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Estuarine oiling increases a long-term decline in mussel growth[☆]

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ABSTRACT

The ribbed mussel, *Geukensia granosissima*, cycles nutrients, contributes to soil stability, and can be a major component of predator-prey communities in salt marshes. Mussels were exposed to the 2010 Deepwater Horizon oil spill in the Gulf of Mexico, and salt marshes remain contaminated eight years later. We hypothesized that the oiled mussels had reduced annual growth, altered population size frequency, and perhaps changed valve morphometrics. We sampled 10 marshes near Port Sulphur, LA, to measure the morphometrics of 133 mussels and their age-specific growth rate, and also the marsh oil content and percent vegetative cover. The relationships between valve weight, length and biomass weight were stable as mussels aged. A Year 1 growth decline from 1994 to 2018 is not easily explained by estuarine acidification, flooding, and temperature rise; freshening of estuarine waters is suggested to be a probable causal factor in the declining growth rate. The average valve length and dry biomass per valve declined with oiling in 2010. A multiple regression equation using the percent cover and oil concentration in 2018 described 70% of the variation in valve length. Sites with the highest oiling had few mussels with 14 annual growth bands and more of the younger mussels compared to sites with the lowest oiling. Valve growth in Year 1 declined for four years after the oil spill and was not compensated by higher growth rates in older mussels. Annual growth was below the amount predicted in a regression equation for the five years after the oil spill. Mussel populations may also have been structured by predators that were also responsive to oiling in subtle ways.

1. Introduction

The ribbed mussels *Geukensia granosissima* and *G. demissa*, are involved in a widely appreciated milieu of functional relationships within salt marshes that include nitrogen cycling (Bilkovic et al., 2017; Jordan and Valiela, 1982; Moody and Kreeger, 2021), water filtration (Landgon and Newell, 1990), soil stability (Bertness, 1984), above- and belowground plant biomass (Bertness, 1984; Hamilton, 1978; Honig et al., 2015), vertical accretion (Moody and Kreeger, 2021) and predator-prey interactions (Kuenzler, 1961; Hughes and Seed, 1981). After settling, *Geukensia* sp. juveniles are permanently anchored in the marsh with byssal threads attached to plants or hard surfaces, including other mussels. They form growth bands in the valve by retraction of the shell-secreting mantle edge back into the shell chamber during slower growth. These growth bands have been used for decades to estimate the age of ribbed mussels (Bertness, 1980; Brousseau, 1984) and an individual mussel can have more than 18 growth bands (Culbertson et al., 2008). The response of some mobile organisms to pollutants may not

be observed, perhaps because of behavioral avoidance (Fodrie et al., 2014; Martin, 2017), whereas the distance between growth bands of these sessile mussels may be useful to disentangle the effects of disturbances at one location.

Marsh elevation has been correlated with mussel food resources (Peterson and Howarth, 1987; Evgenidou and Valiela, 2002) which indirectly may influence widths between growth bands. Franz (1997), for example, demonstrated that limits in feeding time and food supply resulted in mussels of a given valve length having a lower body mass at higher elevations than mussels of equivalent length at the marsh edge. Lent (1969), however, found that there was no relationship between intertidal elevation and the biomass weight/biomass-weight ratio. Food resources, therefore, may affect growth, but other factors are also influential. Culbertson et al. (2008), for example, documented reductions in valve length after a diesel oil spill in Massachusetts that happened 38 years before their reciprocal transplant experiments that tested for legacy effects of oiling. Quade (2019) found that unaged mussels transplanted into heavily oiled 0.25 m² plots located 1 m into

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the marsh in coastal Louisiana exhibited reduced mussel survivorship and recruitment, but not growth. Quade (2019) showed that unaged mussels classified as adults according to their size (>60 mm) were smaller and tended to have less live tissue mass at moderately oiled sites but were larger at heavily oiled sites. Juvenile mussel density, as well as total mussel density, was lower in the heavily oiled plots than in the moderately oiled plots.

The variations in age-specific growth widths and valve morphometrics of the Gulf of Mexico species of ribbed mussel, *G. granosissima*, are explored here within the context of oiling a salt marsh during the 2010 Deepwater Horizon (DWH) oil spill in the Gulf of Mexico (McNutt et al., 2012a, b; Turner et al., 2014). We hypothesized that mussels exposed to the DWH oil spill exhibited a response to the oiling by reducing the age-specific widths between the annual growth bands and perhaps by modifying valve morphometrics. We were uncertain about the longevity of any potential effects. The concentration of oil in the upper 5 cm of oiled coastal wetlands in Louisiana after the oil spill 66 km offshore of the Louisiana coastline were 100–1000 times higher than in the months before the oil began reaching coastal wetlands. It decreased to one-tenth that peak amount after eight years (Turner et al., 2019a,b). Here we ask: 1) did age-specific growth widths slow or increase with oiling, 2) did growth recover after the 2010 oil spill, and 3) how long did this potential recovery last? These three questions were addressed by measuring the growth band number and width between them, total valve length, biomass weight, and height of live mussels collected at ten salt marsh sites in south Louisiana in 2018. We compared these data to measurements of mussels collected in the same area in 2004.

2. Materials and methods

2.1. Site description and sample collection

The study area (Fig. 1) is a salt marsh near Port Sulphur, LA that is dominated by *Spartina alterniflora* interspersed with monotypic stands of *Juncus roemerianus*. It has diurnal 30 cm tides influenced by wind and precipitation. Petroleum exploration and mineral recovery efforts in coastal Louisiana began in the 1930's and peaked in the 1960s and have since declined (Turner and McClenachan, 2018). These efforts created levees built from material dredged from the canals. The wetland around dry wells subsided more than in nearby marshes drained by undredged channels, but subsidence was even higher in wetlands with mineral production (Turner and Mo, 2021). The area was oiled in 2010 during the DWH oil spill in the Gulf of Mexico that lasted for 87 consecutive days, killed 11 men and injured 17, and released 4.9 million barrels of petroleum product beginning April 20, 2010. Live mussels were collected June 27, 2018 from ten salt marshes near Port Sulphur, LA (Fig. 1). The mussels were located by a hand search starting 10 m from shoreline and continuing until at least 10 mussels of any size were found by searching parallel to the shoreline. All additional mussels within a mussel patch were collected after the 10th individual mussel was discovered. Mussel valves broken during collection or afterwards were not used. There were 8–27 mussels from each of 10 sites that provided a total of 133 whole mussel shells used to estimate the size distributions (right-valve length, weight, and height, and soft-tissue (biomass) weight) for each shell. All mussels collected were put into plastic bags in the field and then stored in an ice chest until they were put into a cold room (3°C) by the end of the sampling day. Population density cannot be estimated using these data because the search area was not measured.

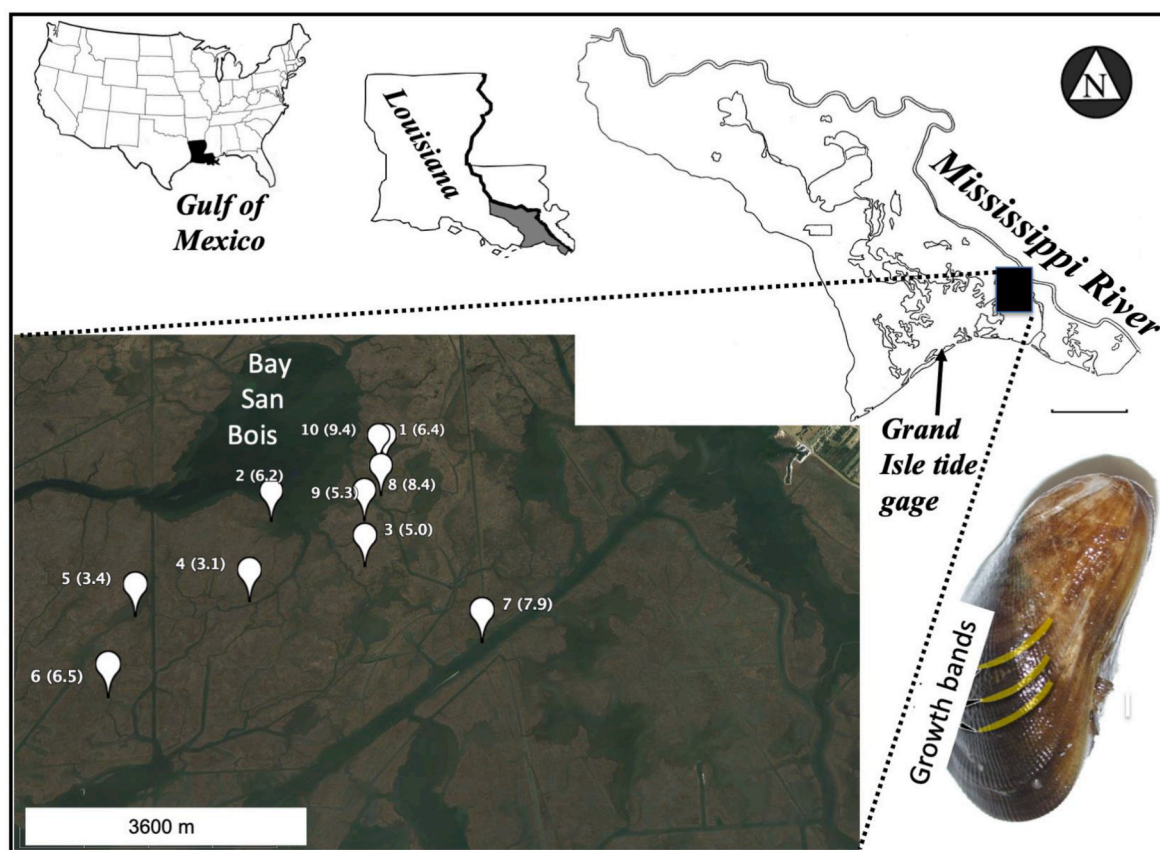


Fig. 1. Location map for the ten stations sampled in 2018 near Bay San Bois, south Louisiana. The concentration of alkanes is in the parentheses (mg kg^{-1}) with each station. The location of the tide gage used at Grand Isle, LA is indicated. A mussel valve is shown with highlighted (yellow lines) growth bands. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

These marshes are in the same region where Spicer (2007) collected mussels >20 mm long in October 2004 that were from four 0.5 m × 0.5 m quadrants at the marsh edge of 22 natural creeks, 20 dredged canals and 8 open water sites.

2.2. Processing

The shells were scrubbed cleaned on the outside and opened by cutting the posterior adductor muscle. The byssus threads were detached, and then the biomass was rinsed in de-ionized water before removing from the shell. The total length of the right valve from the apex to the posterior margin, and its maximum height was measured with calipers to ±0.1 mm. Not all dimensions of some valves could be measured for various processing reasons including edge breakage. The biomass (soft tissues) of animals and the right-valve valves were dried at 60 °C for 72 h, and then weighed to the nearest ± 0.01 g.

Valves were placed in a solution of 50% chlorine bleach for approximately 1 h to increase the visibility of growth bands. The distance from the umbro to each growth ring number was measured along the same axis as for the measurement of total valve length. The birth year was defined as the band number (integer) in sequence where Year 1 was the band nearest the umbro. The width (mm) of each individual growth band was measured by subtracting the previous year's cumulative length from the cumulative length at the end of the next band. These measurements resulted in bandwidth measurements for each year of growth (age-specific) that were assigned a birth year based on the years since collection. The difference in the length from umbro to the year 1 and year 2 growth band, for example, was assigned a birth date of 2016. Only 1 of 133 Year 1 band widths for mussels collected in 2018 was less than 20 mm (19.4 mm) which was similar to the minimum of 20 mm that Spicer (2007) found in her analysis of mussels collected in the same area.

2.3. Oil samples

A single 5 cm deep sample of sediments was collected from the center of each sampling site for oil analyses. The sampling, storage and analysis was done in the same way as described by Turner et al., 2019a and by the same laboratory. Briefly, field samples were put in pre-cleaned amber jars, put on ice and transported to the laboratory where they were either immediately extracted or refrigerated at 4 °C for no more than 14 days until all extractions and analyses were done concurrently. We used a GC/MS-SIM (gas chromatography/mass spectrometry in selective ion monitoring mode) to quantitatively measure C10 to C35 normal alkanes plus pristine and phytane, 2- to 6-ringed parent polycyclic aromatic hydrocarbons (PAHs), and many of their respective C1 to C3 or C4 alkyl homologs. These 28 alkanes and 43 polycyclic aromatic hydrocarbons are part of a standard suite of analyte determinations using good laboratory practices. Only the alkane data were used to indicate relative oil exposure.

2.4. Vegetative cover, salinity and water level

The percent vegetative cover was determined in two 0.5 m × 0.5 m quadrats placed next to each other over the center of the area where live shells were gathered in 2018. Both live and dead emergent plant material were included as vegetative cover. Data on salinity from before and after the oil spill were used in various tests to determine their effects on mussel growth. Salinity data are the average annual salinity for Barataria Bay reported in Turner et al. 2019b that are based on monthly samples. The monthly water level at Grand Isle, LA (Station ID 526; Latitude 29.263°N; Longitude -89.957°W) was downloaded from the Permanent Service for Sea Level Measurements website (<https://www.psmsl.org/data/obtaining/>).

2.5. Statistical analysis

We used Prism 8.0c software © 2020 (GraphPad Software, Inc., La Jolla, CA) to compute various linear regressions of the total valve length (mm) versus valve height (mm), total valve width (mm), valve weight (g) and biomass (g). The mean growth (mm) and standard error of the mean ($\mu \pm 1$ SEM) of all mussels in each birth year was determined for width changes for all mussels with more than 20 age determinations for that year. The average total valve length (mm) and biomass per shell were compared to the oil concentration at each of the ten 2018 station locations. A one-way analysis of variance (ANOVA) was run to determine if there were differences in the total valve length or biomass per shell between three oil concentration groups: 2.5 to 5, 5.1 to 7.5, and 7.6–10 mg kg⁻¹ of alkanes; the data are plotted in violin plots showing the frequency distribution as a proportion of the number of all samples. An ANOVA tested for differences between the three groups and assumed a non-parametric data distribution; the associated Kruskal-Wallis test determined if samples originated from the same data distribution. The percent of valves represented in each age group for all samples collected in 2004 or 2018 were compared. A simple linear regression of year versus average tidal height was made and the residual from the prediction for each year determined.

3. Results

3.1. Valve morphology and weight

Valve dimensions (length, height), valve weight and biomass weight were linearly related with each other in a highly predictable manner at the ten sites ($R^2 > 0.88$; Fig. 2). There were no irregularly formed valves; the valve length vs biomass, length and weight, and the valve weight versus biomass was stable. The standard error of the mean (SEM) was small relative to the range in size or weight. This result means that the morphologies of the smallest and largest valves had the same proportional relationships as growth occurred.

3.2. Tidal variations, growth, and salinity

The average tidal height at Grand Isle rose with variations among years from 1980 to 2019 (Fig. 3A). A simple linear fit of the data indicates a relative sea level rise of 7.9 mm y⁻¹ from a combination of the absolute rise in the ocean's level and subsidence of the gage. Segmenting the years into shorter intervals reveals a recent acceleration in the average relative sea level rise to 11.9 mm y⁻¹ from 1999 to 2019. Birth year ranged from 1980 to 2017. The Year 1 growth declined over the last 20 years (Fig. 3B) as the average water level at the Grand Isle tidal gage increased. The annual growth widths in Year 1 versus the residuals of the annual sea level rise (range = 139 mm; Fig. 3A) are in Fig. 3C along with a dotted line at zero on the Y axis representing the predicted value; the results from a simple linear regression are for all data combined. The growth of Year 1 mussels was unrelated to the tidal residuals for that year. The annual salinity versus Year 1 growth was significantly related (Fig. 3D; $R^2 = 0.34$). Growth in 2010 was significantly outside of the 95% Confidence Interval (CI), as was the sample taken in 2016 for a year with the lowest salinity in the data record.

3.3. Oiling impacts

The average concentration of alkanes (mg kg⁻¹) remaining in 2018 at each of the ten locations sampled was 6.1 ± 0.61 mg kg⁻¹. This concentration is 61% of the average 10.0 ± 1.3 mg kg⁻¹ in spring, 2018, at twenty-five stations in the deltaic plain, which included stations nearby our sampling sites (Turner et al., 2019a,b). The valve length (mm) was negatively related to the oil concentration among the 10 sites (Fig. 4A), as was the average biomass in shells at each site (Fig. 4C). In other words, the sites with higher oil residues remaining had both

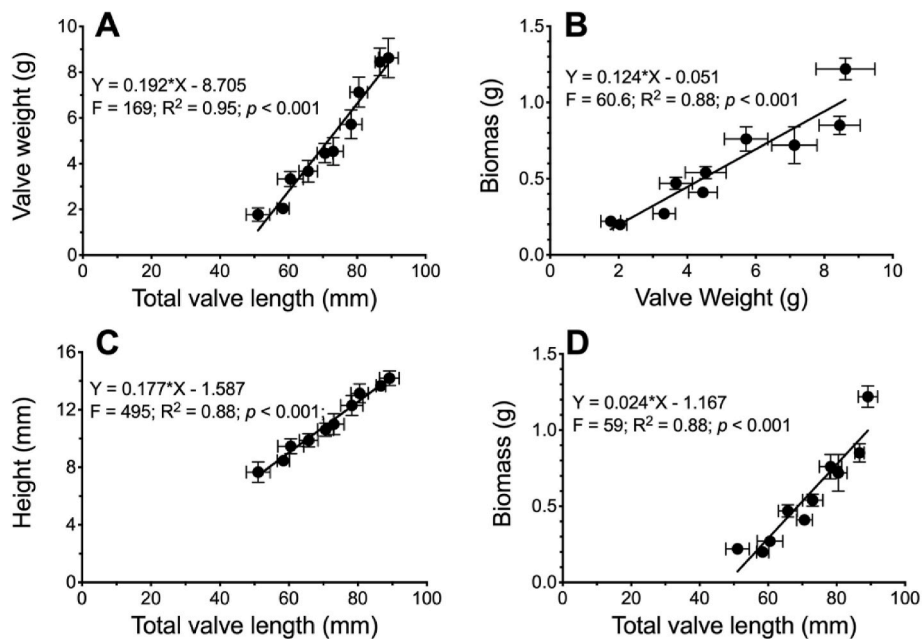


Fig. 2. The relationships between valve morphologies (mm), valve weight (g) and biomass weight (g dry weight) averaged for each of the 10 stations shown in Fig. 1. A) Total shelf length and valve weight. B) Valve weight and biomass weight. C) Total valve length (mm) and maximum height of the valve. D) Total valve length and biomass weight (g). The mean \pm 1 SEM is shown.

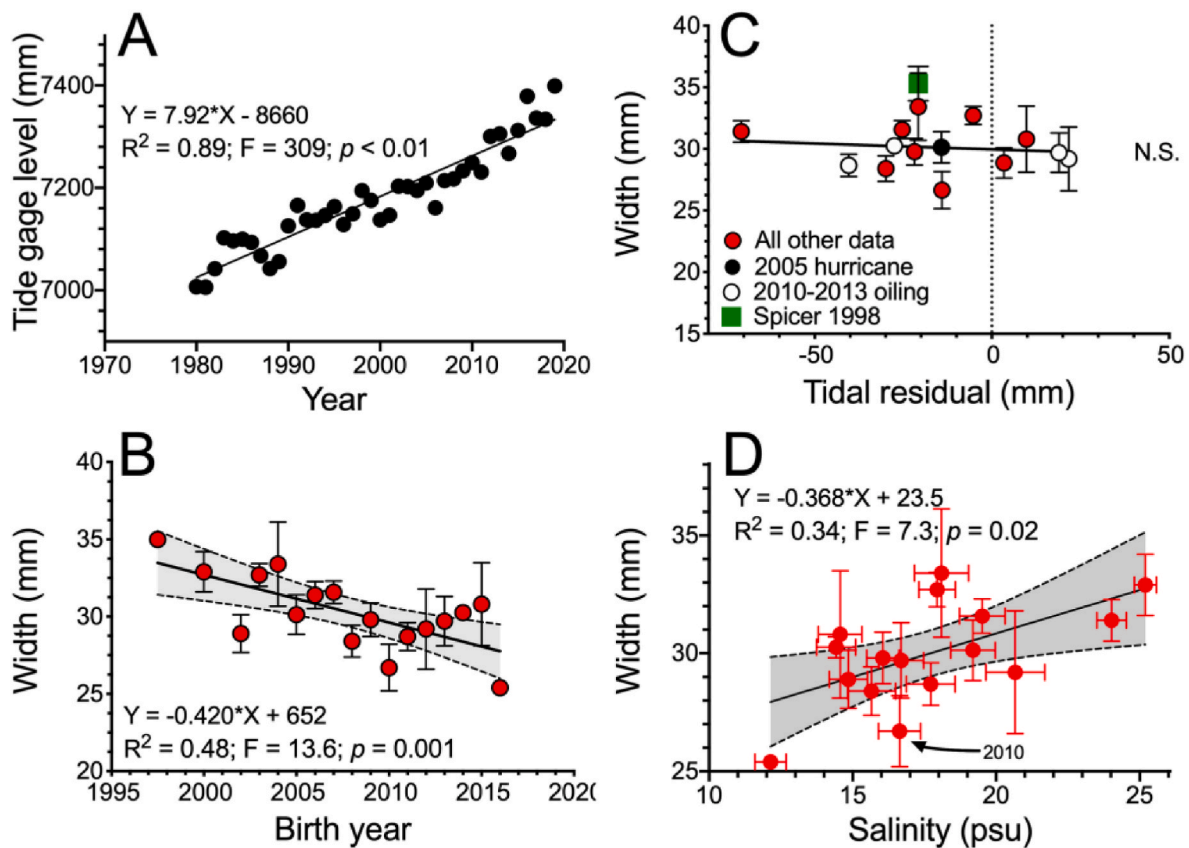


Fig. 3. The tidal variations and growth width (mm) in Year 1. A) Annual tidal height at Grand Isle, LA for each year from 1980 to 2019. B) The width of the Year 1 growth versus the birth year of the mussels. The 95% CI is the shaded gray area. C) The residuals of the simple linear regression shown in Fig. 3A versus the Year 1 growth. The dotted line at zero on the Y axis is the predicted value of the annual tide level for that year; D) The Year 1 growth and the annual salinity. The 2010 year is indicated. The 95% CI is the shaded gray area. N.S. = not significant.

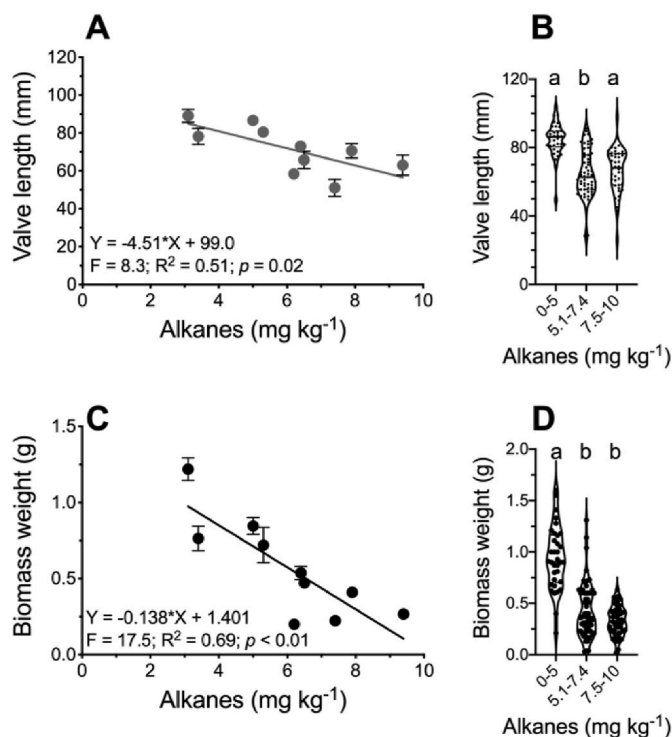


Fig. 4. The relationship between the concentration of alkanes (mg kg⁻¹) at each of the ten locations. A) The average total valve length (mm) versus oil concentration, B) A violin plot of total valve length in three ranges of oil concentration classes. Lower case letters above each plot show differences as determined by a one-way ANOVA test. C) The biomass per shell (g) vs. oil concentration. D) Violin plot of biomass weight in three ranges of oil concentration. Lower case letters above each plot show differences as determined by a one-way ANOVA test. The $\mu \pm 1$ SEM are shown.

smaller valves and less biomass per shell than sites with lower oil alkane content 8 years after the DWH oil spill. The violin plots to the right of these plot (Fig. 4B,D) show the distribution of points (X axis) as being proportional to the number of points in that Y value. The lowercase letters represent the result of a one-way ANOVA testing for differences between each of the three categories of oil concentration. The age-specific growth widths at sites with highest oiling had smaller valve lengths and fewer of the larger valves compared to sites with a lower oil content (Fig. 4B). The biomass content at sites with the highest oil concentrations were much lower (about half) compared to sites in the lowest oiling category (Fig. 4D). Because valves >80 mm are mussels at least >14 years old, we conclude that the oiling of the marsh resulted in a lower percentage of older valves (and biomass per shell) and a higher proportion of smaller valves.

3.4. Year class proportions

There were 194 individuals in each year class for all samples collected in 2004 and 133 in 2018 ($n = 133$). The proportional number of samples by age was lowest for the younger mussels collected in 2004 at the marsh edge and the percent peaked at ages 3 and 4 (Fig. 5). The samples collected in 2004 were collected within 2 m of the marsh edge and had no mussels older than 10 years. The 2018 mussels were collected at 10 m from the marsh/water interface and also had a low percentage of younger aged mussels at the marsh edge but, unlike the 2004 samples, some mussels found there were as old as 18 y. The percent frequency grew gradually from ages between 8 and 12 years old and peaked in the 12th Year, before declining.

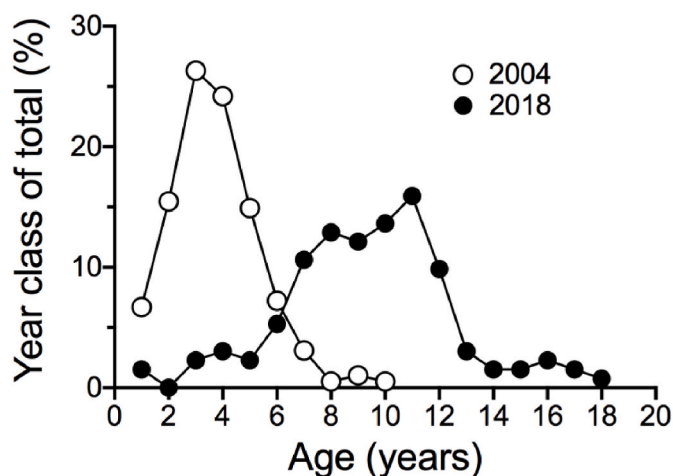


Fig. 5. The percentage of the year class of all samples collected at the marsh edge by Spicer (2007) in 2004 (unfilled circles) and from 10 m into the marsh for samples collected in this study (filled circles).

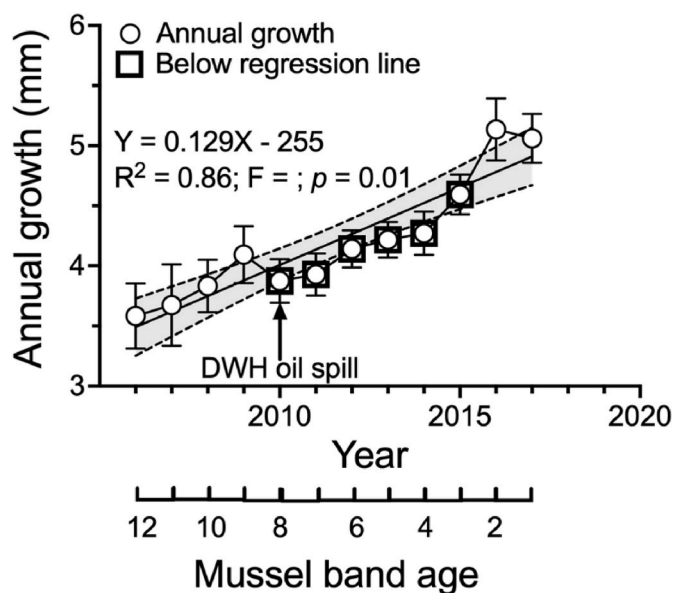


Fig. 6. Age-specific annual growth (mm) for all mussel year classes with more than 20 measurements for that bandwidth age. The higher x axis is the calendar year of the bandwidth and the second (lower) x axis is the age of the bandwidth. A simple linear regression (95% CI) is fitted for all years with more than 20 values for that year. Growth below the predicted value for that year are indicated. Data are the $\mu \pm 1$ SEM.

3.5. Multi-year growth rates

The annual age-specific growth from 2006 to 2017 declined with age (Fig. 6; $R^2 = 0.86$). The annual growth declined after the 2010 marsh oiling and was lower than predicted by the linear regression and below the 95% CI. Recovery to pre-spill growth rates (as determined by the linear regression) took about 5–6 years.

The average valve length (mm) at each of the ten sites sampled in 2018 are positively related to the percent vegetative cover, but weakly (Fig. 7A; $R^2 = 0.19$), whereas the size of the average valve was negatively related to oiling, but stronger (Fig. 4A; $R^2 = 0.51$). A predictive multiple regression relationship incorporating both oiling and % vegetative cover had a predictive equation with an $R^2 = 0.70$ (Fig. 7B). The equation has a negative coefficient for oil content and a positive coefficient for vegetative cover.

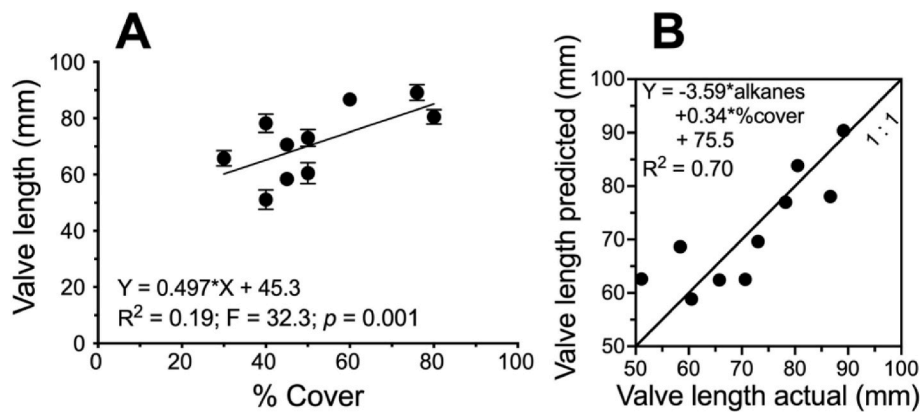


Fig. 7. Valve length, vegetative cover and oiling relationships at the ten sites sampled in 2018. A) The percent vegetative cover and average valve length. The $\mu \pm 1$ SEM are shown for the valve length. B) The prediction of average valve length compared to the actual valve length based on a multiple regression equation that included percent vegetative cover and alkane concentrations.

4. Discussion

The variations in annual growth demonstrated the expected decrease in growth with age observed by Spicer (2007) at this location by others for elsewhere. Growth bands were sometimes difficult to distinguish, but this dating method was useful for comparing population structure in varying environmental conditions and can be valid for up to 18 years at this location. In general, the morphological relationships between length, biomass weight and valve height of individual valves were constant, but the growth of Year 1 mussels has been declining for decades. There could be several reasons for this decline including variations in flooding, temperature, acidification, and salinity.

Higher flooding is expected to enhance mussel growth because mussels feed by filtering primarily plankton during flooding tides (Peterson and Howarth, 1987). Their growth rate, as well as reproduction, may, therefore, be food-limited by submergence time, because more submergence brings more food to the sessile organism (Franz, 1993). Variations in the average sea level rise (residuals) and size, however, were moving in opposite direction, suggesting that variations in flooding and growth for Year 1 mussels were not related. Alternatively, perhaps using the residuals of annual tidal rise was too crude a measure of flooding variations.

The average temperatures are increasing across the world, which means that higher temperatures will, in general, result in smaller sizes for ectotherms including bacteria, benthic invertebrates and fish (Dau-fresne et al., 2009; Hiddink et al., 2015; Turner, 2017). Temperature rise is, therefore, a possible potential factor contributing to the lower growth rate of Year 1 mussels. The annual air temperature at New Orleans, Louisiana, increased at $0.034 \text{ }^{\circ}\text{C y}^{-1}$ from 1985 to 2015 (Powell and Keim, 2015), equal to about 2.7 times the rise in annual global sea surface temperature averaged for the open Gulf of Mexico ($0.0129 \text{ }^{\circ}\text{C y}^{-1}$) over the same time (Belkin, 2009). This rise is equivalent to only $0.68 \text{ }^{\circ}\text{C}$ for the twenty years of growth for these mussels, which seems like a large decline in growth for the amount of temperature rise. The reduced growth in Year 1 mussels also supports the general idea that ocean acidification could affect the calcification necessary for shell growth in mussels. Estuarine acidification is due to a multitude of factors influencing pH in estuaries (Duarte et al., 2013) but is unlikely in Barataria Bay because of two reasons. First, the pH of the Mississippi River entering Barataria Bay through tidal passes mixes with estuarine water to strongly influence salinity in Barataria Bay (Turner, 2019), and the pH in the river has been increasing during the years when these Year 1 growth measurements were made (Turner, 2021). Second, the alkalinity in the Mississippi River has also been rising for more than 100 years (Raymond and Hamilton, 2018). This rise is important because alkalinity and pH are directly related (Hu et al., 2015) and alkalinity buffers

potential changes in acidity. A third factor is the lower salinity in Barataria Bay because the Mississippi River discharge has been increasing over the last 30 years (Wiseman et al., 1990; Turner et al. 2019b; Murawski et al., 2021). A lowered salinity should result in slower growth, perhaps through increased calcification costs as suggested by the results of experiments conducted in the laboratory and field (Riis-gård et al., 2012; Sander et al., 2018). This salinity-stress hypothesis seems to us to be the most likely explanation for the smaller growth of Year 1 mussels, but further investigations may reveal a stronger alternative explanation.

The first year's growth was depressed several years after the oil spill but was not enhanced in subsequent years. This growth decline means that the cumulative effects last for the lifetime of the mussel which could be up to 18 years. The effect of oiling the marsh was to decrease the biomass and valve length of individuals which was reflected in the size frequencies in the populations. There was a shift in the sizes of organisms when oiled which suggests a population effect for mussels 14 years or older in 2018, and that the mussels >6 years old died during the oil spill in 2010 or later. The three to four year-aged valves have an average length between 48 and 53 mm, which makes them small enough to be prey for crabs (Hughes and Seed, 1981). The slower growth rates, valve lengths and amounts of biomass per shell are consistent with results from the short- and long-term mussel transplant experiments observed by Culbertson et al. (2008) at a site oiled 38 years earlier. Oiling did not reduce mussel growth in Quade's (2019) experiments in which he transplanted mussels into plots located 1 m from the marsh edge.

Juvenile recruitment rates by *G. demissa* in Jamaica Bay, NY, were positively correlated with tidal coverage (mean range = 1.5 m; Nielsen and Franz, 1995). But the size frequency of mussels at both the marsh edge and 10 m inland was higher for the older mussels compared to juveniles floating in at the shoreline. Stiven and Gardner (1992) suggested that mussels growing lower in the tidal zone may be more susceptible to predation by blue crab, but Honig et al.'s (2015) 8-month long experiments showed the opposite result. The population is subject to other factors, including predation that influences the length (and age) of mussel populations. Stiven and Gardner (1992), for example, described an interesting tension between: 1) the increased survivorship of small and medium-sized mussels with decreasing clump size in winter, especially in the low tide zone, and 2) greater mussel growth but lower survival in the summer when crab predation was the highest. They also suggested that there was an advantage of clumping as a refuge from crab predation during summer. Lin (1991) found in laboratory studies that blue crabs ate juveniles attached to large mussels at clump edges but did not consume the host. Lin interpreted this to mean that predation created an older and larger size structure that characterized the high marsh zone.

The reason(s) for the smaller frequency of Year 1 mussels collected in 2018, though real, remains obscure but could be related to predation. Jordan and Valiela (1982) showed that mussel density increased with decreasing elevation, and Bertness (1980) suggested that intraspecific competition could be a significant mortality factor at lower elevation sites, thus lowering densities and changing growth rates. Lin (1990), however, found that elevation was not a significant factor in the 48% predation mortality of mussels by the mud crab (*Panopeus herbstii*) that had the largest predation rate at the marsh edge. It may be that predation changes with higher water levels for other predators, but this needs further examination in marshes that have a 30 cm tidal range.

The relationship between *G. granosissima* and *S. alterniflora* may be because of a facultative mutualism involving mussels increasing soil nitrogen through excretion and pseudofeces deposition and because the plant may become an anchoring site. Bertness (1984) showed that the experimental removal of mussels from *Spartina* marsh plots decreased the soil nitrogen by 19%, and plant tissue by 10% in the Great Sippewissett Marsh, MA. The mussel population there has the highest biomass of any other animal population and releases more ammonia than any population of either plants or animals. Because nitrogen usually limits aboveground productivity in the salt marsh (Morris, 1971), increased retention of nitrogen due to filtration by mussels may ultimately enhance the aboveground productivity of the marsh (Jordan and Valiela, 1982). The increased *Spartina* density and biomass can reduce predation on mussels by producing a firm base for attachment of the byssi (Kuenzler, 1961) and increase mussel growth by providing an additional food source (Kreeger et al., 2000) and shading (Kuenzler, 1961). Oiled sites in the area had decreased above- and belowground plant density (McClenachan et al., 2013; Turner et al., 2016; Fleeger et al., 2019) which could have been caused by factors unrelated to mussel densities, perhaps due to a toxic or sublethal effect on plants and other organisms that lingered for years (e.g., Turner et al., 2016; Fleeger et al., 2018; Deis et al., 2020). The influence of oiling on valve size and biomass content, therefore, may be both a direct and indirect effect on mussels, plants, and their consumers and so additional research is required to clarify the relative strength of those relationships.

5. Conclusions

Here we show that the impacts of mussels exposed to the residual petroleum affected individual growth rates, size structure, and biomass content in the first year of the DWH oil spill and afterwards. There were growth reductions in the annual valve growth with oiling and these were accompanied by changes in the proportions of different ages of mussels. Notably, oiling was associated with fewer of the largest mussels. The growth responses occurred eight years after oiling the marsh in 2010 and the oldest mussels were 18 years old, which suggests that it may take a decade or more for populations to recover once the oil content is reduced to its pre-oiling concentration. The first year's growth of mussel was reduced for four to five years and seemed to have recovered by 2018 but the higher post-oil spill growth did not compensate for pre-oil spill growth reductions. These results show how mussel growth bands could be used as bioindicators of environmental change and contaminant stress.

A striking decline in the size of the first year's growth from 1997 to 2017 occurred that has no causal effect conclusively identified. Ocean acidification, flooding and temperature rise do not easily explain this decline, but there are results from lab and field suggesting that the lower salinity in the bay is a causal influence. The effects of oiling mussels may also be dependent upon plants and predators which may have been affected by oiling in subtle ways.

Credit author statement

R. Eugene Turner Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing –

original draft preparation, Visualization, Supervision, Project administration, Funding acquisition, **Jennifer Spicer Plunket** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing-Review and Editing, Project administration

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2021.117506>.

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