Hypoxia-Induced Predation Refuge for Northern Quahogs (*Mercenaria mercenaria*) in a Temperate Estuary

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Abstract

Oxygen depletion in estuaries and coastal waters is often associated with reduced biodiversity, coastal dead zones, and the loss of important ecosystem services. However, some species can benefit from low oxygen conditions due to the indirect effects these conditions have on trophic relationships. In Narragansett Bay, Rhode Island, U.S.A., northern quahogs (*Mercenaria mercenaria*) reach their highest densities in the areas of the Bay most prone to oxygen depletion. One line of evidence suggests that suboxic events (hypoxia and anoxia) can aid quahogs by excluding predators. Here, we analyze data from long-term surveys of water quality and quahog abundances to test whether a hypoxia-induced predation refuge is strong enough to explain quahog population dynamics in Narragansett Bay. We found that quahog cohorts were larger when they had been exposed to low oxygen conditions as juveniles, consistent with the predation refuge hypothesis. However, cohort size was also strongly associated with location and year settled, suggesting that a predation refuge is but one of a suite of factors influencing *M. mercenaria* populations.

Keywords: Anoxia, Dissolved oxygen, Clam fisheries, Eutrophication, Marine mollusks, Narragansett Bay

1. Introduction

Low oxygen events, such as hypoxia and anoxia, often have negative impacts on coastal biodiversity, ecosystem services, and fisheries (Altieri and Diaz 2019). Coastal hypoxia has increased globally since 1951, primarily from anthropogenic nutrient loading (especially nitrogen) and subsequent eutrophication of coastal waters (Altieri and Diaz 2019; Diaz and Rosenberg 2008; Gilbert et al. 2010). Eutrophication increases microbial respiration such that oxygen demand outstrips oxygen input from photosynthesis and atmospheric exchange (Altieri and Diaz 2019; Levin et al. 2009; Rabalais et al. 2001), creating dead zones where suboxic conditions can be so extreme that almost no fauna survive (Altieri and Diaz 2019; Rabalais et al. 2002). Dead zones are sometimes permanent, but are more likely to be seasonal or episodic. These cyclic events exert direct and indirect ecosystem effects that alter species distributions and trophic relationships (Diaz and Rosenberg 2001; Levin et al. 2009). For example, juvenile fish in the Neuse River estuary in North Carolina successfully dispersed away from hypoxic events but suffered from reduction in growth rates due to increased density when they aggregated in normoxic waters (Campbell and Rice 2014). In the Chesapeake Bay, hypoxia limited prey availability for planktivorous pelagic fishes by reducing spatial overlap with their more hypoxia-tolerant mesozooplankton prey (Ludsin et al. 2009). Low oxygen conditions have also been associated with reductions in abundance of sessile benthic species that are not able to escape suboxic events (Levin et al. 2009).

In Narragansett Bay, Rhode Island, U.S.A., recent upgrades to wastewater treatment facilities and subsequent reductions in nutrient pollution have reduced summertime hypoxia by up to 34% in some areas of the Bay (Oviatt et al. 2017). Biodiversity and ecosystem services should be enhanced by these water quality improvements (Deacutis 2008; NBEP 2017).

However, some estuarine species may be negatively impacted by the upgrades in wastewater treatment because they responded positively to suboxic conditions in the past (Altieri and Diaz 2019). It is likely that the northern quahog (*Mercenaria mercenaria*) is one of those species (Altieri 2008). Quahogs provide key ecosystem services (Vaughn and Hoellein 2018) and sustain a local fishery that generates over $5 million per year in ex-vessel landings by over 500 active shellfishers (McManus et al. 2020b). Quahogs also reach high densities in the areas of the Bay most often subject to suboxic conditions (Altieri 2008; Marroquin-Mora and Rice 2008).

One proposed explanation for quahogs' higher densities in the areas of Narragansett Bay that experience suboxic conditions is that they benefit from a hypoxia-induced predation refuge (Altieri 2008). This hypothesis is deduced from quahogs' relative resilience to suboxic conditions, especially when compared with that of their predators. For example, *in situ* studies in Narragansett Bay have found that quahogs were unaffected by suboxic events that led to the depletion or local extinction of other sessile shellfish species (Altieri 2008; Altieri and Witman 2006). Laboratory studies confirmed quahogs' relative resilience to suboxia as both larvae and juveniles (Gobler et al. 2017; Morrison 1971; Stevens and Gobler 2018). Quahog predators, however, are generally more susceptible to suboxia than their prey (Altieri 2008; Sagasti et al. 2001). In Narragansett Bay, these predators include mud crabs (*Dyspanopeus sayi*), rock crabs (*Cancer irroratus*), Jonah crabs (*Cancer borealis*), spider crabs (*Libinia emarginata*), green crabs (*Carcinus maenas*), knobbed whelk (*Busycon carica*), channeled whelk (*Busycotypus canaliculatus*), drills (*Urosalpinx cinerea* and *Eupleura caudata*), and sea stars (*Asterias forbesi*) (Altieri 2008; Jeffries 1966; Kraeuter 2001). In general, mobile epibenthic predators such as these tend to respond to suboxic events by reducing foraging rates and seeking normoxic conditions (Sagasti et al. 2001). For example, blue crabs reduced their feeding behavior in the presence of suboxia (Bell et al. 2003b) and attempted to avoid suboxic events (Bell et al. 2003a) in the Neuse River estuary. They also displayed reduced foraging (Taylor and Eggleston 2000) and increased movement (Bell et al. 2009) in response to experimental manipulations of dissolved oxygen in laboratory-based studies. In the Seekonk and Taunton rivers, two tributaries of Narragansett Bay, blue crab abundance was lower during suboxic events (Taylor and Fehon 2021). Sea stars in Narragansett Bay also dispersed away from suboxic events (Altieri and Witman 2006). These behavioral responses by quahog predators to suboxia may have strong effects on quahog population dynamics as top-down effects can be a significant driver of quahog survivorship and abundance (Altieri 2008; Bricelj 1992; Mackenzie 1977; Ólaffson et al. 1994; Peterson 1979; Wilson 1990). Furthermore, Altieri (2008) found evidence for a hypoxia-induced predation refuge in Narragansett Bay, observing that predator exclusion cages led to increased quahog survivorship at normoxic study sites but not at hypoxic sites.

There are, however, alternative explanations that could also explain the distribution of quahogs in Narragansett Bay. Water quality concerns in the Bay have led to permanent or conditional fishing closures in the most hypoxic areas (NBEP 2017). These closures act as *de facto* marine reserves, allowing quahogs to reach high densities in the absence of fishing pressure (Marroquin-Mora and Rice 2008), in the same places presumed to be intermittently free from non-human predators due to hypoxia (Altieri 2008). Other environmental variables that sometimes overlap with hypoxia, such as primary production, temperature, and salinity, could also affect quahog population dynamics (Ólaffson et al. 1994).

Therefore, despite evidence that a hypoxia-induced predation refuge exists in Narragansett Bay (Altieri 2008), the contribution of this refuge to quahog population dynamics remains in question. It has not yet been determined whether hypoxia enhances the quahog population, or whether the predation refuge is strong enough to explain the high densities of quahogs found in the Bay's suboxic areas. If, however, hypoxia is positively related to quahog density, ongoing water quality improvements (Oczkowski et al. 2018; Oviatt et al. 2017) may expose quahogs to increased predation at the same time managers begin opening more areas of the bay to harvest (RIDEM 2021). This could increase the likelihood of recruitment overfishing, a phenomenon that has been documented for quahogs in Great South Bay, New York (Kraeuter et al. 2008), and central North Carolina (Peterson 2002). Here, we used data from two long-term monitoring programs that surveyed sessile shellfish stocks and water quality in Narragansett Bay to better understand the effects of cumulative low oxygen events on the cohort size of northern quahogs. We hypothesized that cohort size would be positively correlated with the cumulative hypoxic and anoxic histories to which cohorts had been exposed as juveniles.

2. Methods

2.1 Study Site

Narragansett Bay is a 324 km^2 north temperate, partially mixed estuary in New England, U.S.A., with a mean depth of 8.8 m and mean tidal ranges of 1.4 m at its head (northern terminus) and 1.1 m at its southern entrances (Hicks 1959) (Fig. 1). The estuary is connected to the Atlantic Ocean at its southern end via three passages to Rhode Island Sound (Hicks 1959). Many water quality variables follow a north-south gradient in the Bay: temperature and chlorophyll *a* tend to decrease toward the Bay's mouth, whereas salinity and dissolved oxygen increase, especially during summer months (Hicks 1959; Oviatt et al. 2002; Saarman et al. 2008). The Bay's mean residence time is 26 days (Pilson 1985).

Narragansett Bay experiences low oxygen conditions intermittently, with hypoxic events lasting 1-14 days, primarily from late June through August, although with a high degree of interannual variability (Codiga et al. 2009). These events are spatially variable, in some instances affecting only a single subestuary, or covering up to 40% of the Bay by surface area in others (Codiga et al. 2009; NBEP 2017). Anthropogenic nutrient inputs serve a prominent role in initiating low oxygen events in Narragansett Bay (Oviatt et al. 2017; Saarman et al. 2008). Nutrient sources also interact with physical factors that control stratification and flushing patterns, and these physical factors help determine the severity and duration of low oxygen events (Codiga et al. 2009). Summertime winds, for instance, contribute to increased stratification and weak horizontal circulation that give suboxic conditions more time to develop in the bottom waters of the Bay (Balt 2014; Pfeiffer-Herbert et al. 2015; Rogers 2008). Both physical (meteorological and oceanographic) and biological (nutrients and eutrophication) factors therefore contribute to suboxic conditions in Narragansett Bay (Oczkowski et al. 2018; Oviatt et al. 2017), and their relative contributions often vary spatiotemporally (Codiga 2012; Codiga et al. 2009; NBEP 2017; Nixon et al. 1995).

Our study focused on regions of Narragansett Bay where quahogs are abundant, where they inhabit areas subject to varying levels of hypoxia and anoxia, and where adequate data on abundances, dissolved oxygen, and von Bertalanffy growth function parameters were available. These criteria led us to select the Shipping Channel, Greenwich Bay, and the upper West Passage as sampling regions (Fig. 1). Suboxic events in each of these three regions generally affect the entire region in which they occur, rather than affecting only part of each region (Saarman et al. 2008). This made them useful spatial replicates. However, the Shipping Channel spans multiple shellfish management areas, which are subject to different levels of fishing pressure (McManus et al. 2020b; NBEP 2017).[1] We thus divided the Shipping Channel into its component management areas: the Providence River, Conditional Area A, Conditional Area B, and the upper East Passage (Fig. 1). Greenwich Bay and the upper West Passage span only one shellfish management area (Fig. 1; NBEP 2017).

2.2 Hydraulic Dredge Survey

Quahog data were available from hydraulic dredge surveys conducted by the Rhode Island Department of Environmental Management's Division of Marine Fisheries (RIDEM DMF). The dredge survey is based on a sampling technique originally used in Greenwich Bay in 1993 that divided Greenwich Bay into a grid of 149 quadrats measuring 250 m^2 and sampled each quadrat twice (Lazar et al. 1994). For each sample, the dredge was towed for a length of 30.5 m. Quahogs were counted and measured for hinge width (mm HW). In 1994, the dredge survey was expanded to other parts of Narragansett Bay, with bay-wide data first collected in 1996 (Gibson 2010). Since 1996, the survey has sampled 19 strata distributed across the Bay (Greenwich Bay is now one stratum). Each stratum contains a grid of up to 44 of the above-described sampling quadrats, which are now termed stations (Gibson 2010). The survey followed a random stratified sampling design until 2010, with a subset of the stations in each stratum sampled annually (Gibson 2010). Then, from 2010-2019, every station in each stratum was sampled every other year. Only the Greenwich Bay stratum deviated from this, being sampled completely every year (McManus et al. 2020a). The catch efficiency of the hydraulic dredge used in this survey is 0.73 ± 0.23 (SD) on hard bottom types and 0.48 ± 0.28 (SD) on soft bottoms (McManus et al. 2020a).

[1] These management areas have been modified as of May 2021 (RIDEM 2021). Here, we use the management areas that were in force for the duration of this study (2001-2019) (NBEP 2017).

We examined only littleneck quahogs from each survey, defined by a size range of 25-34 mm HW. This is the smallest size class sampled by the dredge and the youngest life stage consistently quantified in the Bay (McManus et al. 2020a); this size class represents a snapshot of quahog abundance that is closer in time to the period in which quahogs are most susceptible to predation. We used count and size data from the dredge survey and the von Bertalanffy growth function parameters estimated by Robinson et al. (2020) for Narragansett Bay to calculate frequency at age for all littleneck quahogs. Estimating ages in this way provided a second reason to focus only on littlenecks: because quahog growth rates become slower over time, these age estimates would have been unreliable for larger size classes (Robinson et al. 2020). We could not track sublegal cohort abundance through time because the dredge has a mesh size of 25.4 mm and does not reliably capture quahogs smaller than the minimum legal size (McManus et al. 2020a).

2.3 Water Quality Monitoring

Water quality data were obtained from the Narragansett Bay Fixed-Site Monitoring Network (NBFSMN 2019), which consists of buoys equipped with YSI brand multi-parameter sensors that measure surface and bottom physical water quality parameters every 15 minutes (RIDEM 2020). We compiled time-series for dissolved oxygen (DO) in our three sampling regions from the following NBFSMN buoys: Bullock's Reach (BR) (2001-2019), Conimicut Point (CP) (2005-2019), Poppasquash Point (PP) (2004-2019), Greenwich Bay Marina (GB) (2003-2019), Sally Rock (SR) (2008-2019), and Quonset Point (QP) (2005-2019) (Fig. 1). These buoys were chosen based on their proximity to the quahog study areas. We focused on bottom water dissolved oxygen data between June 1 and August 31 of each year, the months in which hypoxic conditions are most frequent and severe in Narragansett Bay (Codiga et al. 2009; NBEP 2017; Oviatt et al. 2017; Saarman et al. 2008). These dates also represent the time when water quality data were most consistently available for the NBFSMN buoys included in this study.

2.4 Dissolved Oxygen Summary Statistics

We counted the number of hypoxic and anoxic episodes (see below for our definition of these terms) for six overlapping windows of time that corresponded to the early years of each quahog cohort's life. We chose to use these cumulative windows because they integrate conditions experienced by each cohort over the period when they are most vulnerable to predation (Kraeuter 2001). The shortest time window corresponded to the presumed summer in which a cohort settled (age 0; a one-year suboxic event history), the longest time window corresponded to all six summers between settlement and recruitment to the fishery (a six-year suboxic event history, ending at graduation to the littleneck size class), and intermediate time windows captured by two- through five-year suboxic event histories. All time windows began in the year a cohort settled and were continuous throughout the years measured.

We tested these six time windows because, although quahogs become less vulnerable to predation as they grow (Altieri 2008; Kraeuter 2001; Mackenzie 1977), the rate of this reduction has not been defined in Narragansett Bay. Kraeuter (2001) found that quahogs are less vulnerable to predation after they reach approximately 25 mm shell length (SL), or approximately 13 mm HW (Pratt et al. 1992). Combining this assumption with growth rates observed in Narragansett Bay (Robinson et al. 2020), quahogs would be considered most vulnerable to predation in the first two years of their lives (three summers of suboxia). Altieri (2008) postulated instead that quahogs in Narragansett Bay are vulnerable to predation until they reach the minimum legal size for harvest in Rhode Island at 25 mm HW. Thus, sublegal quahogs above 13 mm HW would also be vulnerable to predation, albeit at reduced predation rates (Kraeuter 2001). Our six time windows, representing the cumulative suboxic event histories experienced by quahog cohorts from their first through sixth summers, account for a range of possible sizes and ages that could be subject to a hypoxia-induced predation refuge.

Hypoxic and anoxic events were defined in accordance with Rhode Island state regulations, where a hypoxic event is a continuous 24-hour period with a maximum mean DO concentration of 2.9 mg/L and an anoxic event is a 1-hour period with a maximum mean DO concentration of 1.4 mg/L (Oviatt et al. 2017; RIDEM 2018). These thresholds were designed to help managers make policy decisions that would protect the larval stages of marine species found in Narragansett Bay (EPA 2000; RIDEM 2018), but it is also likely that they are meaningful for the behavior and distribution of epibenthic predators. Quahogs in Narragansett Bay become less susceptible to predation as DO drops below 5.0 mg/L (Altieri 2008), which suggests that the Rhode Island state threshold (2.9 mg/L) is a conservative estimate of the concentrations required to generate a predation refuge. The anoxia event definition (1.4 mg/L * 1 hr) is also expected to be meaningful. Observations in the Gulf of Mexico, for instance, found no motile organisms in waters with DO concentrations below 2.0 mg/L (Rabalais et al. 2002). Following Codiga (2008), hypoxic events were discarded where data were missing for half or more of the 15-minute intervals in a 24-hour period. Anoxic events with fewer than three data points in one hour were also discarded. We ended with 12 DO summary statistics against which to compare littleneck abundances: one- through six-year cumulative event histories for both hypoxia and anoxia.

2.5 Modeling Littleneck Abundances Against Suboxic Event Histories

Each dredge sample was matched to the suboxic event histories collected by the nearest NBFSMN buoy in the same sampling region (Shipping Channel, Greenwich Bay, and the upper West Passage). This distance-based matching procedure was particularly important for the Shipping Channel, where three buoys were available, and Greenwich Bay, where there were two buoys (Fig. 1). The upper West Passage and Mount Hope Bay each have only one NBFSMN buoy, so the suboxic histories from those buoys could be matched to their respective dredge samples by region alone. Dredge samples and their assigned suboxic histories from the Shipping Channel were also subdivided by management area (Providence River, Conditional Area A, Conditional Area B, and Upper East Passage) as discussed in section 2.1 (Fig. 1).

Generalized linear mixed models were used to test relationships between cohort size (counts) and each of the summary statistics for suboxic histories (one- through six-year hypoxia and anoxia). We used mixed models to control for spatiotemporal variability in environmental conditions that could otherwise confound our results. Models were implemented using the "glmmTMB" function in the eponymous R package (Brooks et al. 2017) using the same model structure for each summary statistic:

$$\begin{aligned} \mathit{Cohort\ Size} \sim \mathit{Suboxic\ Event\ History} + \ (1|\mathit{Management\ Area}{:}\mathit{Year\ Settled}) \\ + (1|\mathit{Management\ Area}{:}\mathit{Dredge\ Station}) + (1|\mathit{Bottom\ Type}) \\ + \mathit{offset}(\log \mathit{Tow\ Area}) \end{aligned}$$

The year a cohort settled was included as a nested random effect within each management area to account for the temporal and spatial variability across management areas in factors that affect quahog population dynamics, such as primary production, larval production, and larval transport and settlement (McManus et al. 2020b; Mercer et al. 2016; Oviatt et al. 2017). The Management Area: Dredge Station term reflected the spatial structure of our data by accounting for the fact that, while some environmental variables, such as freshwater runoff, will affect an entire management area (Codiga 2012; Codiga et al. 2009), others, such as sediment characteristics, vary on a much finer scale (McManus et al. 2020a). This term also controlled for the effects of fishing closures in hypoxic areas of the Bay by testing for the effects of suboxia within these areas as well as among them. A term for bottom type was also included to account for the difference in dredge catch efficiency observed between hard and soft bottoms (McManus et al. 2020a). Although the dredge survey uses a target tow length of 30.5 m, there is some variation in the tow distance among individual samples, so tow area was included in the model to account for these differences in sampling effort. A version of this model that did not include the *(1|Management Area: Dredge Station)* term was also tested, but a likelihood ratio test supported the model structure presented here for all twelve predictor statistics ($p < 0.001$ in all cases). A negative binomial error structure was used in case of overdispersion. We evaluated model residuals for deviation from the fitted values using Kolmogorov-Smirnov tests and visual inspections of quantile-quantile plots, implemented in R using the “simulateResiduals” and “testUniformity” functions in the “DHARMa” package (Hartig 2020). Models using different suboxic event histories were compared by Akaike Information Criterion (AIC), the KS test statistic (D), and overdispersion parameter; the model with the lowest AIC was deemed the best fitting model, and models with scores within 4 AIC points of the best model and which also returned nonsignificant KS and overdispersion test results ($p > 0.05$) were considered well supported.

The results of the best fitting model were visualized in R using the “ggpredict” function in the “ggeffects” package (Lüdecke 2018). The resulting plots present simulated predictions based on the estimated model parameters. For each management area, results are simulated for the observed range of suboxic load found in each location in Narragansett Bay. The prediction error includes uncertainty attributed to the relationship between suboxic load and cohort size (confidence interval), as well as all additional sources of variance in the model, including the random effects components. The prediction error associated with the total model variance represents the most accurate presentation of the *in situ* conditions for both suboxic load and cohort size at each location.

3. Results

3.1 Quahog Abundances

442 hydraulic dredge survey samples from 2006-2019 were analyzed. Littleneck quahog densities ranged from 0.0-20.1 m^{-2} with a bay-wide mean of 1.0 ± 0.1 m^{-2} (SE). Littlenecks were most abundant in the Providence River, where their mean density was 1.7 ± 0.2 m^{-2} (SE) (Fig. 2). Sampling effort was not distributed evenly among management areas. Greenwich Bay and the Providence River were sampled 159 and 142 times, respectively. Only six samples were made in the upper East Passage and the other three management areas were sampled between 29 and 64 times.

3.2 Suboxic Event Histories

94 buoy-summers of DO conditions were analyzed. The mean hypoxia load for all buoys and summers analyzed in this study was 6.9 ± 0.8 days (SE) and the mean anoxia load was 43 ± 8 hours (SE). Although hypoxia was most prevalent in the Providence River, where the Bullock's Reach buoy recorded a mean summertime hypoxia load of 13 ± 3 days (SE), anoxia was most prevalent at the two buoys located in Greenwich Bay (Sally Rock and Greenwich Bay

Marina) (Fig. 3). While we observed a clear down-bay gradient of decreasing hypoxia, anoxia was mostly limited to Greenwich Bay (Fig. 3).

3.3 Quahog Response to Suboxic Conditions

While all six anoxia models converged with the data and were within four AIC units of the best fitting anoxia model (six-year anoxia), they also produced incorrect residuals as detected by significant KS tests (p-value < 0.003 in all cases) (Table 1). For that reason, we do not present the anoxia model predictions here.

All six hypoxia models converged to the parameter estimates. The model that used three-year hypoxia load as the predictor statistic was the best fit model (Table 1). Models in which two, four, five, and six-year hypoxic event histories were used as predictor statistics were also well supported (Table 1). These five models all found a positive, significant correlation between cohort size and exposure to hypoxia (Table 2, all $p \leq 1.05 \times 10^{-5}$). With a mean cohort size of 3.4 $\pm$ 0.2 quahogs (SE) at age per dredge sample and a median effect size of 1.6 additional individuals per cohort across management areas, as predicted by the three-year hypoxia model, these results suggest a biologically significant effect of hypoxia on cohort size (Fig. 4). However, there is appreciable error around these model estimates when all sources of variance are considered (Fig. 4), indicating that a cohort’s response to hypoxia can be variable, and that hypoxic history is not likely to be the primary driver of cohort size. The model outputs further suggest that variation among dredge survey stations was a key correlate of quahog abundance (Table 3). When the variance for the attributable random effects is removed, however, the model predictions’ confidence intervals were reduced (Fig. S1), which is consistent with the strong evidence for a positive correlation between two- through six-year hypoxia and cohort size presented in Table 2.

4. Discussion

The positive correlation between quahog cohort size and juvenile exposure to hypoxia is consistent with a previously posited hypoxia-induced predation refuge in Narragansett Bay (Altieri 2008). Our best supported models indicate that cohort size is increased by hypoxic conditions across multiple years of a cohort's life history, suggesting that quahogs in Narragansett Bay are subject to top-down control by predators during all six summers of their sublegal lives. These results are not a signal of the *de facto* marine reserves created by fishing closures as we controlled for this pattern with the spatial terms in our models. We note, however, that hypoxia only explains a small portion of the variance in cohort size, which indicates that other factors, such as larval recruitment (McManus et al. 2020b; Mercer et al. 2016) and fishing pressure (Kraeuter et al. 2008; Marroquin-Mora and Rice 2008; Peterson 2002), are likely to be more important.

Variation among dredge stations was the strongest random effect (Table 3), which is consistent with the patchy distribution of quahogs in Narragansett Bay (Gibson 2010; Saila and Gaucher 1966). Interannual variation in cohort size was also notable (Table 3; Fig. 5), which is consistent with previous work that found high interannual variability in larval supply and recruitment associated with weather-induced changes to hydrodynamics in the Bay (McManus et al. 2020b). Cohort size also varied among management areas, with the largest cohort sizes observed in the Providence River (Table 3; Fig. 4). This is consistent with findings that have connected high larval and adult quahog abundances with fishing closures and proximity to warm, shallow tributaries of the upper Bay (Marroquin-Mora and Rice 2008; McManus et al. 2020b; Mercer et al. 2016). The additional sources of variance detected by the random-effects components of our models indicate that, while hypoxia has a biologically significant effect on quahog abundance, it cannot independently predict cohort size.

Although quahogs appear to have benefited from the levels of hypoxia present in some parts of Narragansett Bay, it should still be noted that quahogs are not entirely resilient to low oxygen. Hypoxia has been shown to have negative effects on growth rate and survival for both larval and juvenile quahogs (Clark and Gobler 2016; Gobler et al. 2014, 2017; Morrison 1971; Stevens and Gobler 2018) and laboratory-based experiments have found negative interactions between acidification, thermal stress, and hypoxia (Gobler et al. 2014; Stevens and Gobler 2018).

Moreover, though we found evidence consistent with a hypoxia-induced predation refuge, others have not (Long and Seitz 2008; Polyakov et al. 2007). This may be due to differences in focal species and their predators. Long and Seitz's (2008) Chesapeake Bay study, which found that Baltic clams (*Macoma balthica*) experienced more predation during hypoxic events, focused on predators like blue crab (*Callinectes sapidus*), Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and hogchoker (*Trinectes maculatus*). While blue crabs are also present in Narragansett Bay, other significant quahog predators in the Bay, such as whelk (*Busycon carica* and *Busycotypus canaliculatus*) and sea stars (*Asterias forbesi*) are unlikely to increase foraging during hypoxic events as they do not have the ability to move quickly in and out of hypoxic waters. In Great South Bay, no evidence was found that mud crab (*Dyspanopeus sayi*) predation on quahogs influenced patterns in quahog distribution

(Polyakov et al. 2007). It is possible, however, that the suite of predators found in Narragansett Bay exerts stronger top-down control on quahog populations than mud crabs in Great South Bay.

The positive correlation between cohort size and juvenile exposure to hypoxia could also be the result of other environmental factors that are closely correlated with hypoxia, rather than changes in the distribution of epibenthic predators. For example, the concentration of chlorophyll *a*, a common proxy for primary production, is strongly correlated with hypoxia on a seasonal timescale in Narragansett Bay (Codiga 2020), and increased abundances of phytoplankton have been found to enhance quahog growth rates and reproduction in nearby systems (Carmichael et al. 2004; E.T. Weiss et al. 2002; M.B. Weiss et al. 2007). However, recent studies found no significant relationship between quahog growth rates and concentrations of chlorophyll *a* in Narragansett Bay (Henry and Nixon 2008; Robinson et al. 2020) and quahogs in the most eutrophic areas of the Bay have decreased reproductive capacity, as indicated by histological analysis of gonadal tissue samples (Marroquin-Mora and Rice 2008). The same studies of quahog growth rates in the Bay also found no relationship with temperature or salinity (Henry and Nixon 2008; Robinson et al. 2020). This suggests that these factors do not exhibit enough variance in Narragansett Bay to strongly control quahog population dynamics.

Decreased interspecific competition is a second pathway that could explain the correlation between hypoxia and cohort size. Quahogs are more resistant to hypoxia than other suspension-feeding bivalves in the Bay, including softshell clams (*Mya arenaria*) and blue mussels (*Mytilus edulis*), and are heavily dominant in areas where suboxic conditions are more prevalent (Altieri 2008). Although food limitation is unlikely (Robinson et al. 2020), it is possible that hypoxia-driven depletion of potential competitor species led to increased available benthic surface area and decreased predation on quahog larvae by other filter feeders. However, quahogs are still able to achieve high densities despite strong intraspecific competition in hypoxic areas of Narragansett Bay (Altieri 2008; Kraeuter et al. 2005; Marroquin-Mora and Rice 2008), and lower shellfish densities elsewhere (Altieri 2008; Pratt 1988) make it unlikely that competitive pressures could be as high in down-bay normoxic areas. We thus do not consider interspecific competition to be a likely explanation of our data.

Unfortunately, there are no long-term data for epibenthic predator distributions in Narragansett Bay that would allow us to more completely test the effects of the hypoxia-induced predation refuge on the food web in Narragansett Bay. Future research should consider modeling the relationship between quahog populations and other environmental parameters to better describe the relative importance of the most significant pre- and post-settlement processes in structuring the soft sediment benthic communities of north temperate estuaries. Additional field work would also yield important insights. This work could include surveys of the abundance and distribution of epibenthic predators as well as direct or indirect observations of predation on quahogs with sufficient spatial coverage and resolution to determine bay-wide patterns.

This study provides additional evidence that hypoxic events provide quahogs with a refuge from epibenthic predators in Narragansett Bay and demonstrates that the hypoxia-induced predation refuge is but one part of a complicated suite of drivers of population dynamics. As water quality continues to improve in Narragansett Bay (Oczkowski et al. 2018; Oviatt et al. 2017), quahogs may experience increased predation in their up-bay hypoxic refugia.

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Table 1 Model fits for all 12 models. Test results of the best supported models (determined by AIC) for both hypoxia and anoxia are in bold. The best fitting models, as indicated by nonsignificant KS and dispersion tests (p > 0.05), are in italics.

			Dispersion Test		KS Test	
	Predictors	AIC	Parameter	p-value	D	p-value
Hypoxia Models	1-yr	5878	0.811	0.934	0.0402	0.010
	2-yr	*5867*	*0.731*	*0.846*	*0.0194*	*0.565*
	3-yr	***5864***	***0.752***	***0.836***	***0.0132***	***0.935***
	4-yr	*5865*	*0.749*	*0.818*	*0.0117*	*0.977*
	5-yr	*5866*	*0.773*	*0.848*	*0.0192*	*0.577*
	6-yr	*5865*	*0.770*	*0.892*	*0.0199*	*0.527*
Anoxia Models	1-yr	5884	0.814	0.924	0.0481	0.001
	2-yr	5884	0.787	0.932	0.0475	0.001
	3-yr	5884	0.762	0.824	0.046	0.002
	4-yr	5884	0.811	0.956	0.0502	0.000
	5-yr	5882	0.768	0.894	0.0446	0.003
	6-yr	**5881**	**0.780**	**0.898**	**0.0458**	**0.002**

Table 2 Fixed effect predictions of the supported models. The best fit model is in bold. Estimates are logistic correlation coefficients showing the effect of each predictor on cohort size.

	Estimate	Std. Error	z value	p-value
2-yr Hypoxia	0.0235	0.0053	4.407	1.05E-05
3-yr Hypoxia	**0.0203**	**0.0042**	**4.853**	**1.22E-06**
4-yr Hypoxia	0.0161	0.0035	4.648	3.35E-06
5-yr Hypoxia	0.0129	0.0029	4.488	7.20E-06
6-yr Hypoxia	0.0112	0.0025	4.505	6.64E-06

Table 3 Random effects predictions of the supported models. Each pair of columns corresponds to one row (model) in Table 2. The best fit model is in bold. The rows in each variance column are read relative to each other, with each value indicating how much variance was explained by the random effect listed in the groups column.

	2-yr Hypoxia		**3-yr Hypoxia**		4-yr Hypoxia		5-yr Hypoxia		6-yr Hypoxia	
Groups	Variance	Std. Dev.	**Variance**	**Std. Dev.**	Variance	Std. Dev.	Variance	Std. Dev.	Variance	Std. Dev.
Management Area : Year Settled	0.4428	0.6654	**0.3975**	**0.6305**	0.4543	0.6740	0.5091	0.7135	0.5151	0.7177
Bottom Type	0.1173	0.3425	**0.1174**	**0.3426**	0.1164	0.3412	0.1160	0.3406	0.1160	0.3405
Management Area : Station	1.4300	1.1958	**1.4212**	**1.1922**	1.3802	1.1748	1.3499	1.1618	1.3417	1.1583

Fig. 1 Map of study area in Narragansett Bay. Narragansett Bay Fixed-Site Monitoring Network buoys are (from north to south) Bullock's Reach (BR), Conimicut Point (CP), Greenwich Bay Marina (GB), Sally Rock (SR), Poppasquash Point (PP), and Quonset Point (QP).

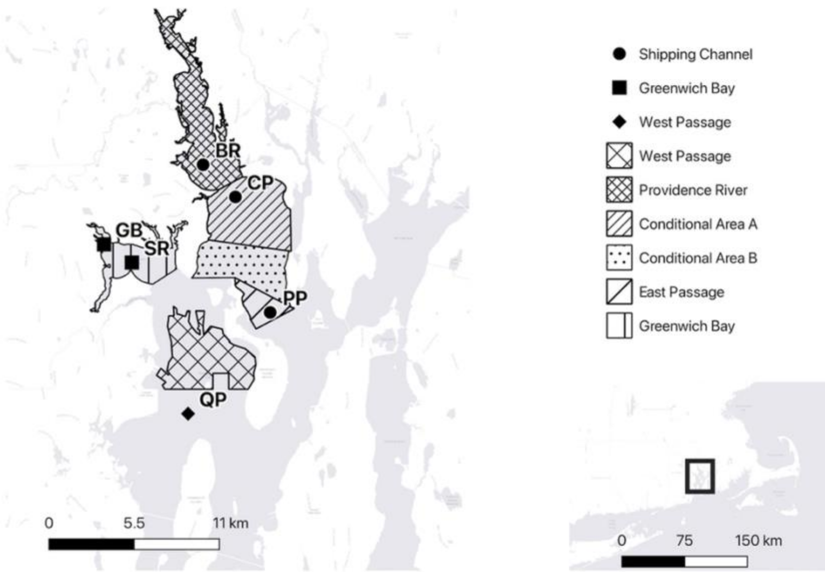

Fig. 2 Mean densities of littleneck and legal quahogs for all RIDEM DMF hydraulic dredge survey samples included in this study. Management areas are arranged left to right by location from south to north: West Passage (WPsg), East Passage (Epsg), Greenwich Bay (Gbay), Conditional Area B (CondB), Conditional Area A (CondA), and Providence River (ProvRiv). The spatial relationship between these management areas and the monitoring buoys used to collect dissolved oxygen data is depicted in Fig. 1. Error bars indicate SE.

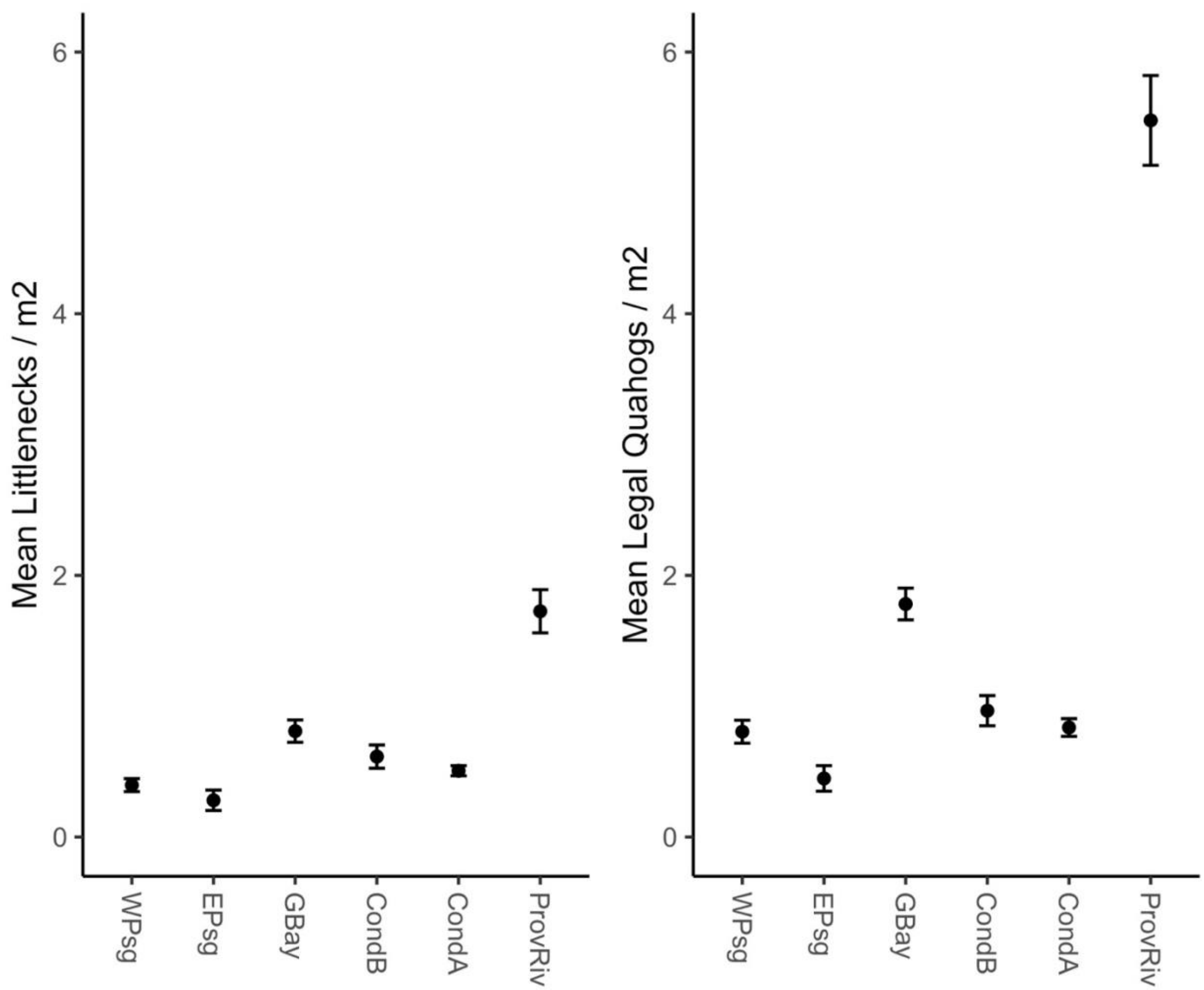

Fig. 3 Mean annual summer hypoxia (24 hrs of DO ≤ 2.9 mg/L) and anoxia (1 hr of DO ≤ 1.4 mg/L) observed at each NBFSMN buoy. Buoys are arranged from left to right in order of increasing hypoxia: Quonset Point (QP), Poppasquash Point (PP), Conimicut Point (CP), Sally Rock (SR), Greenwich Bay Marina (GB), and Bullock's Reach (BR). The spatial relationship between NBFSMN buoys and quahog management areas is depicted in Fig. 1. Error bars indicate SE.

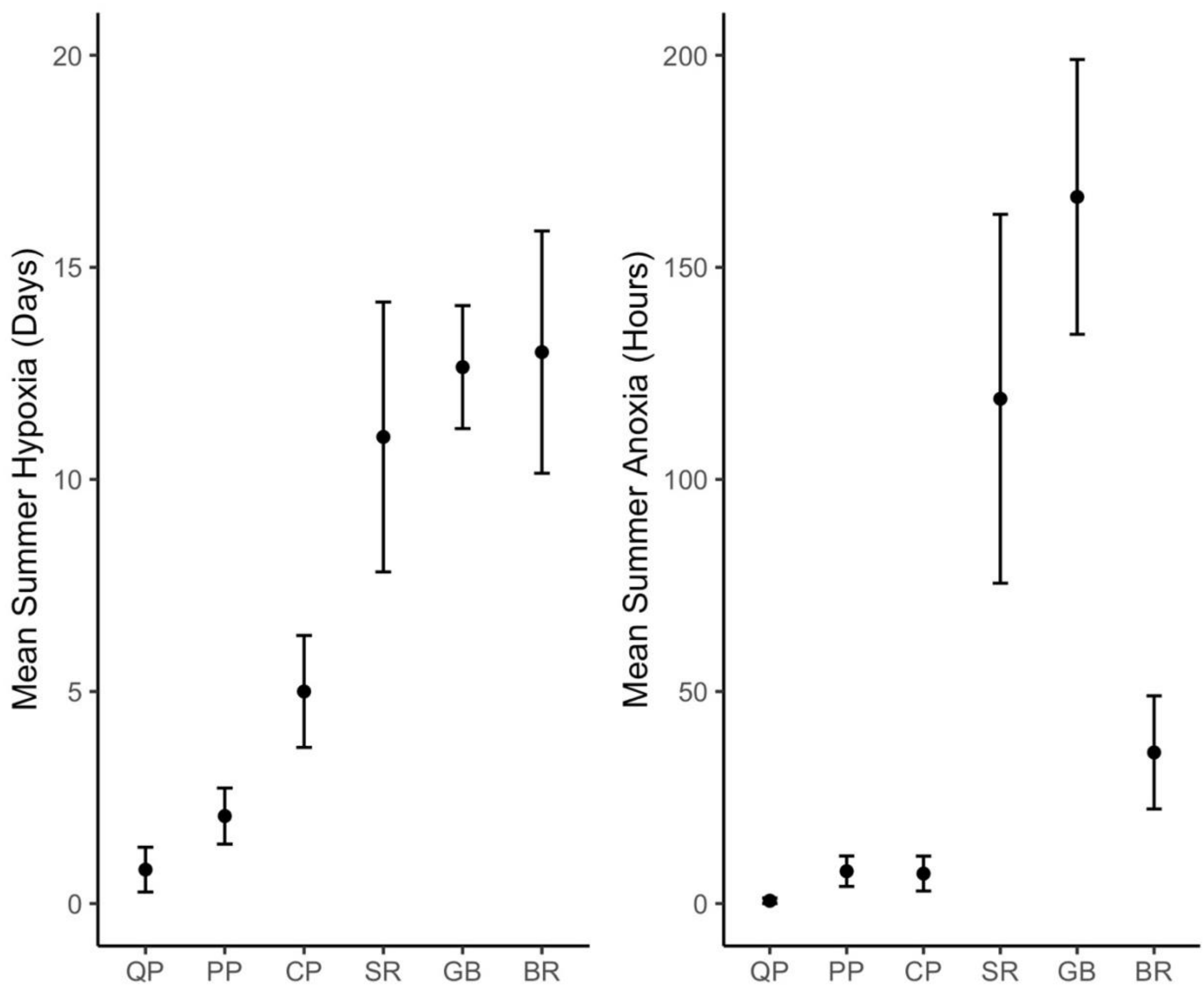

Fig. 4 Effect of hypoxia on cohort size for each management area as predicted by the best fit model (3-year hypoxia). N indicates sample size (number of cohorts) for each management area. Gray ribbons indicate prediction intervals, which are composed of a 95% CI around the predicted relationship between hypoxia and cohort size as well as all additional sources of variance in the model, including random effects. Model predictions are only simulated across the range of hypoxia observed at each location.

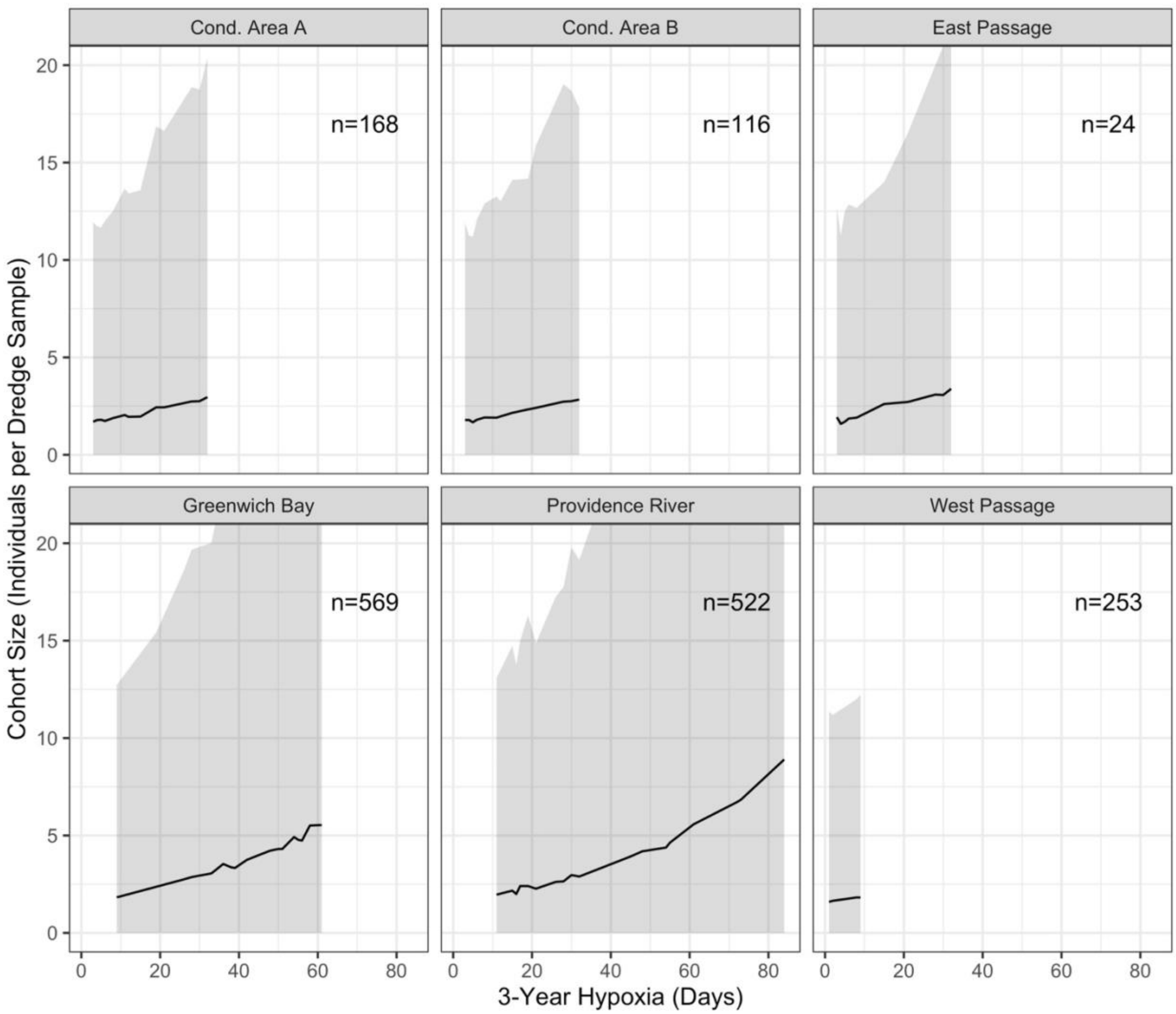

Fig. 5 Intercept of each year by management area for the 3-year hypoxia model, back transformed to indicate effect size (individuals per cohort per tow). In this case, the intercept indicates the predicted cohort size in each management area before taking hypoxia into account. Error bars indicate SE.