu (central bay in CHE, Fig. 1) tend to grow better than in BAR and BRE, a trend reversed in older individuals. Simulation outputs predicted similar trends with higher potential for aquaculture and restoration, calculated using measures of shell growth and tissue weight, respectively. Sehlinger et al. (2019) further noted that oysters in BAR consistently grew faster than oysters in BRE, which we also found in our simulations (Table 2).

Rarely reported in the literature, to our knowledge, but extremely important for aquaculture operations, are predictions of the time necessary to reach market size (determined by growth rates). Here, simulations showed differences between Louisiana and Texas estuarine zones, with Texas estuarine zones predicted to take more than 365 days to reach market size (< 1 % areas achieved enough growth in CAS and GAL), while all Louisiana estuarine zones had areas reaching market size in less than 300 days. Louisiana's higher food availability (i.e., chlorophyll-a) likely explains this pattern. But had simulations been extended for a few weeks or months, the shell height threshold would have been reached in > 82 % of each Texas estuarine zone within three months of the second year of growth (Table S3). The faster growth and greater food availability may also contribute to the higher fecundity reported for Louisiana oysters, which were predicted to release up to 6.1–7.8 10^6 eggs compared to 3.6–4.8 10^6 eggs for Texas oysters. These numbers match the few existing reports for reproduction in the GoM, such as that by Choi et al. (1993), indicating between 3.7 and 65.4 10^6 eggs per spawning event for 7–12 cm oysters in GAL, or by Marshall et al. (2020) who reported up to 5.5 10^6 eggs per individual spawning event. Considering that reproduction increases in older oysters and that >2 spawning events usually occur in a year in nGoM (Walton et al., 2013; Lavaud et al., 2017), our estimates of 2.4–4.5 10^6 eggs per year for 1-year-old oysters (Table 2) are in the same order of magnitude. While reproduction and cumulated eggs are critical for the sustainability of wild oyster populations and reefs, linking these outputs to larval transport, settlement and survival on reefs is critical for understanding the effect of these events on reef development and conservation (La Peyre et al., 2021; Sable et al., 2023).

Despite, on average, faster growth and greater reproduction, Louisiana estuarine zones showed greater areas with no oyster survival compared to Texas estuarine zones. Some of this is explained by the more complex estuarine areas in Louisiana, with wetlands and low salinity areas comprising high proportions of these estuaries. Oysters would not perform well in such areas, and in fact, no oysters or reefs are reported in many of these low-scoring aquaculture and restoration zones (e.g., east side of CHE or up-estuary in BAR; LDWF, 2022). In contrast, predicted mortality in CAS and other Texas estuarine zones was restricted to very limited areas compared to Louisiana estuaries (scores of 0 in Figs. 2 and 3). Importantly, this pattern disappears in extreme conditions and inter-annual variability, as revealed by simulations using individual years (Table 4). While Louisiana estuarine study zones experience better food conditions and showed more spatiotemporal variability than Texas, the percent area where oysters survived was very similar across all estuarine study zones. Mortality in our model exclusively reflects the effect of different environmental conditions as model parameters remained unchanged between individuals and across locations, and this model does not incorporate biotic effects, such as mortality from predators. The fact that the DEB model can reproduce the different patterns of the physiology and the life history of eastern oysters in the nGoM further demonstrates the strength of this tool.

One important aspect of our study is that we rely on daily data to force the oyster DEB model. Daily averages over several years allowed us to evaluate long-term trends and compare study zones over long periods. But a crucial point in our analysis is the availability of data for each year, which permits more in-depth analysis of the patterns observed with means. For instance, while the SI_{Aqua} was in the majority above 0.33 in all estuaries (Table 2), exploring the cumulated survival success from single years (Fig. S3) indicated that many of these locations experienced mortality in multiple years between 2014 and 2020, particularly in Louisiana estuaries. The focus on a long-term period versus a year-to-year analysis matters for aquaculture and restoration, which have different goals. Locations in which oysters may be expected to grow well on average but that experience deadly conditions in 4 or more years over our 7-year study (10.6–21.3 % across all study zones; Table 4) may not be appropriate for aquaculture production as repeated crop failure would not be economically sustainable. In a restoration context where efforts are limited in time, this can also mean the failure of a project. However, restored reefs may be more flexible as long-term success is preferred to annual productivity. Restoration managed at the metapopulation level may expand their covered areas for restoration by monitoring success based on the sustainability of the overall metapopulation, with the expectation that populations (reefs) at the upper and lower ends of the metapopulations distribution within an estuary would serve as refuges during extreme year and events (i.e., Lipcius et al. 2015, Swam et al. 2022).

As in any modeling exercise, the quality, availability, but also the processing of data before use in a model condition the outcome of simulations. Most methods of exploring the potential of organisms to grow, reproduce and survive in an environment rely on defining forcing conditions on a monthly or annual basis (Beseres Pollack et al., 2012; Sable et al., 2023). However, recent evidence indicates that monthly means, or averaged means over many years may fail to identify potential extreme or acute events affecting the resource (Zabin et al., 2022; La Peyre et al., 2022; Briscoe et al., 2023). For example, laboratory studies have shown that either acute changes in salinity, frequent changes in

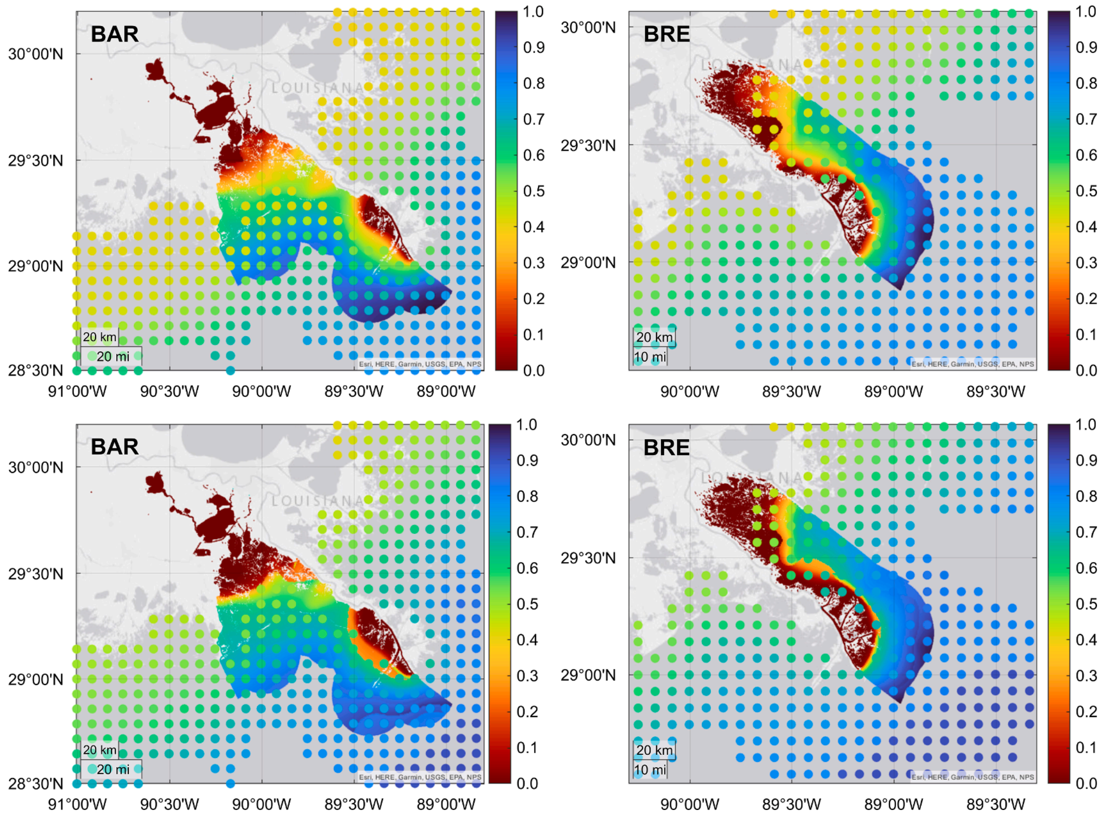

Fig. 6. Superimposition of current (solid colored area) and future (large dots) aquaculture potential index (SI_{Aqua}; top panels) and restoration potential index (SI_{Resto}; bottom panels) calculated using averaged environmental conditions over the 2014–2020 and 2041–2050 periods, respectively, in Barataria Bay (BAR; left panels) and Breton Sound (BRE; right panels). Current index represents a 200 m grid resolution while future index represents a 1/12° (about 10 km) grid resolution, based on the best available environmental forcing data for each period. Color bars represent the SI_{Aqua} and SI_{Resto} scales, with 0 indicating a low score and 1 a high score, calculated using Eq. (1) and Eq. (2), respectively. Map background is from Matlab, created using Esri (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

salinity, or cumulated days of exposure, while not necessarily changing the annual mean, might be mortal to oyster populations (Marshall et al., 2021a, 2021b; Coxe et al., 2023). Extreme events such as salinity freshets or marine heat waves are usually brief (days to weeks), but may have direct lethal, or sub-lethal effects conditions. Statistical models relying on general tolerance ranges may be unable to account for such events. Considering the effect of extremes in environmental conditions is therefore critical in providing insight to restoration managers.

4.2. Future conditions

The approach employed here compares to existing methods developed for terrestrial organisms to model species distribution and performance (Kearney et al., 2021), which are also based on DEB theory and query available satellite-driven data to inform individual biophysical modeling. Simulating oyster performance under future conditions proved more challenging due to the limited availability of projected salinity and temperature in the future coastal zone. A compromise was made in the selection of the model to provide both a high enough spatial resolution, which enabled comparison to model outputs under current conditions, and a high temporal resolution (i.e., daily), which is necessary to capture low salinity events that put oysters near their physiological limits and can lead to mortality outbreaks (Marshall et al., 2021a).

Comparing current years (salinity: 2015–2020; temperature: 2014) from HadGEM3-GC3.1 used for future conditions with observed current conditions of the same time frame showed a clear overestimation of salinity in BAR and BRE estuaries, but relatively similar temperature projections (Fig. S2). As a result, comparisons of simulation results between current and future conditions were not straightforward. The higher simulated salinity of HadGEM3-GC3.1 indicates that the model fails to reproduce coastal and estuarine processes and predicts inshore and estuarine salinity and temperature largely driven by resulting in minimal variation between offshore and estuarine conditions. Moreover, the lack of interannual variability in future conditions led to consistent survival across time and space, including in areas of BAR and BRE with no oysters currently. Another limitation in our interpretation of the results lies in the lack of good projections for food availability (i.e., chlorophyll-a) in the coastal and estuarine zones. With the development of regional models currently being developed for the Gulf of Mexico (Xue and Warner, 2022), future model efforts may have better forcing variables and be able to better integrate oceanic forcing conditions with coastal and estuarine processes driving salinity (i.e., freshwater inflow, local precipitation events, evapotranspiration rates) and temperature.

Nevertheless, the pattern of better aquaculture and restoration scores shifting toward offshore areas in the future (Fig. 4) is an important result of our study and has been pointed out by Swam et al. (2022), who defined the area extending 5 km from the Louisiana coast as an area with high aquaculture production potential. This pattern in our results corroborates the conclusions of recent reports identifying offshore areas for mariculture in the nGoM (Riley et al., 2021) and zones of resilience (Swam et al., 2022), suggesting exploration of these offshore areas for future oyster production. The zones identified in these studies correspond to the highest index values we predicted. Continued improvement and the need for spatial and temporally accurate data along coastal and estuarine areas are critical to increasing the accuracy and resolution of this application.

4.3. Model needs and limitations

The model and approach outlined here rely on the biological potential for oyster growth, reproduction and survival, incorporating only salinity, temperature and food resources. The definition of the suitability indices used could be refined; for instance considering logistics and regulatory aspects, substrate, wave energy, distance from launch and other ecosystem actors and processes, among other factors (i.e., Puckett et al. 2018). Tissue weight may be relevant for aquaculture too as condition index changes with reproduction activity. But shell height determines the marketability of oysters, not biomass, and triploid oysters, which do not reproduce, are often used in aquaculture. Currently, no feedback exists between oysters in our model and the environment, but drawing from carrying capacity studies could provide estimates of the production potential based on interactions with other trophic levels in the ecosystem; a version of the DEB model used here was already applied in such context (Lavaud et al., 2020). In addition, increasing evidence of potentially lethal acute events from anoxic events (Rabalais and Turner, 2019; Coxe et al., 2023), high suspended sediment loads, or large-scale human engineering projects (CPRA, 2021) may be critical in selecting locations for the development of off-bottom aquaculture farms in the region, and were not accounted for in this work.

Similarly, the selection of locations for restoration from this work are based exclusively on biological potential at each site and does not account for bottom type, competing uses, regulatory limitations, or connectivity between reefs within a metapopulation (Puckett et al., 2018). However, our model provides a means to move beyond the typical use of historical data only to guide restoration projects, which is valuable with climate change exacerbating extreme events and creating new ranges of environmental conditions, the success (in time and magnitude) of restoration efforts may be more unpredictable. Here, we provided a powerful way to measure potential metapopulation success by including reproductive output; estimating cumulative reproductive outputs over the years and across environmental variability can be critical to manage existing reefs and support the creation of new ones. Our model was run independently in each cell of the estuarine study zone grids, but considering larval development can provide even more valuable insights. This constitutes a priority for local agencies (La Peyre et al., 2021, 2022) and efforts are currently put towards the creation of an oyster metapopulation model, taking advantage of the capacity of DEB theory to cover the entire life cycle with the same equation and parameters as in the present study (La Peyre et al., 2021). As opposed to aquaculture (refer to paragraph above; Riley et al. 2021), the interpretation of offshore predictions related to restoration purposes should be taken with caution as only active management (artificial reef creation) could support the development of oyster populations in these areas, which would probably be expensive for state agencies to conduct.

Inter-individual variability in oyster physiological rates can be rather large and can be accounted for through IBM approaches (Lavaud et al., 2021b). The high spatial and temporal resolution of our approach conflicted with computing limitations which restricted the current mapping efforts to simulations of a single average individual in each cell of the grid. But the existing diversity within natural populations (or on reefs set for restoration) in terms of physiological tolerance, may result in increased resilience to environmental variations, including extreme events. To go further, we analyzed some choices made in this study, such as the start date of simulations, based here on the time at which aquaculture farmers usually deploy spat obtained from hatcheries. The effect of deploying newly set oysters (6 mm) at different times of the year revealed that current practices match maximized outputs in length (Table S4). This information could also be useful for restoration planning management. Finally, our mechanistic approach could help investigate triploid mortality phenomena faced by the aquaculture industry in the nGoM over recent years (Bodenstein et al., 2023) by exploring possible physiological causes linked to changes in energy allocation.

5. Conclusion

As a foundation species, it is important to understand how climate change and human activities affect eastern oysters and the multiple ecological services the species provides. Using a mechanistic bioenergetic DEB model, our approach allows the identification of suitable areas based on the physiological capacity (materialized by the ecological niche) of oysters with great accuracy. Moreover, we provided a variety of indicators that could be useful for managers, planners and farmers in their restoration and cultivation activities. The model reproduced observed gradients in production and distribution, but also provided insight into key life-history traits such as reproductive potential, survival or time to reach market size at a spatial scale never achieved before. Thanks to the universal mechanistic nature of the DEB framework, the method we developed here could be used to investigate the effects of changing environmental conditions on other species or on ecosystem-level processes. Importantly, better projections for the future remain dependent upon the availability of climate model outputs. Our simulations could benefit from better coverage, especially in coastal areas. Even with such uncertainty in future conditions, the present work still provides valuable predictions of the physiological response of oysters under the currently studied future scenario.

CRediT authorship contribution statement

Romain Lavaud: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Megan K La Peyre:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Brady Couvillion:** Conceptualization, Methodology, Software, Writing – review & editing. **Jennifer Beseres Pollack:** Conceptualization, Writing – review & editing. **Vincent Brown:** Methodology, Software, Writing – review & editing. **Terence A Palmer:** Writing – review & editing. **Barry Keim:** Resources, Writing – review & editing.

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

All data used were referenced in the article. The code can be made available upon request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2023.110603.

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