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Dynamic Energy Budget modelling to predict eastern oyster growth, reproduction, and mortality under river management and climate change scenarios

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Abstract

Eastern oysters growing in deltaic Louisiana estuaries in the northern Gulf of Mexico must tolerate considerable salinity variation from natural climate variability (e.g., rainfall and stream run-off pushing isohalines offshore; tropical storms pushing isohalines inshore) and man-made diversions and siphons releasing freshwater from the Mississippi River. These salinity variations are predicted to increase with future climate change because of the increased frequency of stronger storms and also in response to proposed large-scale river diversions. Increased Mississippi River flow into coastal estuaries from river diversions, along with potential changes in rainfall and stream run-off from climate change will alter spatial and temporal salinity patterns. In this study we used an individual Dynamic Energy Budget model to predict growth and reproductive potential of eastern oysters across observed and simulated salinity gradients corresponding to different climate and river management scenarios. We used validated model outputs of salinity from a coupled hydrology-hydrodynamic model to assess the current impacts of Davis Pond diversion discharge on oysters located downstream. Under a high diversion discharge scenario oyster growth potential was reduced by 9%, 4%, and 1% in Upper, Mid, and Lower Bay locations, respectively, as compared to a limited discharge year. Reproductive outputs decreased by 34% and 2% in the Upper and Lower Bay locations, respectively, and increased by 2% at the Mid Bay site. In scenarios combining predicted increased temperature with the effect of diversions, all oysters located in the Upper and Mid Bay sites died due to severe summer conditions (high temperatures combined with low salinity). Overall, oysters in down-estuary locations, influenced by both estuarine river management and gulf conditions demonstrated significant tolerance to changing salinity and temperature conditions from diversions alone and when combined with climate change. In contrast, oysters located up-estuary, and exposed to more extreme salinity impacts from river management, demonstrated potentially lethal impacts through direct mortality, and reduced sustainability through decrease in reproductive output. These predictions at the individual level may translate into less sustainable populations in the most extreme scenarios; restoration and production plans may benefit from accounting for these impacts on reproductive output particularly as decision makers seek to restore critical oyster areas.

Keywords

Bioenergetics; Salinity; Physiology; northern Gulf of Mexico; *Crassostrea virginica*; Louisiana.

1. Introduction

Coastal marine ecosystems are, by definition, transition zones between the terrestrial and marine domains, subject to constant fluctuations due to many factors including tidal regimes, hydrodynamics, terrestrial inputs, coastal erosion and development. These ecosystems provide a fundamental environment to a wide range of organisms both aquatic (nursery and feeding grounds) and terrestrial (access to marine food supply, protection from storms). However, because of their location, coastal marine ecosystems are particularly subject to rapid perturbations from natural and anthropogenic events including storms, sea level rise, tsunami, hypoxia, acidification, urbanization, industrialization, pollution, fishing, and eutrophication. The pressure on these ecosystems grows with increased impacts of climate change, and increasing settlement of human populations near the coasts, which threaten the preservation of the resources and services coastal environments provide.

In Louisiana, the Mississippi River has been channelized by a system of levees since the 1930s in order to protect the human population from floods and facilitate industrial development through fluvial trade. While the levees effectively provide safety to populations and development opportunities to local and supra-local economies, major side-effects to this engineering work include a reduction of river inflow and a drop in sediment input to the delta area, resulting in more intense salinity variations and land loss (Coastal Protection and Restoration Authority of Louisiana, 2017). In the past, this freshwater input carried a load of sediment equivalent to the annual natural subsidence of the lands (Hatton et al., 1983; Coleman et al., 1998) and helped maintain the natural protection that wetlands provide from hurricanes. In 1991, the first diversion in the levee system, Caernarvon, with a discharge capacity of 8,000 CFS (cubic feet per second), was created on the east bank of the Mississippi River for the explicit purpose of maintaining optimal salinity in the Breton Sound coastal area for commercial oyster production (Chew et al., 1984). This was followed by the creation of the Davis pond diversion, with capacity of 10,650 CFS, on the west bank of the Mississippi River to discharge freshwater into Barataria Bay. After the devastating hurricanes Katrina and Rita in 2005, efforts intensified to enhance shoreline protection, including proposed large-scale diversions into Barataria Bay and Breton Sound estuaries that would divert an order of magnitude more freshwater compared to the current Davis Pond and Caernarvon diversions (Coastal Protection and Restoration Authority of Louisiana, 2017). However, the benefits of such structures are under debate (Nittrouer et al., 2009; Turner, 2009; Kearney et al., 2011; Nyman, 2014) and concerns have been raised regarding the impacts of increased freshwater fluxes on coastal fisheries (Piazza and La Peyre, 2011; Adamack et al., 2012; Soniat et al., 2013; Wang et al., 2017). The first of the proposed four large-scale diversion projects, the mid-Barataria sediment diversion, is expected to be completed in 2021. However, research to evaluate its impacts on wildlife and fisheries remains scarce (de Mutsert et al., 2017).

The eastern oyster, *Crassostrea virginica*, serves as an ecosystem engineer across coastal bays and estuaries, and supports an important industry. However, this species may be threatened by changes in the hydrology of their environment. Unlike many fish or crustaceans, once established, oysters are sessile and cannot escape adverse conditions by migrating to more suitable waters. As a result, changes in water quality, from either direct anthropogenic activities including restoration (e.g., diversions, barrier island restoration, shoreline protection), and impacts from changing climate such as increased storms, precipitation and altered river flows, can impact eastern oysters in many ways. Many of these changes are predicted to impact estuarine salinity over historic oyster habitats. Lower salinity in particular has been shown to increase mortality (Newell et al., 2000; Casas et al., 2015; Rybovich et al., 2016), reduce physiological rates such as clearance (Loosanoff, 1953; Casas et al., 2018), respiration (Shumway and Koehn, 1982; Casas et al., 2018), growth (La Peyre et al., 2013; Lowe et al., 2017), gametogenesis (Butler, 1949), and alter spat (Rybovich et al., 2016) and larval development and settlement (Calabrese and Davis, 1970), overall reducing the fitness of oyster populations in impacted areas.

Numerical modeling can be used to predict and quantify the effect of stressors on an organism including the assessment of interactive effects of multiple stressors. Models developed on the basis of the Dynamic Energy Budget (DEB) theory (Kooijman, 2010) have been increasingly used over the past decade in part because of their mechanistic nature, their replicability, and a drive to unify biological organization representation (Augustine and

Kooijman, 2019), but also because of their flexibility and a wide range of applications. Lavaud et al. (2017) developed an individual DEB model for the eastern oyster, which allows the simulation of all physiological rates (growth, feeding, respiration, reproductive investment) and the quantification of the effect of salinity on these metabolic processes. Such individual based models require environmental condition inputs (temperature, food availability, salinity, etc.), which can be provided by direct measurements but may also originate from spatialized and temporal models of the system they live in (e.g. Saraiva et al., 2017). A high-resolution, coupled hydrology-hydrodynamic model was developed for Barataria Bay by Das et al. (2012) and used to study the effects of the opening of the Davis Pond diversion on salinity gradients in the bay. The combination of an individual bioenergetic model and a coupled hydrology-hydrodynamic model, along with the available time-series of observational data, offer a powerful simulation tool for the quantification of the effects of environmental conditions on living resources (Filgueira et al., 2015; Le Goff et al., 2017; Saraiva et al., 2017). More importantly, this type of mechanistic approach, as opposed to empirical ones, is more suitable for assessing and predicting the probable impacts of management policies and future environmental conditions.

This paper examines impacts of river management and climate change on eastern oyster in Barataria Bay, Louisiana, and provides new insights into the consequences of higher freshwater inputs on oyster biology. Specifically, using DEB modeling and scenario building, our objectives were to: 1) assess the current effects of environmental variability on oyster physiology (growth and reproduction) in coastal Louisiana, 2) evaluate how oyster physiology may be affected by operation of large diversions, and 3) estimate the combined effects of river management and climate change on oyster physiology. We addressed the first objective using environmental monitoring data from 2002–2015 records in Barataria Bay as inputs to the individual oyster DEB model (Lavaud et al., 2017). We then used outputs from a coupled hydrology-hydrodynamic model of Barataria Bay to determine the effects of diverted freshwater on oysters to address the second objective. Finally, we built environmental scenarios based on projections of future climate conditions and present-day river management endpoints to explore the combined consequences of environmental changes and river management on oyster productivity.

2 Material and Methods

2.1 Study area

Barataria Bay is a shallow, turbid, 120 km long estuary located in Louisiana, USA (Figure 1). The 1,673 km^2 (413,407 acres) system is bordered by the Mississippi River delta to the east, Bayou Lafourche to the west, the Gulf of Mexico to the south through four tidal passes, and is fringed by a complex system of bayous, canals, channels and small embayments (USEPA, 1999). The tropic diurnal tidal range averages 0.3 m and salinities range from near zero in the upper reaches of the estuary to about 25 in the southernmost section of the estuary (Conner and Day, 1987; Das et al., 2012). Freshwater inputs to the Barataria estuary originate from rainfall, stream runoff, man-made diversions and siphons from the Mississippi River, and from the Gulf Intracoastal Waterway. Eastern oysters occupy most of the area between Hackberry Bay and the Barataria waterway to the north to the barrier islands of Grand Isle and Grande Terre to the south.

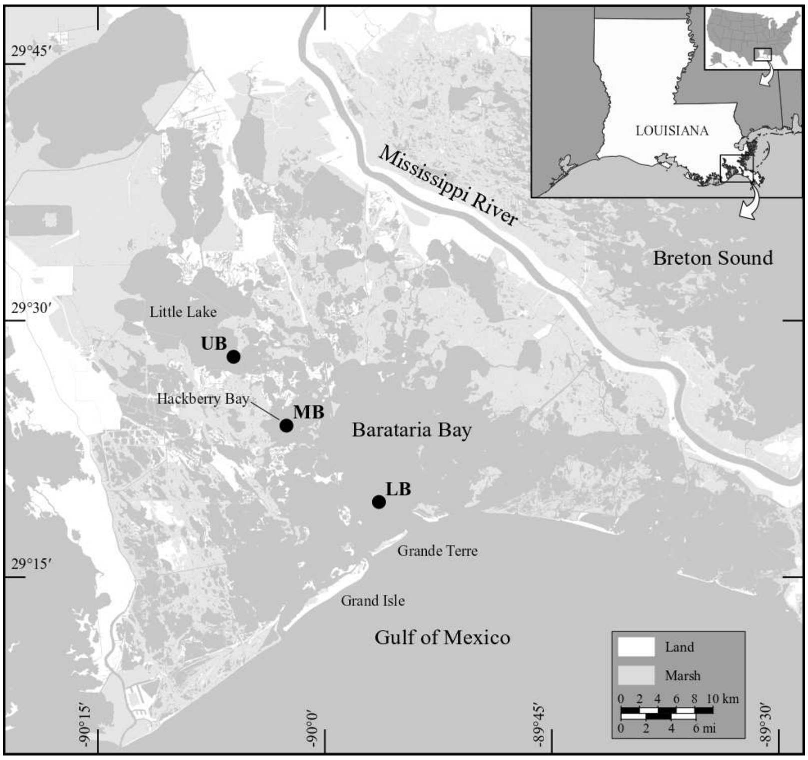

Figure 1. Location of the U.S. Geological Survey monitoring stations (circle) in Barataria Bay, southern Louisiana, USA. Abbreviations for site locations stand for: Upper Bay (UB), Mid Bay (MB), and Lower Bay

(LB).

Barataria Bay has historically supported some of the more productive oyster grounds within Louisiana, with 563 km^2 (139,164 acres) of managed private oyster leases (LDWF, 2018), 162 km^2 (40,031 acres) of public seed grounds (LDWF, 2013), and contains the first, and currently only, permitted oyster aquaculture park within coastal Louisiana. Extensive oil and gas activities, and shrimping and fishing are also supported across the entire bay.

2.2 Individual oyster DEB model

The individual bioenergetic model for the eastern oyster based on DEB theory and including the effects of salinity was recently presented by Lavaud et al. (2017). All model equations and parameters used in the present work were described by these authors and are available in the Supplementary Information file. Briefly, the DEB model describes all energy fluxes between the environment and four state variables: reserve, structure, maturity, and maturation (for juveniles) or reproduction buffer and gametes (for adults). Energy from food is assimilated into reserves, which are mobilized and split between the somatic (structure) and reproductive (maturity, buffer, and gametes) branches at a fixed proportion according to the kappa-rule. In each branch, mobilized energy is first used to fulfill maintenance costs, i.e. somatic maintenance and maturity maintenance. Parameters of the eastern oyster DEB model were estimated and validated using field data on shell height, whole tissue and gonad dry weight across the northern Gulf of Mexico. Lavaud et al. (2017) showed that across the northern Gulf of Mexico coast, the impact of low salinity on ingestion rates explained most of the variation in eastern oyster growth. The model thus includes a correction function of the ingestion rate $\dot{p}_X$, which is unaltered when salinity remains over 10, is progressively reduced from salinities of 10 to 3, and becomes null under the lower threshold.

We added two new features to the existing oyster DEB model: 1) variability in some parameter values and initial state conditions, and 2) mortality criteria based on temperature, salinity, and condition index. Inter-individual variability in the response to environmental conditions is characteristic of oysters (Thomas et al., 2016), therefore, simulations were carried out on 21 individuals, whom initial size, maximum ingestion rate ($\{\dot{p}_{Xm}\}$) and upper salinity tolerance threshold (i.e. the salinity at which physiological rates start to be impacted) were either increased or decreased by up to 10% from the species' parameter values, following a normal distribution. Individual model outputs were then pooled to create an average and inter-individual standard deviation (reported as ± SD).

Mortality was introduced in the model as the result of energetic failure or extreme environmental conditions. Energetic failure corresponds to a deficit in energy to fulfill essential maintenance costs (turnover of structural proteins, concentration gradients across membranes, muscle work, maintenance of maturity level; Kooijman, 2010). Before reaching this lethal stage, energy can be reallocated to maintenance from the reproduction buffer (Table S1, $\dot{p}_{LR}$) and, if a deficit remains, structure can be broken down (Table S1, $\dot{p}_{Lm}$). Extreme environmental conditions can induce rapid and severe stress not related to internal energy shortage. Based on field and laboratory observations documenting disruption of osmotic gradients that are beyond the regulating capacities of oysters (Newell et al., 2000; La Peyre et al., 2013; Casas et al., 2015; Rybovich et al., 2016), modeled oysters were assumed to die when they were exposed for more than 7 days to salinity lower than 1 and temperature above 20 ºC, or salinity below 5 and temperature above 32 ºC. Finally, cumulated egg production was computed using an energy density of 2.566 10^{-4} J g^{-1} (dry mass, Powell et al., 1995) and an average dry mass of 4 10^{-8} g egg^{-1} (Gallager et al., 1986).

2.3 Coupled hydrology-hydrodynamic model

The high-resolution (100 m), two-dimensional (2-D), coupled hydrology-hydrodynamic model described in Das et al. (2012) was used to produce salinity fields to the DEB model for two contrasting years with limited (2002) and strong (2008) river diversion influence. The model forcing functions used in this depth-integrated model are tides coming in from the Gulf of Mexico, rainfall and evaporation over the model domain, local runoff, salinity at the ocean boundary, water temperature, wind, and freshwater diversions from the Mississippi River (Das et al., 2012). Model-derived salinity time series were obtained for locations where validation data were available (see the next paragraph). Temperature data were gathered from nearby U.S. Geological Survey (USGS) monitoring stations. Additional USGS salinity values were also collected to complete salinity fields from the coupled hydrology-hydrodynamic model which only started at day 79 due to forcing data availability (Das et al., 2012), in order to provide a full year of environmental conditions to the individual DEB model.

2.4 Environmental and validation data

Three sites in Barataria Bay were selected (Figure 1), Upper Bay, Mid Bay, and Lower Bay (UB, MB, and LB respectively), based on their proximity to USGS water monitoring stations and the availability of oyster growth data provided by the Louisiana Department of Wildlife and Fisheries. Water temperature and salinity were retrieved from USGS monitoring station #292800090060000 in Little Lake (29°28'00"N, 90°06'00"W) for the UB site, station #73802512 in Hackberry Bay (29°23'54"N, 90°02'28"W) for the MB site, and station #291929089562600 near Grande Terre Island (29°19'29"N, 89°56'26"W) for the LB site. Records from the period 2002–2015 (http://waterdata.usgs.gov/la/nwis/nwis) showed the lowest salinity values at the UB site with an average of 5.8 ± 2.0 (SD), medium range values at the MB site with an average of 10.6 ± 2.3, and the highest salinities were measured at the LB site with an average of 19.7 ± 3.3.

2.5 Simulation experiments

We designed three specific studies with a total of eight scenarios focusing on: 1) natural variability under present-day conditions, 2) effects of river diversions, and, 3) effects of hypothetical environmental conditions at the end of the 21st century in response to global warming (Table 1).

Study 1: Natural variability under present-day conditions

In the first study, we used current environmental data (temperature and salinity) recorded at the three USGS stations in Barataria Bay during typical dry years (2006 and 2012) and typical wet years (2010 and 2013), selected based on yearly mean conditions. These time series were used to force the individual DEB model at the UB, MB, and LB sites, in order to demonstrate how current natural conditions shape oyster's bioenergetics. Simulations were conducted on a time period based on the availability of forcing data, starting in March and ending in December of each year. Initial oyster length at each site was set to 76.8 mm (average size of wild-caught oysters in Barataria Bay in their third year of life, Banks et al., 2016) and the initial state of reserves was set at 80% (values subsequently applied in study 2 and 3).

Table 1. Summary information for the three studies and eight scenarios designed to investigate natural variability under present-day conditions (Study 1, four scenarios), the effect of diversions (Study 2, two scenarios), and the effect of hypothetical environmental conditions at the end of the 21st century (Study 3, two scenarios). USGS = U.S. Geological Survey.

Study	Scenario	Temperature conditions	Salinity conditions
1	2006 – dry	USGS data from 2006	
	2010 – wet	USGS data from 2010	
	2012 – dry	USGS data from 2012	
	2013 – wet	USGS data from 2013	
2	Standard	USGS data from 2002	Das et al. (2012) model outputs for 2002
	Diversion	USGS data from 2008	Das et al. (2012) model outputs for 2008
3	Low Flow	2002-2015-seasonal average from USGS data + 2.6 °C	USGS data from 2006
	High Flow		USGS data from 2010

Study 2: Effects of river diversions

In the second study, we investigated the effects of river diversions by using model outputs of salinity from the coupled hydrology-hydrodynamic model to simulate oyster growth under two different salinity scenarios originally developed by Das et al. (2012). In the *Standard* scenario, the model used actual tides, rainfall, evaporation, wind, and the actual Davis Pond discharge during 2002 (Figure 2a), which occurred only during the July-December period and was very limited in scope. In the *Diversion* scenario, the 2002 diversion discharge data were replaced with the 2008 data, a high Davis Pond discharge year (Figure 2b), in order to illustrate a representative fully operational annual diversion schedule, while keeping all other forcing identical. As in Study 1, temperature data were retrieved from USGS monitoring stations. This exercise was originally conducted by Das et al. (2012) to investigate the hydrodynamic and hydrologic consequences of a fully operational Davis Pond diversion, in an attempt to constrain as many parameters as possible. In the present study we explore the consequences of these hydrologic changes on oyster physiology. Oyster growth data were compared to shell length observations during years 2002 and 2008.

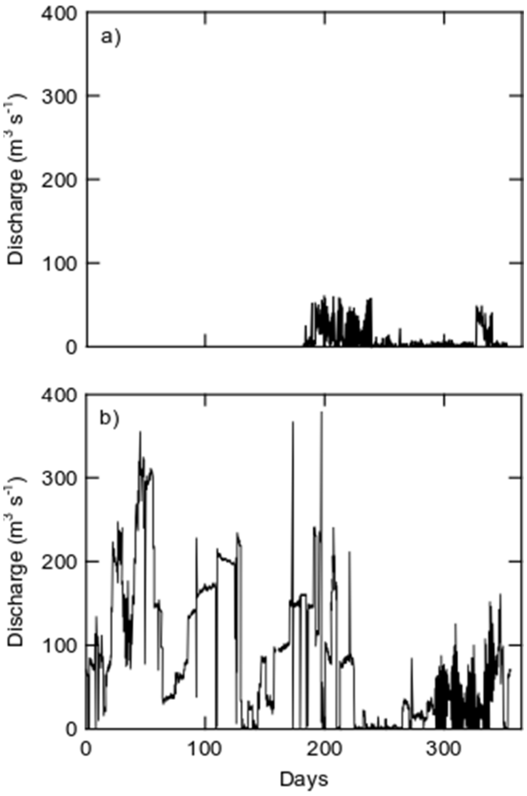

Figure 2. Discharge rates from the Davis Pond diversion during 2002 (a) and 2008 (b) used in the *Standard* and *Diversion* scenarios of Study 2, respectively (adapted from data in Das et al. (2012).

Study 3: End of the century conditions

In the third study, we explored the interaction between the effects caused by river management and climate change on the energy budget of oysters. A recent review of sea surface temperature (SST) model predictions indicated that yearly average SST in the Gulf of Mexico may increase by 0.30 to 0.35 °C per decade until the end of the 21st century (Alexander et al., 2018) under the RCP8.5 “business as usual” scenario (IPCC, 2014). This would translate to a temperature increase of 2.4 to 2.8 °C in the study area. Alexander et al. (2018) also indicate that the predicted SST seasonal cycle in the Gulf of Mexico would only slightly diverge from current observations, with a slight extension of the summer period. Based on this report, we constructed a time series of temperatures for Barataria Bay, based on daily average data over the period 2002–2015 (USGS) increased by 2.6 °C. We used salinity data sets from Study 1 to illustrate the variety of salinity regimes encountered at each of the three sites (UB, MB, and LB). A *Low flow* scenario was created using data from 2006, a typical dry year with limited diversion operations and a *High flow* scenario was created using data from 2010, a year with increased freshwater flow due to repeated and prolonged diversion opening. Data from these years were preferred to data from the coupled hydrology-hydrodynamic model as the latter do not cover a full year – starting mid-March (day 79) – omitting important effects from winter climatic conditions on salinity patterns.

3 Results

3.1 Study 1: natural variability in current conditions

Records of environmental variables in Barataria Bay at the lower, mid and upper sites showed very similar temperature time series across sites (Table 2), while salinity varied considerably between years and location (Table 2, Figure 3). Little variation in average temperature was observed between the studied years (2006, 2010, 2012, and 2013), with a mean of 22.9 ± 0.7 °C (± SD, Table 2). Mean salinity at the lower bay site (LB, Table 2) averaged 20.4 ± 6.2 and showed little variation between years with a difference of 3.3 between 2006 and 2010, the two most extreme years. At the upper bay site (UB, Table 2) mean salinity averaged 8.2 ± 5.3 and varied more between years (difference of 5.80 between 2006 and 2010). Mean salinity at the mid bay site (MB, Table 2) was 11.5 ± 6.5 and showed the highest variation between years (difference of 10.6 between 2006 and 2010).

Model predictions in 2006 showed similar oyster growth at the three sites (Figure 3a) with an average length of 118.5 mm and similar standard deviation of only 5.8 mm between the three sites. In 2012, a slightly less dry year, this variation increased to 10.9 mm, with expected length at the UB site dropping to 95.4 mm (Figure 3k); note that this value is impacted by the absence of individuals who died from energetic failure at this location (only three individuals out of twenty one survived). Due to mortality at the UB site, the number of eggs spawned was only 5% of the amount spawned in 2006. The number of eggs spawned by oysters at the MB site was close to the amount from 2006 and an additional late spawn occurred for some individuals at the LB site, resulting in a higher number of eggs spawned in 2012 at this location (Table 2). During the wettest year in the collection, 2010, the model predicted massive oyster mortality at the UB and MB sites during the summer (Figure 3i). All oysters from the UB site succumbed from exposure at extremely low salinity (<1). Only three oysters survived at the MB site while all others died from energetic failure. Salinity in the summer of 2010 (between day 182 and 273) averaged 2.4 ± 2.3 (SD) and 4.9 ± 3.1 (SD) at the UB and MB sites, respectively (Figure 3j). In 2013, also a wet year but not as extreme as 2010, oysters at the UB site died at the beginning of summer, mostly from energetic failure (Figure 3s). Reproductive activity was impacted at the MB site where oysters spawned only twice (Table 2). Inter-individual variability in the parameters of the model created a range of growth potential and reproductive activity in all simulations but small differences in survival, i.e. when oysters died at a given site, almost all individuals succumbed despite their physiological differences.

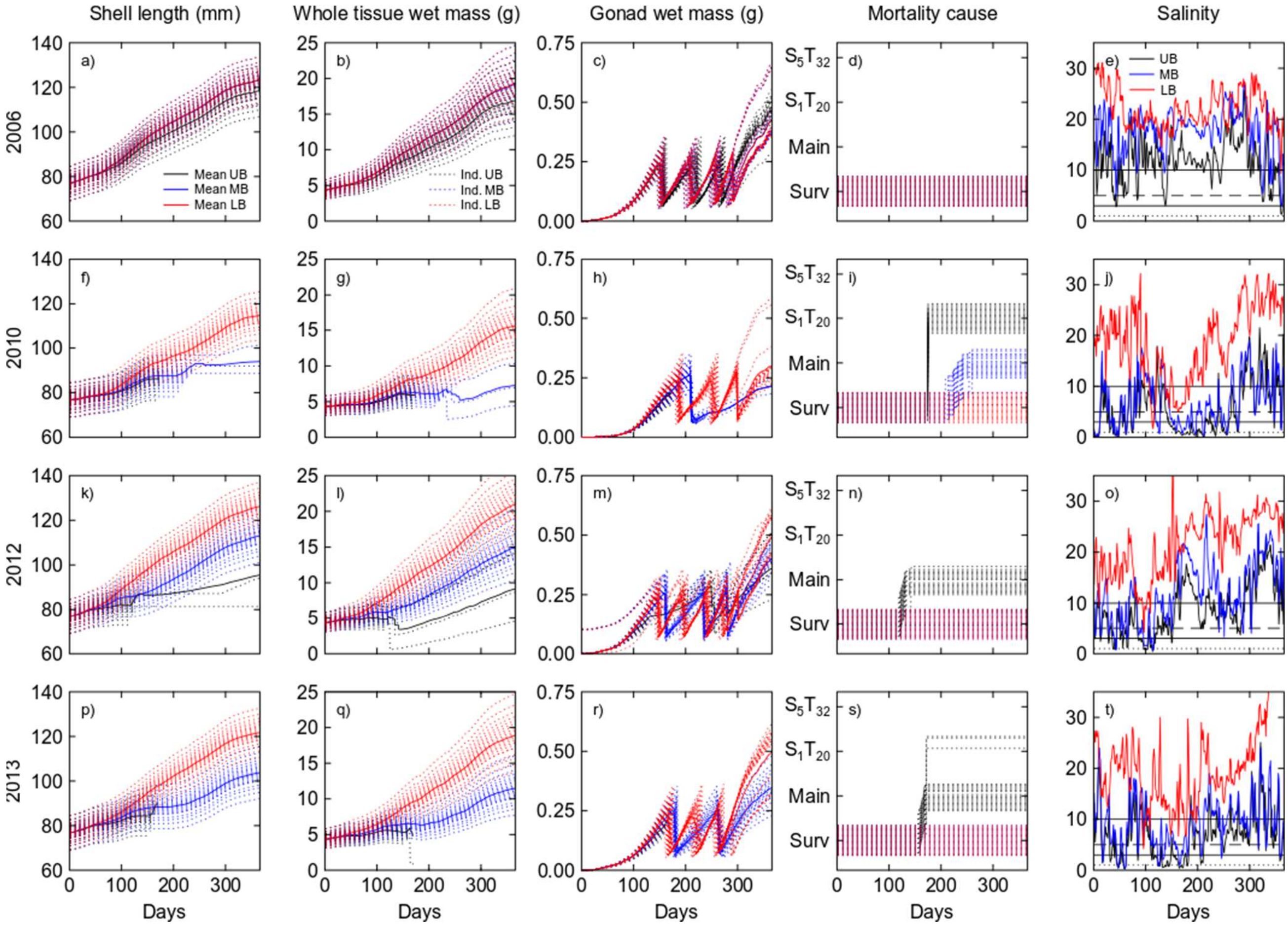

Figure 3. Oyster Dynamic Energy Budget (DEB) model outputs under typical present conditions (Study 1), using U.S. Geological Survey (USGS) salinity data (right column) from three locations in Barataria Bay: Upper Bay (UB, blue), Mid Bay (MB, red), and Lower Bay (LB, black). Four years are presented: 2006 (top row) and 2012 (third row) both typically hot and dry years; 2010 (second row) and 2013 (bottom row) both typically mild and wet years. Shell length (mm, first column), whole tissue wet mass (g, second column), and gonad wet mass (g, third column) are presented as the average (solid line) of 21 oysters (dotted lines) differing from each other through individual variation in 4 parameters. Cause of mortality (fourth column) indicates if oysters survived (Surv) or died from energy deficit to fuel maintenance costs (Main), exposure at salinity under 1 and temperature over 20 °C (S_1T_{20}) or exposure at salinity under 5 and temperature over 32 °C (S_5T_{32}), for more than a week. Salinity profiles (fifth column) are presented together with the different thresholds (horizontal lines) for filtration and survival used in the model.

Table 2. Mean temperature (°C), salinity, final shell length (mm), whole tissue wet mass (g), and total number of eggs spawned (N = 21 or remaining live oysters) in simulations conducted during two typically dry years (2006 and 2012) and two typically wet years (2010 and 2013) (study 1). Abbreviations for site location stand for: Upper Bay (UB), Mid Bay (MB), and Lower Bay (LB).

Year	Site	Mean temperature (SD)	Mean salinity (SD)	Shell length (SD)	Whole tissue wet mass (SD)	# eggs spawned (SD)
2006 dry	UB	23.3 (6.4)	11.6 (4.3)	118.5 (5.7)	17.1 (2.6)	1.4 10^7 (0.2 10^7)
	MB		17.6 (4.4)	123.2 (5.3)	19.4 (2.7)	1.8 10^7 (0.2 10^7)
	LB		22.0 (3.8)	123.4 (5.3)	19.6 (2.7)	1.8 10^7 (0.2 10^7)
2010 wet	UB	22.2 (7.7)	5.8 (5.0)	0.0 (0.0)	0.0 (0.0)	0.0 10^7 (0.0 10^7)
	MB		7.0 (4.8)	*93.9 (6.6)	*7.3 (3.0)	0.4 10^7 (0.2 10^7)
	LB		18.7 (7.3)	114.6 (5.4)	15.6 (2.4)	1.4 10^7 (0.1 10^7)
2012 dry	UB	23.5 (5.6)	8.6 (5.1)	*95.4 (14.8)	*9.1 (4.8)	0.1 10^7 (0.2 10^7)
	MB		12.1 (6.0)	113.0 (6.0)	15.0 (2.5)	1.4 10^7 (0.2 10^7)
	LB		21.5 (6.0)	126.2 (5.5)	21.0 (3.0)	2.1 10^7 (0.2 10^7)
2013 dry	UB	22.4 (6.4)	6.8 (4.7)	0.0 (0.0)	0.0 (0.0)	0.0 10^7 (0.0 10^7)
	MB		9.3 (5.0)	103.7 (5.8)	11.5 (2.1)	0.9 10^7 (0.1 10^7)
	LB		19.3 (6.4)	121.7 (5.5)	18.9 (2.8)	1.5 10^7 (0.2 10^7)

*N = 3.

3.2 Study 2: effect of river diversions

In the *Standard* scenario, mimicking the actual Davis Pond discharge during 2002 (i.e., a reduced opening of the Davis Pond diversion), salinity decreased <5 only for seven non-consecutive days at the UB site and remained above 5 and above 10 at the MB and LB sites, respectively. Oysters grew up to 114.4 ± 5.6 mm on average at the UB site, up to 118.5 ± 5.3 mm at the MB site, and up to 118.3 ± 5.3 mm at the LB site (Figure 4, first column). Mean tissue wet mass was also lower at the UB site, with 15.2 ± 2.4 g, as compared to 17.5 ± 2.5 g at the MB site and 17.5 ± 2.5 g at the LB site (Figure 4, second column). All oysters but one spawned three times at the UB site under this scenario. At the MB and LB sites two spawning events were simulated, except for three individuals at the MB site and two individuals at the LB site, who spawned a third time late in the year (Figure 4, third column).

In the *Diversion* scenario, oysters shell length was reduced to 103.9 ± 6.1 mm on average at the UB site, 113.9 ± 6.1 mm at the MB and 117.7 ± 5.4 mm at the LB site (Figure 4, first column), which correspond to a change of –9%, –4%, and –1%, respectively, as compared to the *Standard* scenario (Table 3). Variations in whole tissue wet mass between the two scenarios were even more evident as the average mass dropped to 11.1 ± 2.0 g (–27%) at the UB site and 15.3 ± 2.6 g (–13%) at the MB site. At the LB site whole tissue wet mass almost remained steady with an average value of 17.2 ± 2.5 g (Figure 4l), corresponding to a –2% change between scenarios (Table 3). Oysters from the UB site experienced only two spawning events under the *High flow* scenario, which resulted in an average 34% decrease in the total number of eggs released over the year (Table 3). Spawning activity was less impacted at the LB site where the average number of eggs released decreased by only 2%. With four individuals experiencing a third spawning at the MB site, the average number of eggs released increased by 2%. Finally, no mortality was predicted in any of the simulations run in this study.

Table 3. Mean percent change in final shell length, whole tissue wet mass, and total number of eggs spawned (N = 21) between simulations conducted under the *Standard* and *Diversion* scenarios (study 2). Negative numbers represent decreases under the *Diversion* scenario and Max and Min represent maximum and minimum change, respectively. Abbreviations for site location stand for: Upper Bay (UB), Mid Bay (MB), and Lower Bay (LB).

	Shell length (%)	Whole tissue wet mass (%)	# eggs spawned (%)

	UB	MB	LB	UB	MB	LB	UB	MB	LB
Mean	–9.3	–3.9	–0.5	–27.4	–13.0	–1.5	–34.0	1.6	–1.8
SD	0.9	0.8	0.1	1.9	2.5	0.3	8.7	7.1	5.9
Max	–11.0	–5.6	–0.8	–31.8	–18.1	–2.0	–40.0	32.6	–25.0
Min	–7.7	–2.4	–0.3	–24.6	–8.5	–0.1	0.1	0.1	0.0

3.3 Study 3: end of the century conditions

Projected environmental conditions used at the end of the century scenarios are presented in Figure 5. According to these simulations, temperatures would remain above 30 °C for 145 days a year, as compared to 48 on average over the period 2002–2015 (Figure 5a). The number of days with concomitant temperatures above 30 °C and salinities below 5, one of the thresholds for mortality defined in the model after 7 consecutive days of exposure to such conditions, would more than double under both scenarios at the UB and MB sites.

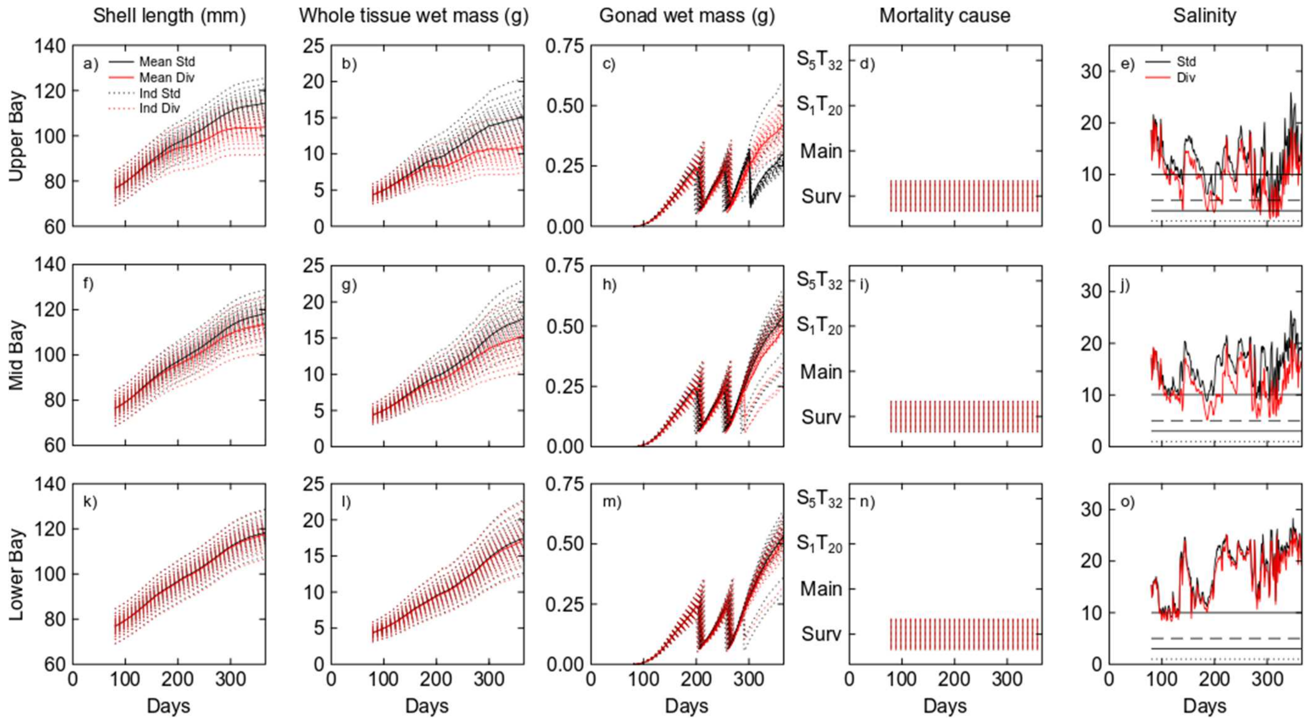

Figure 4. Oyster DEB model outputs from Study 2, under limited diversion operations in the *Standard* scenario (Std, black lines) and under the *Diversion* scenario with a fully operational diversion (Div, red lines). Shell length (mm, first column), whole tissue wet mass (g, second column), and gonad wet mass (g, third column) are presented as the average (solid line) of 21 oysters (dotted lines) differing from each other through individual

variation in 4 parameters. Cause of mortality (fourth column) indicates if oysters survived (Surv) or died from energy deficit to fuel maintenance costs (Main), exposure at salinity under 1 and temperature over 20 °C (S_1T_{20}) or exposure at salinity under 5 and temperature over 32 °C (S_5T_{32}), for more than a week. Salinity profiles (fifth column) are presented together with the different thresholds (horizontal lines) for filtration and survival used in the model.

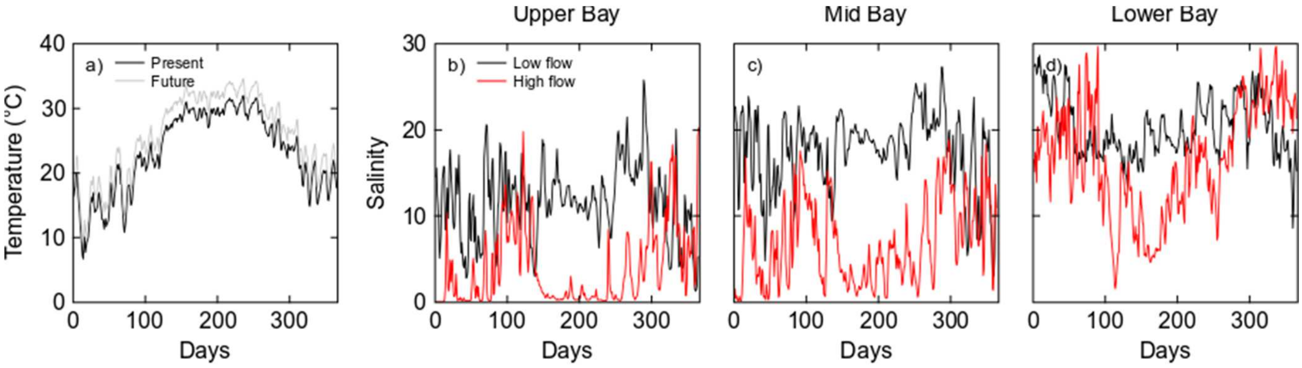

Figure 5. Environmental variables used in the simulations for conditions at the end of the century (study 3). Present (black) and future (grey) temperatures are presented in the left panel (a). Salinity time series used at the Upper Bay (b), Mid Bay (c), and Lower Bay (d) in the *Low flow* scenario (black) come from 2006 U.S. Geological Survey (USGS) data and from 2010 USGS data in the *High flow* scenario (red).

Under projected environmental conditions for the end of the century, oysters in the three study sites performed well in the *Low flow* scenario, reaching lengths over 114.9 mm on average (Figure 6, first column). More variation was observed in oyster tissue wet weight at the different sites but estimated values were in the same range as in present-day conditions (Table 2, Study 1 year 2006). Reproductive patterns were similar in all three sites and showed three spawning events during the simulated year. The number of eggs spawned was slightly below the values estimated in 2006 in Study 1 (Tables 2, 4). Under this *Low flow* scenario, no mortality was predicted at any site.

In the *High flow* scenario, Oysters at the LB site performed almost as well as in the *Low flow* scenario, with an average final length of 117.3 ± 5.4 mm and an average tissue wet weight of 16.9 ± 2.5 g (Table 4, Figure 6k,l). However, despite the inter-individual variability in some model parameters, all individuals at the MB and

UB sites died (Figure 6d,i). Oysters at the MB site, notably, succumbed from exposure to temperature above 32 °C combined to salinity below 5, about 50 days after their first and only spawning event, which was delayed by about a month.

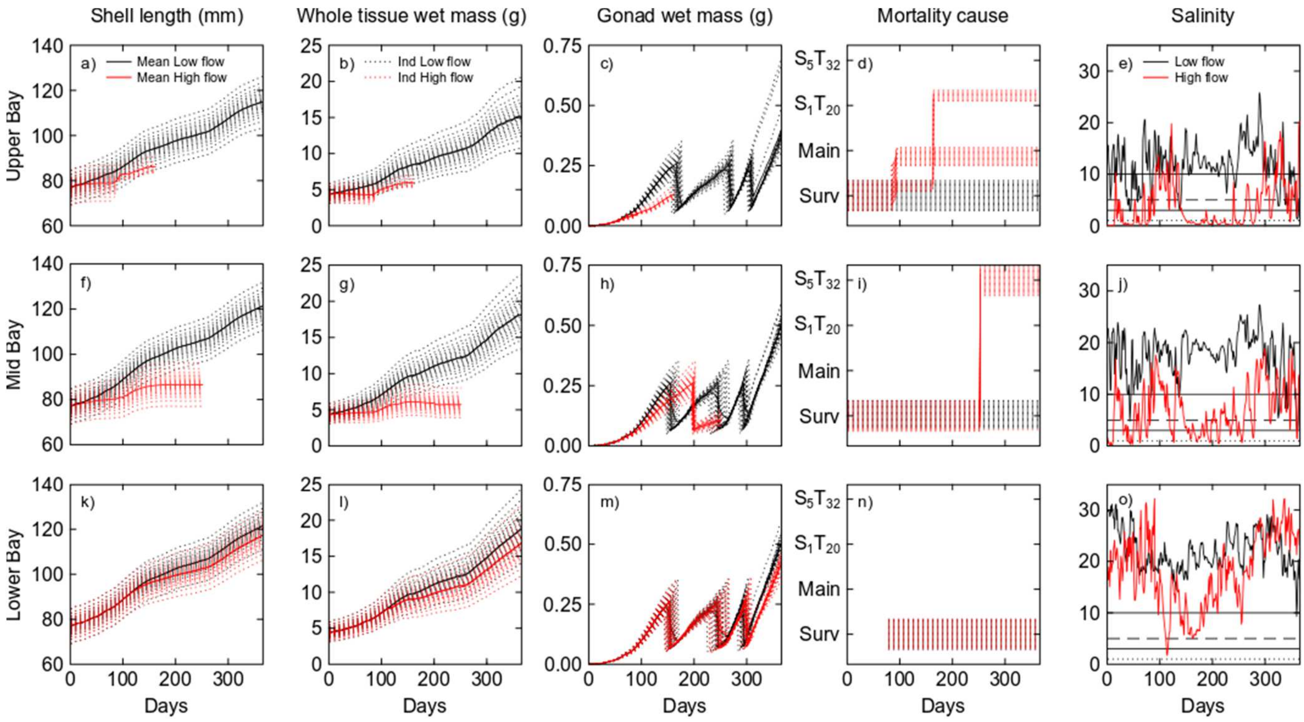

Figure 6. Oyster DEB model outputs under the *Low flow* scenario (black) and the *High flow* (red) scenario for the end of the century (Study 3). Shell length (mm, first column), whole tissue wet mass (g, second column), and gonad wet mass (g, third column) are presented as the average (solid line) of 21 oysters (dotted lines) differing from each other through individual variation in 4 parameters. Cause of mortality (fourth column) indicates if oysters survived (Surv) or died from energy deficit to fuel maintenance costs (Main), exposure at salinity under 1 and temperature over 20 °C (S_1T_{20}) or exposure at salinity under 5 and temperature over 32 °C (S_5T_{32}), for more than a week. Salinity profiles (fifth column) are presented together with the different thresholds (horizontal lines) for filtration and survival used in the model.

Table 4. Mean final shell length (cm), whole tissue wet mass (g), and total number of eggs spawned (N = 21) in simulations conducted with projected conditions at the end of the century (study 3). Abbreviations for site location stand for: Upper Bay (UB), Mid Bay (MB) and Lower Bay (LB).

Scenario	Site	Shell length (SD)	Whole tissue wet mass (SD)	# eggs spawned (SD)
Low flow	UB	114.9 (5.7)	15.1 (2.4)	1.3 10^7 (0.2 10^7)
Low flow	MB	120.9 (5.3)	18.2 (2.5)	1.4 10^7 (0.2 10^7)
Low flow	LB	121.5 (5.2)	18.8 (2.6)	1.4 10^7 (0.2 10^7)
High flow	UB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
High flow	MB	0.0 (0.0)	0.0 (0.0)	0.5 10^7 (0.1 10^7)
High flow	LB	117.3 (5.4)	16.9 (2.5)	1.4 10^7 (0.2 10^7)

4 Discussion

Oysters have a high tolerance to the dynamic nature of estuarine and coastal water quality but face increased threats from human activities (fishing, river management, pollution, etc.) as well as rapidly changing environmental conditions. In this study we aimed to quantify the effects of freshwater diversions from the Mississippi River, and some of the climate change consequences on oyster bioenergetics through numerical modeling. While oysters located in the southern part of Barataria Bay seem to tolerate the potential salinity and temperature conditions explored in the different scenarios, growth, reproduction, and survival of oysters present in more up-estuary waters may be negatively impacted. These results indicate that oysters may remain abundant in the south of the bay under the current diversion framework, but the anticipated changes in the north may cross thresholds that would impact oyster harvest sustainability in Barataria Bay.

4.1 Present-day oyster productivity

Using records of past environmental conditions we first demonstrated how the current variability of estuarine water chemistry affected oyster bioenergetics. High variability in individual shell growth was predicted between sites, with values ranging from 1.1 ± 0.3 mm mo^{-1} at the UB site in 2010 to 4.1 ± 0.1 mm mo^{-1} at the LB site in 2012. Our predictions match calculations for wild-caught oysters (i.e., sack oysters; >75.0 mm) in Barataria Bay over the last two decades done by Lowe et al. (2017), who reported average monthly growth rates values ranging from 1.7 ± 0.1 mm mo^{-1} to 3.6 ± 0.4 mm mo^{-1} for the entire bay (i.e., all sites considered). Sehlinger et al. (2019) reported average monthly growth rates ranging between 0.1 mm mo^{-1} and 6.0 mm mo^{-1} for oysters growing in trays in Barataria Bay (mean = 1.5 ± 0.4 mm mo^{-1}). The modeled average growth rate at the LB site across years (3.7 ± 0.4 mm mo^{-1}) also compares well with the average growth rate of oysters growing in Grand Isle, a few km South of the LB site: 4.1 ± 0.3 mm mo^{-1} (Lavaud et al., 2017).

Under present-day conditions, the model predicted a release of about 1.5 ± 0.5 10^7 eggs (maximum: 2.7 10^7 eggs) per oyster per year on average. To our knowledge, there are no reports of fecundity observations for Louisiana oysters in the literature, but our model mean estimate is in agreement with previous studies from Texas (2.1 ± 1.3 10^7 eggs on average per oyster per year; Choi et al., 1993), Virginia (1.5 ± 0.8 10^7 eggs per oyster; Cox and Mann, 1992), Maryland (1.0 ± 0.6 10^7 eggs per oyster per year; Glandon et al., 2016), and New York (0.4 ± 0.4 10^7 eggs; Gallager and Mann, 1986). Looking at these values from the literature, there seem to be a latitudinal gradient in oyster fecundity. Our mean model predictions fit in this apparent pattern although it appears closer to the value from Virginia than the one from Texas. The particularly low salinity in Louisiana deltaic estuaries compared to other regions where oysters grow might explain the lower amount of eggs released by oysters from Louisiana (Marshall et al., 2020).

While oysters are known to tolerate high fluctuations in salinity (Calabrese and Davis, 1970), extended exposure to low salinities affects their feeding behavior (Galtsoff, 1964; MacFarland et al., 2013; Casas et al., 2018) and can lead to increased mortality (La Peyre et al., 2009; Rybovich et al., 2016). Under warm and dry conditions, oysters in all sites performed similarly (Figure 3, year 2006), indicating no significant phenotypic variation between individuals in the different locations. However, in colder and wetter years, a pronounced negative gradient in both growth and reproductive activity appeared from south to north, associated with decreased salinity at the UB site and, to a lesser extent, the MB. Upstream locations are also more likely to experience mortality due to extreme low salinities (<1, Figure 3), which has been consistently reported in the literature (La Peyre et al., 2009; Rybovich et al., 2016). Therefore, natural variability in environmental conditions must be considered as a crucial determinant in oyster productivity and fitness as well as survival. Additional pressures may then accentuate or balance the effects of such dynamics with longer-term consequences on population sustainability.

Oysters respond differently to salinity variations depending on their size. Past studies suggest that larval development is especially impacted when salinity decreases (Davis and Calabrese, 1964), but that smaller settled oysters (i.e., spat) may be more tolerant of salinity variations, including low salinity (Rybovich et al. 2016; Lowe et al., 2017). We only modeled adult oysters in this study but the DEB model could be used to evaluate the effects on the whole life cycle of oysters. Smaller individuals have lower reserve capacity relative to larger individuals. Because in DEB theory maintenance costs are fueled by reserves, the ability of smaller individuals to cope with prolonged freshwater inputs, during which oysters seclude themselves from the environment by closing their valves, could be significantly less compared to larger individuals. However, this pattern only applies up to a certain size because volume specific maintenance costs increase with size according to DEB theory, ultimately becoming the major energy expenditure to the soma by large organisms (Kooijman, 2010). This means that in a situation of prolonged valve closure, small and large individuals should be impacted before mid-sized oysters. This prediction from the theory is difficult to confirm as other factors such as predation and diseases affect growth and mortality traits. Nevertheless, La Peyre et al. (2013) reported that growth of seed oysters (~65.0 mm) in the adjacent bay of Breton Sound occurred throughout 2010 despite the extreme summer conditions, while market size oysters (>75.0 mm) showed low to no growth that same year. Large individuals also produce more gametes than smaller ones (Galtsoff, 1964), which is again expected according to DEB theory: the kappa rule of energy allocation dictates that a fixed amount of reserve is used for reproduction and maturity maintenance. While somatic maintenance increases with volume – leaving close to no energy for growth at some point – maturity maintenance relates to the level of maturity, which tops at puberty and is maintained for the rest of life, leaving an increasing amount of energy to be allocated to reproduction.

4.2 Effect of diversions

Our results indicate that under high diversion opening, oysters located in the upper sections of Barataria Bay experienced a reduction in growth of up to 11% as compared to <1% in the lower part of the Bay (Table 3). The outcome of these simulations is particularly relevant given that all other environmental conditions (temperature, precipitation, evaporation, tides, wind) were kept constant (Das et al., 2012). The only factors not considered in our study were food quantity and quality. While food quantity should not be limiting, as suggested by the elevated concentration of phytoplankton in the water (Lane et al., 2007; Schaeffer et al., 2012), phytoplankton species composition in diverted riverine waters may cause significant changes in the food quality for oysters (Bargu et al., 2011; Schaeffer et al.,2012; Riekenberg et al., 2015).

Reproductive outputs at the UB site decreased by 34% under low salinities conditions, while this number slightly increased at the MB site (+2%). The increased gonado-somatic index of oysters in the middle part of the bay, due to a reduction in whole tissue wet weight while reproductive products accumulated, must have led more individuals to spawn (Table 3). Nevertheless, as survival salinity is higher during early stages of development (>7.5; Carriker, 1951; Davis and Calabrese, 1964), oyster larvae present at this site would likely die in the days or weeks following fertilization given the very low salinities (~7) at this period of the year (Figure 4j).

The construction of river diversions and associated river management to regulate estuarine salinities, protect downstream human populations from flooding risk, or to counterbalance the deficient sediment budget of coastal marsh due to the channelization of the river, can, therefore, cause severe, rapid, and at times prolonged changes in the water chemistry of adjacent bays and estuaries where oysters grow. Such changes in salinity regimes can harm estuarine and marine life. Previous studies in an adjacent Louisiana estuary of Breton Sound, found similar trends with large-scale freshwater diversions pushing optimal salinities seaward, resulting in significant reduction in oyster growth rates, and production. For example, Wang et al. (2017) found that a large diversion decreased estuarine oyster production by up to 60%, while increasing the area of sustainable oyster harvest areas in the southern part of the estuary. Similarly, Soniat et al. (2013) identified a shift down-estuary of areas suitable for oyster production, with over 6 000 ha of estuarine area becoming unsuitable for oyster production. Similar trends are found in other regions as well. For instance, in Matagorda Bay (Texas, United States), harvestable oyster reefs disappeared in the four years following the installation of the Colorado River diversion (Wilber and Bass, 1998). In another example in Doubtful Sound (New Zealand), freshwater inputs from a hydro-electrical power station modified the salinity environment of coastal waters, resulting in a more than ten-fold reduction in abundance in two common clam and cockle species (McLeod and Wing, 2008). Additional consequences such as species invasion (Rilov et al., 2004), and changes in biodiversity (Bargu et al., 2011) may also occur.

No mortality was reported at any site in these simulations in response to Davis Pond operations (Figure 4), which suggests that the effects of Davis Pond discharges on oyster fitness are sub-lethal under present-day conditions. However, the size of the Davis Pond diversion in Barataria Bay and the Caernarvon diversion in Breton Sound, 10,650 CFS and 8,000 CFS, respectively, is relatively small in comparison with the new Mid Barataria Bay diversion currently under construction, which is expected to operate at rates of around 50,000 CFS (Coastal Protection and Restoration Authority of Louisiana, 2017). The effects of this increased diversion rate (~6x) may result in stronger impacts on hydrology, and resident oyster populations. In a recent study that used the Ecopath with Ecosim model, combined discharges from four proposed diversions into the lower Mississippi River deltaic region, resulted in a shift in abundance of oysters and several fish and crustacean species further away from the future diversion outfalls (de Mustert et al., 2017). Similarly to our results, oyster biomass was predicted to decrease in all bays, including Barataria Bay, with a small increase in oyster landings region-wide. This means that oyster harvest and cultivation activities in Barataria Bay would have to be relocated further south, near the barrier islands of Grand Isle and Grande Terre (Figure 1). While this solution could be possible, it requires the placement of hard substrate for oyster settlement, since much of this area consists of soft bottom habitats not currently suitable for oyster settlement.

4.3 Climate change and river management

With the expected change in climatic conditions for the current century, it makes sense to approach the study of future river management in the context of rising temperatures. The modeling exercise conducted in the third study of this paper showed that oysters living in locations under the influence of strong salinity changes (UB site) caused by diversion operations may be further impacted by the predicted temperature increase (2.6 °C), particularly when combined with impacts of decreased salinities. Under full diversion operation alone, these oysters showed a reduction in shell length, whole tissue wet weight and reproductive outputs and their survival was not impacted (Figure 4, top row). However, they experienced 100% mortality when diversion operation was associated with an increase in temperature by 2.6 °C (Figure 6, top row). This was also the fate of oysters at the MB site, which currently only face such mortality in extremely wet years, like in 2010 (Figure 3, second row).

One of the criteria for mortality used in the oyster DEB model is the exposure for more than 7 d to salinity <5 combined to temperature >32. Higher mortality rates were predicted in low salinity areas (UB and MB sites) in conditions for the end of the century, meaning that these oysters would be more threatened in a warmer environment. Moreover, while prolonged exposure to low salinity ([0–5]) can lead to increased mortality (e.g. Rybovich et al., 2016), higher salinity (>25) combined to elevated temperature (>30 °C) increase the prevalence of the deadly parasite *Perkinsus marinus* (La Peyre et al., 2009). Such conditions only occurred for 17 non-consecutive days in the *Low flow* scenario of projected conditions at the end of the century. *P. marinus* is also known to multiply in oysters at salinity >12 and temperature >20 °C, with increasing prevalence and infection intensities at higher salinities and temperatures (La Peyre et al., 2006, 2010). The proliferation of the pathogen within future oyster populations and the lethal and sub-lethal effects of dermo disease caused by the parasite could be included in further developments of the oyster DEB model in the same way. Flye-Sainte-Marie et al. (2009) modeled host-pathogen interactions between the Manila clam, *Ruditapes philippinarum*, and the bacteria *Vibrio tapetis*.

The combination of the impact of higher temperatures and large salinity changes due to diversion operations shows again the importance of considering multiple environmental factors in functional trait-based modeling approaches (Matzelle et al., 2015; Thomas and Bacher, 2018). In this work we used actual time series of salinity (years 2006 and 2010) to predict future oyster physiological response, which may lack accuracy. However, given that salinity regimes are difficult to predict, this approach provides at least a first estimation. As opposed to temperature, salinity records show high variability throughout the year (due to extremes in precipitations, instantaneous freshwater discharge, etc.), which makes it harder to design scenarios for future conditions. The expected increase in extreme climatic conditions due to climate change (IPCC, 2014) is particularly concerning in this perspective. Climate change drivers are already affecting the coast and their impact will grow more severe during the 21st century (Day et al., 2019). Evidence indicates that extreme weather events, such as storms and flooding, will intensify in response to climate warming (Rahmstorf and Coumou, 2011), which could impose increasing pressure on oysters in vulnerable areas. Under such conditions, diversions like the Davis Pond diversion may then be used more frequently. Consequently, the effects of increased variability in salinity time series and associated oyster responses should be investigated as well.

4.4 Conclusions

In this study we provided model outputs for oyster growth and reproductive activity under scenarios of changing river management and climate. We showed that while the natural variability of the coastal and estuarine environment characterises oyster growing areas, existing diversions already significantly impact oyster fitness in the upper parts of Barataria Bay, but have less impact in lower parts of the Bay closer to the Gulf. In up-estuary, these effects may have fatal consequences for oysters when combined with the predicted alterations of environmental conditions due to climate change. In particular, the findings that reproductive output would essentially be non-existent is particularly important as regional oyster restoration planning seeks to develop broodstock sanctuary reefs, and identify threshold conditions to help in locating restoration and protected areas (i.e., DWH NRDA, 2017). The ability to predict reproductive output, and identify potential conditions detrimental to oyster population sustainability provides a critical step forward to inform decision-makers.

As the state of Louisiana moves towards construction of new diversions in Barataria Bay, the presence of oysters in the northern part of the bay may be compromised. Fishing activities may then have to shift further south, around the barrier islands of Grand Isle and Grande Terre. The CPRA master plan projects to restore and create oyster reefs in this area, which may help balance the potential losses deeper in the bay (Coastal Protection and Restoration Authority of Louisiana, 2017). The fate of oysters and the oyster industry in this bay may well depend on the operational strategies for the diversions, the seasonal variation of climatic conditions and river flow, and the incorporation of monitoring, modeling and input from stakeholders to evaluate the changes brought by the diversions to the surrounding environment.

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CrediT authorship contribution statement

Romain Lavaud: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing – Review & Editing, Visualization. **Megan K. La Peyre**: Conceptualization, Investigation, Resources, Data Curation, Writing – Review & Editing, Visualization, Supervision. **Dubravko Justic**: Conceptualization, Methodology, Software, Formal analysis, Data Curation, Resources, Writing – Review & Editing. **Jerome F. La Peyre**: Conceptualization, Investigation, Data Curation, Resources, Writing – Review & Editing, Supervision.

Competing interest statement

The authors have no competing interests to declare.

Annexes

Table A1. Dynamic Energy Budget (DEB) model variables and equations (from Lavaud et al., 2017).

Model dynamics			*Energy fluxes equations*		
			Assimilation flux	$\dot{p}_A$	$\{\dot{p}_{Am}\}f \quad ^{2/3}c_T c_S$
Structural volume	—	$\frac{\dot{p}_G}{[E_G]} - \dot{p}_{Lm}$	Mobilization flux	$\dot{p}_C$	$E\,\frac{[E_G]m^{2/3}\dot{v}c_T + \dot{p}_M}{\kappa E + E_G}$
Reserve	$\frac{E}{\quad}$	$\dot{p}_A - \dot{p}_{Cm}$	Somatic maintenance flux	$\dot{p}_M$	$[\dot{p}_M]c_T$
			Allocation flux to growth	$\dot{p}_G$	$ax(0, \kappa\dot{p}_C - \dot{p}_M)m$
Reproduction buffer	$\frac{E_R}{\quad}$	$\dot{p}_R\kappa_R - \dot{p}_{Go} - \dot{p}_{LR}$	Maturity maintenance flux	$\dot{p}_J$	$E_H^p k_J c_T$

Energy in gonads	$\frac{E_{Gom}}{}$	$\dot{p}_{Gom} - E_{spm}$
Model outputs		
Shell length	L_w	$\frac{1/3}{\delta_M}$
Whole tissue wet mass	W	$+\frac{(E+E_R)w_E}{\mu_E}+\frac{E_{Go}}{\rho_{egg}}$
Number of spawned eggs	N_{egg}	$\frac{E_{sp}}{\rho_{egg}W_{egg}}$

Allocation flux to reproduction	$\dot{p}_R$	$ax\big(0,(1-\kappa)\dot{p}_C-\dot{p}_J\big)$, if $T > T_{Go}$, otherwise 0
Allocation flux to gonads	$\dot{p}m_{Go}$	$\kappa_R E_R\left(\frac{\dot{v}c_T}{1/3}+\frac{[\dot{p}_M]c_T}{[E_G]}\right)\left(1-\kappa\frac{E}{[E_G]m+\kappa E}\right)$, if $T > T_{Sp}$ and $gsi > gsi_{Sp}$, otherwise 0
Gonado-somatic index	gsi	$\frac{E_{Go}}{\rho_{egg}W}$
Spawned energy (via eggs)	E_{sp}	$\frac{E_{Go}\kappa_{sp}}{}$
Maintenance deficit	Mn	$ax\big(0,\dot{p}_M+\dot{p}_J-\dot{p}_C\big)$
Lysis of reproduction buffer	$\dot{p}m_{LR}$	$in\left(Mn,\frac{E_R\kappa_R}{}\right)$
Lysis of structure	$\dot{p}_{Lm}$	$in\left(Mn-\dot{p}_{LR},\frac{\mu}{w}\right)$

Environmental forcing		
Temperature correction function	c_{Tm}	$exp\left(\frac{T_{Am}}{T_{ref}}-\frac{T_{Am}}{T}\right)\frac{1+exp\left(\frac{T_{AL}}{T_{refm}}-\frac{T_{AL}}{T_{Lm}}\right)+exp\left(\frac{T_{AH}}{T_{Hm}}-\frac{T_{AH}}{T_{ref}}\right)}{1+exp\left(\frac{T_{AL}}{T}-\frac{T_{AL}}{T_L}\right)+exp\left(\frac{T_{AH}}{T}-\frac{T_{AH}}{T_{ref}}\right)}$
Salinity correction function	c_{Sm}	1, if $S > S_H$ $\frac{S-S_{Lm}}{S_{Hm}-S_L}$, if $S_{Lm} > S > S_H$ 0, if $S < S_L$

Table A2. Eastern oyster Dynamic Energy Budget (DEB) model parameters (from Lavaud et al., 2017).

Parameter	Value	Unit	Description
$\{\dot{p}_{Am}\}m$	187.125	J d^{-1} cm^{-2}	maximum surface area-specific assimilation rate
$\dot{v}m$	0.03453	cm d^{-1}	energy conductance
κ	0.82	-	fraction of energy allocated to soma
κ_R	0.95	-	reproduction efficiency
k_J	0.002	d^{-1}	maturity maintenance rate
$[\dot{p}_M]m$	38	J d^{-1} cm^{-3}	volume-specific somatic maintenance rate
$[E_G]m$	5230	J cm^{-3}	volume-specific cost for structure
E_H^p	369.9	J	maturity at puberty
δ_M	0.2	-	shape coefficient
	0.2	g cm^{-3}	specific density of structure
w	23.9	g mol^{-1}	molecular weight of structure
w_E	23.9	g mol^{-1}	molecular weight of reserve
μ	500,000	J mol^{-1}	chemical potential of structure
μ_E	550,000	J mol^{-1}	chemical potential of reserve
κ_{sp}	0.5	-	spawning efficiency
gsi_{sp}	0.08	-	gonado-somatic index threshold for spawning
ρ_{egg}	2.566 10^{-4}	J g^{-1}	energy density of an egg
W_{egg}	4 10^{-8}	g egg^{-1}	dry mass of an egg
T_{ref}	293	K	reference temperature
T_L	283	K	temperature at the lower boundary of tolerance range
T_H	303	K	temperature at the upper boundary of tolerance range
T_A	6700	K	Arrhenius temperature
T_{AL}	21820	K	Arrhenius temperature at the lower boundary
T_{AH}	45380	K	Arrhenius temperature at the upper boundary
T_{Sp}	25	°C	temperature threshold for spawning
T_{D1}	20	°C	lethal temperature when exposed for >7 d at S_{D1}
T_{D2}	32	°C	lethal temperature when exposed for >7 d at S_{D2}
S_H	10	-	upper salinity threshold of the feeding correction function
S_L	3	-	lower salinity threshold of the feeding correction function
S_{D1}	1	-	lethal salinity when exposed for >7 d at T_{D1}
S_{D2}	5	-	lethal salinity when exposed for >7 d at T_{D2}

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