

## RESEARCH ARTICLE

# Warming and hypoxia reduce the performance and survival of northern bay scallops (*Argopecten irradians irradians*) amid a fishery collapse

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## Abstract

Warming temperatures and diminishing dissolved oxygen (DO) concentrations are among the most pervasive drivers of global coastal change. While regions of the Northwest Atlantic Ocean are experiencing greater than average warming, the combined effects of thermal and hypoxic stress on marine life in this region are poorly understood. Populations of the northern bay scallop, *Argopecten irradians irradians* across the northeast United States have experienced severe declines in recent decades. This study used a combination of high-resolution (~1 km) satellite-based temperature records, long-term temperature and DO records, field and laboratory experiments, and high-frequency measures of scallop cardiac activity in an ecosystem setting to quantify decadal summer warming and assess the vulnerability of northern bay scallops to thermal and hypoxic stress across their geographic distribution. From 2003 to 2020, significant summer warming (up to ~0.2°C year<sup>-1</sup>) occurred across most of the bay scallop range. At a New York field site in 2020, all individuals perished during an 8-day estuarine heatwave that coincided with severe diel-cycling hypoxia. Yet at a Massachusetts site with comparable DO levels but lower daily mean temperatures, mortality was not observed. A 96-h laboratory experiment recreating observed daily temperatures of 25 or 29°C, and normoxia or hypoxia (22.2% air saturation), revealed a 120-fold increased likelihood of mortality in the 29°C-hypoxic treatment compared with control conditions, with scallop clearance rates also reduced by 97%. Cardiac activity measurements during a field deployment indicated that low DO and elevated daily temperatures modulate oxygen consumption rates and likely impact aerobic scope. Collectively, these findings suggest that concomitant thermal and hypoxic stress can have detrimental effects on scallop physiology and survival and potentially disrupt entire fisheries. Recovery of hypoxic systems may benefit vulnerable fisheries under continued warming.

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## KEYWORDS

*Argopecten irradians*, bay scallop, diel cycling, estuarine heatwave, fishery collapse, hypoxia, marine heatwave, multiple stressors, shellfisheries, warming

## 1 | INTRODUCTION

The signature of sustained, anthropogenic warming has emerged across the continents, oceans, and coastal seas (Abram et al., 2016) with the global ocean absorbing ~90% of the excess heat generated by anthropogenic activities (Bindoff et al., 2019). Warming oceans contain less O<sub>2</sub> and are expected to exhibit increased stratification and reduced ventilation rates, leading to further ocean dissolved oxygen (DO) reductions (Keeling et al., 2010; Shepherd et al., 2017) beyond the 2% decline measured over the last half century (Schmidtko et al., 2017). In coastal aquatic systems, reported deoxygenation rates integrated over a decade or longer exceed those of the open ocean (Gilbert et al., 2010). Climate change likely contributes to these trends as the shallow bathymetries and complex topographies can lead to rapid warming (Scanes et al., 2020), and shifts in watershed processes (e.g. nutrient delivery) accelerate DO declines in many regions (Breitburg et al., 2018; Howarth et al., 2011).

Recurrent or persistent coastal hypoxia (low DO) can have lasting ecological impacts on marine life, resulting in the loss of certain functional traits (e.g., suspension-feeding or provision of structured habitat) and profoundly altering the community composition (Diaz & Rosenberg, 1995, 2008; Tomasetti & Gobler, 2020). A recent meta-analysis identified hypoxic events as the only global change stressor (of warming, acidification, and oxygen loss) to consistently elicit negative effects on abundance, development, growth, metabolism, reproduction, or survival, across all taxonomic groups tested (Sampaio et al., 2021). Under higher temperatures, the vulnerability of coastal organisms to hypoxia is also heightened, with mollusks exhibiting more rapid mortality and significantly higher lethal DO thresholds than those exposed to lower temperatures (Vaquer-Sunyer & Duarte, 2011).

Current temperature and oxygen trends present significant challenges for the effective management of coastal systems, as reports of hypoxia and warming-related impairment continue to expand (Breitburg et al., 2018; Diaz et al., 2011; Smith et al., 2021). Exposure to combined thermal and hypoxic stress can have negative impacts on benthic macroinvertebrate development (Vasquez et al., 2015), growth (Donelan et al., 2021), and larval bivalve abundance (Weinstock & Collin, 2021), although there are few thermal/hypoxic stressor experiments relative to other stressor pairs (see Sampaio et al., 2021). At higher temperatures the physiological demand of marine ectotherms for O<sub>2</sub> is increased while hypoxia limits its supply, potentially reducing an organisms' aerobic scope for growth and diminishing energy reserves (Pörtner, 2010; Sokolova, 2013). Hence, thermal and oxygen conditions that produce energy limitation and fitness reduction for a given species may correspond to the species' distributional limits (Deutsch et al., 2015; Sokolova, 2013).

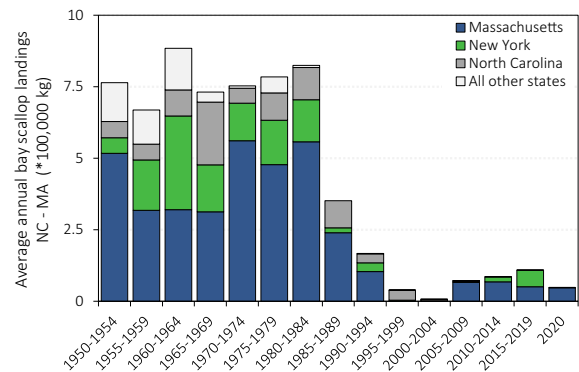


FIGURE 1 Average annual commercial bay scallop landings over 5-year periods from 1950 to 2020. Colors denote the commercial landings of different states.

The Northwest Atlantic Ocean, with recent and projected warming rates that are more than double the global average (Pershing et al., 2015; Saba et al., 2016), encompasses a suite of ecoregions that transition across markedly different physical and biological regimes (Spalding et al., 2007). Many coastal systems in the region suffer from a legacy of eutrophication and severe hypoxic impairment, particularly in the heavily urbanized US East Coast (Bricker et al., 2008; Jewett et al., 2010; Wallace et al., 2014). The distribution of *Argopecten irradians* (bay scallop) is concentrated along the US East Coast and the Gulf of Mexico, with two subspecies comprising commercially important fisheries: the northern *Argopecten irradians irradians* in Massachusetts (MA) and New York (NY) and the southern *Argopecten irradians concentricus* primarily in North Carolina (NC) (MacKenzie Jr., 2008). Bay scallops typically live 18–24 months (Tettelbach et al., 1999; Tettelbach & Smith, 2009) and engage in one to four spawning events during their life (MacFarlane, 1991) for which the timing depends on the latitude of the population. Populations in NY and MA generally spawn sometime between June and October, at ~1 year of age (Hall et al., 2015; Tettelbach et al., 1999) prior to harvests in the late fall and winter months.

Landings of *A. irradians*, which approximate abundance since most harvestable scallops are collected each year in each state, abruptly declined in the mid-1980s (Figure 1; MacKenzie Jr., 2008; NOAA, 2021). Declines during the twentieth century were linked to harmful algal blooms (Gobler et al., 2005; Summerson & Peterson, 1990; Tettelbach & Wenzel, 1993), loss of seagrass habitat (Casper et al., 1987; Fonseca & Uhrin, 2009), and increasing predation pressure (Peterson et al., 2001). The life history of bay scallops generally precludes overfishing as a driver of population decline because adults are now harvested in the months following their spawning activity and populations are generally limited to two generations (Belding, 1910; MacKenzie Jr., 2008). In NY, over a decade of extensive restoration efforts aimed at overcoming

recruitment limitations in the Peconic Estuary—the epicenter of the NY bay scallop fishery—had led to notable improvements in recruitment and landings (Tettelbach et al., 2011, 2013, 2015; Tettelbach & Smith, 2009), but consecutive summer mass mortality events from 2019 to 2021 have erased this recovery (Figure 1).

Little is known regarding the spatial and temporal trends in summer temperature and DO across the *A. i. irradians* ecoregion, and the combined effects of thermal and hypoxic stress on adult bay scallop behavior, physiology, and survival are also unknown. Here, remote sensing and biogeochemical monitoring data are combined with field and laboratory experimental approaches to assess the vulnerability of northern bay scallops to warming and hypoxic events individually and in combination, across their geographic distribution. We specifically analyzed the National Aeronautics and Space Administration (NASA) multi-scale ultra-high resolution (MUR) sea surface temperature (SST) dataset (Chin et al., 2017) to quantify rates of summer temperature change from 2003 to 2020. In addition, northern bay scallops were deployed across four field sites (two in NY and two in MA) to assess differences in survival, DO, and temperature across sites. To characterize scallop physiological responses to natural fluctuations in temperature and DO, scallop cardiac activity (heartbeat rate) was also measured in situ every 15 min throughout a month-long deployment. Finally, to complement the field data, we conducted a laboratory experiment to determine the impacts of high temperature and low DO, individually and in combination, on the survival and feeding rates of northern bay scallops.

## 2 | MATERIALS AND METHODS

### 2.1 | Multi-year temperature and dissolved oxygen records

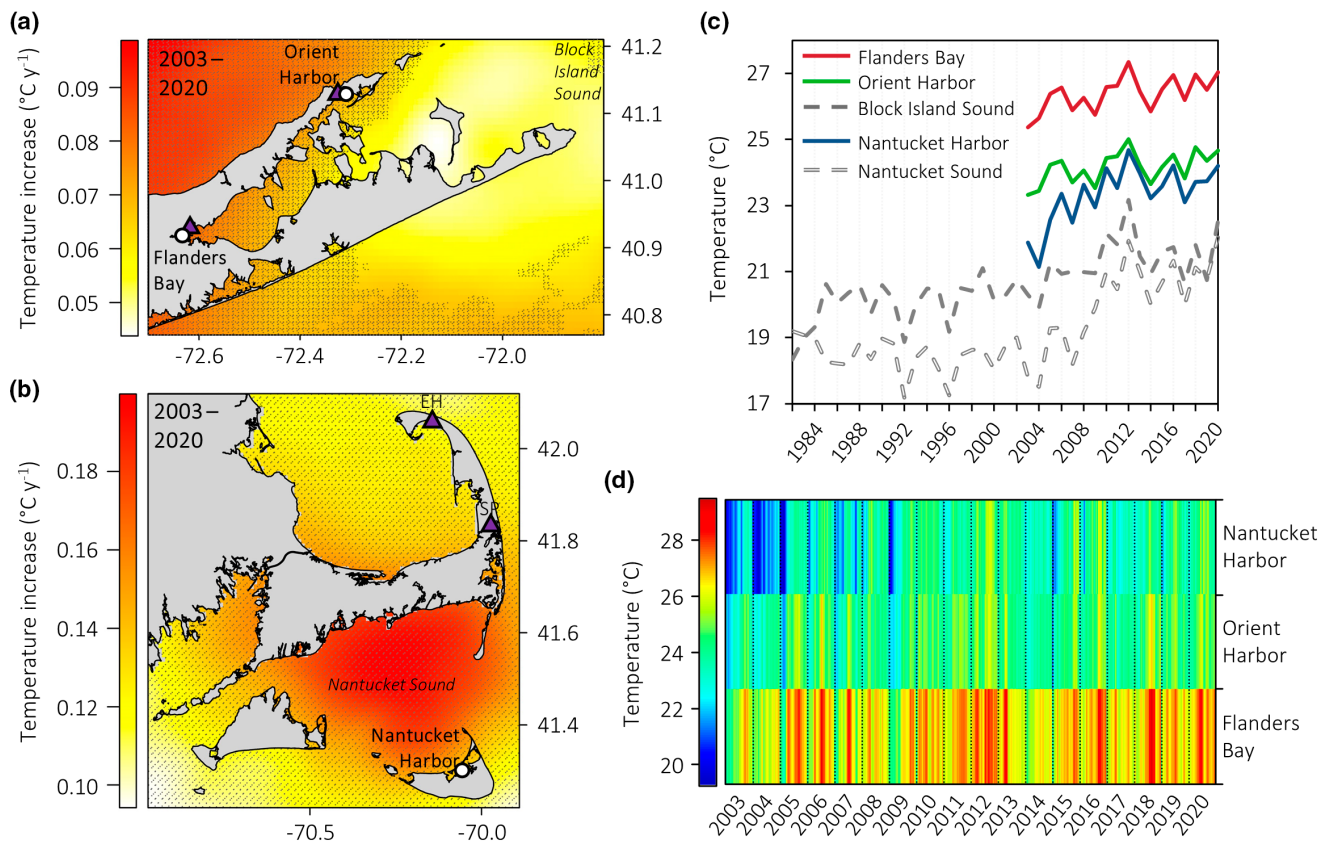
Daily sea surface summer temperature records (July 1–August 31) from 2003 to 2020 for regions hosting commercially viable populations of northern bay scallops over the last decade were obtained from NASA's Group for High-Resolution Sea Surface Temperature (GHRSSST) Level 4 MUR SST Analysis v. 4.1. This data product merges MODIS satellite SST retrievals, other satellite infrared and microwave retrievals, and in situ SST measurements from ships, drifters, and moorings, in combination, to provide optimally interpolated nighttime SST temperature across a  $0.01^\circ$  (~1 km) grid (Chin et al., 2017). Nighttime retrievals of SST are made to avoid the impacts of irregular solar heating (Chin et al., 2017). However, use of nighttime retrievals can introduce a negative (cold) bias in the record, as diurnal solar heating can increase daily SST by over  $5^\circ\text{C}$ , particularly in shallow, tidally mixed estuaries (Griffith et al., 2019). We performed a simple bias correction which used high-frequency summer temperature records collected at United States Geological Survey (USGS) and National Oceanic and Atmospheric Administration (NOAA) monitoring stations in NY and MA, respectively. This allowed for site-specific bias reductions of daily temperature records (i.e. bias reductions of single grid cells according to monitoring data)

and direct comparisons between specific sites that have hosted commercially viable northern bay scallop populations (Flanders Bay, NY; Orient Harbor, NY; Nantucket Harbor, MA; see Figure 1a,b for locations). NASA MUR SST outputs were bias-corrected by applying a linear correction according to 8 years of high-frequency summer temperature observations made at two USGS monitoring stations in the Peconic Estuary (one corresponding with the Flanders Bay site, the other with the Orient Harbor site; Figure S1a,b) and 16 years of summer data from the NOAA Nantucket Island buoy in Nantucket Harbor (Figure S2). An average  $\pm$ SD increase of  $4.11 \pm 0.35^\circ\text{C}$ ,  $2.21 \pm 0.45^\circ\text{C}$ , and  $3.19 \pm 0.33^\circ\text{C}$  was applied to the NASA MUR data for single grid cells corresponding with the Flanders Bay, Orient Harbor and Nantucket Harbor sites, respectively. The corrected values provide estimates of the actual daily mean (including both day and night) summer temperatures from 2003 to 2020 at each individual site (one grid cell), but when comparing temperature trends broadly across a region (> one grid cell) the uncorrected MUR SST data were used. NOAA optimum interpolation SST data [available from 1982 at  $\frac{1}{4}^\circ$  (~25 km) scales] were used to contextualize recent site-specific summer temperature changes (via NASA MUR SST) within the regional summer warming occurring from 1982 to 2020. Trends in daily and mean summer temperatures were compared across sites and regions using the MUR SST data. The occurrence, duration, and timing of 2020 estuarine heat waves, defined as a period of 5 or more days when daily average water temperature exceeded the 90th percentile of the baseline daily climatology (Hobday et al., 2016), were also determined. Additionally, annual summer DO observations from NY USGS monitoring stations in Flanders Bay and Orient Harbor were compared from 2013 to 2020 to assess the severity of hypoxic impairment.

### 2.2 | 2020 Northern bay scallop deployment at sites along a temperature and dissolved oxygen gradient

#### 2.2.1 | Site selection and environmental monitoring

Four sites in two regions known for significant bay scallop fisheries were selected for field experiments and concurrent environmental monitoring: two sites from the Peconic Estuary in NY and two sites from the Cape Cod National Seashore in MA (see Figure 2a,b for deployment locations). The differing geography, regional climates, ocean circulation patterns, and anthropogenic impacts between the Cape Cod National Seashore and Peconic Estuary provided natural environmental gradients of both DO and temperature, against which scallop responses could be assessed; specific sites were selected based on previous scallop surveys and/or water-quality measurements (Ralston et al., 2015; pers. obs.; Wall et al., 2013). The Peconic Estuary sites consisted of Orient Harbor ( $41^\circ 8' 15.87''\text{N}$ ,  $72^\circ 19' 6.32''\text{W}$ ), a site of bay scallop restoration efforts since 2006 (Tettelbach et al., 2013, 2015), and Flanders Bay ( $40^\circ 56' 15.3''\text{N}$ ,  $72^\circ 37' 7.5''\text{W}$ ), a shallow eutrophic embayment where scallops have



**FIGURE 2** Trends in average sea surface summer (July 1–August 31) temperature increase from 2003 to 2020. Summer temperature trends in (a) the Peconic estuary and (b) Cape Cod regions over a  $0.01^\circ$  ( $\sim 1$  km) spatial grid from the NASA multiscale ultrahigh resolution sea surface temperature data analysis. Stippling indicates statistically significant warming (Mann–Kendall). Purple triangles denote deployment locations for the northern bay scallop field deployment (SP: Salt pond, EH: East Harbor). White circles indicate the locations of USGS or NOAA monitoring sites that were used to implement site specific temperature bias reductions. (c) Bias reduced annual mean summer temperatures of Flanders Bay, Orient Harbor, and Nantucket Harbor sites. Block Island Sound and Nantucket Sound annual summer temperatures from 1982 to 2020 (available via NOAA optimum Interpolation Sea surface temperature data across a  $\frac{1}{4}^\circ$  grid) are included to provide broader regional estimates and contextualize the temperature increase at the specific sites. (d) Bias reduced daily summer temperature from 2003 to 2020 at the Flanders Bay, Orient Harbor, and Nantucket Harbor sites. Dotted vertical lines indicate the annual summer start.

been planted periodically (Tettelbach et al., 2013, 2015). The Cape Cod National Seashore sites included East Harbor ( $42^\circ 03' 21.9''$ N,  $70^\circ 07' 24.6''$ W), a salt marsh lagoon with seagrass habitat, and Salt Pond ( $41^\circ 50' 12.0''$ N  $69^\circ 58' 19.7''$ W), a kettle pond with limited tidal exchange, restricted circulation, and strong vertical gradients in DO (Chong, 2018).

Monitoring activities occurred across the four field sites simultaneously for  $\sim 1$  month, from mid-July to mid-August 2020. Flanders Bay and East Harbor were outfitted with calibrated, data logging multiparametric sondes (Yellow Springs Instruments, Model: 599503-01) that recorded measurements of temperature, salinity, and DO every 15 min. At Salt Pond, temperature, salinity, and DO concentrations were measured every 10 min using a combination of calibrated data-logging conductivity and optical DO sensors (ONSET HOBO). All sensors were cleaned every 2 weeks. For Orient Harbor, environmental temperature, salinity, and DO monitoring data were obtained from US Geological Survey (USGS) Station 01304200 in Orient Harbor ( $41^\circ 08' 11.9''$ N,  $72^\circ 18' 24.3''$ W).

## 2.2.2 | Northern bay scallop deployment

Prior to their deployment across field sites, 75 individual bay scallops originally reared at the Cornell Cooperative Extension (CCE) of Suffolk County Shellfish Hatchery in Southold, NY, were obtained from lantern nets at the Orient Harbor restoration site at  $\sim 1$  year old. All individuals were from the same cohort and shared the same environmental history. To that end, gonad indices (ratios of gonad tissue mass to full body tissue mass) for other individuals from adjacent lantern nets indicated the cohort had spawned before and potentially during the start of the scallop deployment (Figure S3). Retrieved scallops were transported to the Stony Brook Southampton—Marine Laboratory where they were stored in a flowing seawater table with seawater filtered through a  $200\mu\text{m}$  sock filter and supplied with air via multiple air stones for  $<10$  days.

Shell height (SH:  $51 \pm 4$  mm) was measured for replicate scallops ( $n = 7$ –16 per site) that were subsequently transported to field sites and deployed in two PVC field chambers (length: 45 cm, width: 45 cm,



height: 15 cm) with nine cubic divisions each, in a 3×3 grid covered with plastic mesh (2 cm mesh size) on all sides (Gurr et al., 2018) that were affixed atop cinderblocks to be ~10 cm off the bottom sediment and staked down with rebar. Individuals were deployed at the two Cape Cod sites on July 17 and the two Peconic Estuary sites on July 16 and 19. Sensors and cages were cleaned of any biofouling with bristle brushes every 2 weeks when scallop conditions (live/dead) were also noted. NY field deployments persisted until August 4, coinciding with the arrival of Tropical Storm Isaias, while MA field deployment ended on August 20 when remaining scallops were retrieved and transported to the Stony Brook-Southampton Marine Station.

## 2.3 | High-frequency observations of cardiac activity and environmental parameters

### 2.3.1 | In situ measures of heartbeat rate

At East Harbor, seven individuals were deployed with reflective optical infrared sensors (Vishay Intertechnology CNY70) to measure cardiac activity, a suitable proxy for *A. irradians* respiration over the range of summer temperatures observed in this study (Gurr et al., 2018, 2021), along with the temperature, salinity, and DO recorded by the multiparameter sonde on site. Regular contractions of the heart result in regular alterations of the quantity of reflected infrared light detected by the sensor, allowing for the quantification of heartbeat rates when measured for a discrete time period (Burnett et al., 2013; Gurr et al., 2018, 2021). A microcontroller board (Arduino Uno), SD shield (Adafruit), and amplifier board comprise an amplifier/logging system for recording infrared signals over time (Burnett et al., 2013).

Cardiac activity sensors were affixed to the replicate scallops at the Stony Brook, Southampton—Marine Laboratory on the surface of the scallops' left valves, posterior to the longitudinal axis directly above the hearts of the animals, with glue (Loctite). Sensors were attached 1 day prior to scallop deployment. Custom-built PVC waterproof structures protected all electronics, including the amplifier/logging system and a 15V battery pack. The battery pack allowed for 28 days of continuous data logging. The logger was programmed to record 60 s of infrared data for seven separate channels corresponding to the seven scallops, sequentially, every 15 min (Gurr et al., 2018, 2021). Each scallop with an attached sensor was placed in a separate compartment of the constructed field chambers. Cardiac activity sensors had no effect on scallop survival, and all scallops survived throughout the entirety of the deployment. An interactive R script written for data analysis enabled visual inspection of data and quantification of every individual heartbeat rate (Gurr et al., 2018, 2021), and five of seven scallops provided nearly continuous heartbeat rate data logging over a 28-day period. Data from these five scallops were used in the analyses.

## 2.4 | Laboratory experiment assessing impacts of temperature and dissolved oxygen on feeding and survival

### 2.4.1 | Experimental design

To determine the individual and combined impacts of thermal and hypoxic stress on adult northern bay scallops, we quantified time until death and algal clearance rates of 64 individual scallops exposed to a combination of one of two temperatures (25 or 29°C) and DO levels [22% air sat. (1.4–1.6 mg L<sup>-1</sup> depending on temperature) or 96% air sat. (6.3–6.7 mg L<sup>-1</sup> depending on temperature)] at the Stony Brook Southampton—Marine Laboratory. Target temperatures of 25 and 29°C were chosen to match the highest 24-h mean temperature at the warmest site (Flanders Bay, NY) and the average 24-h mean temperature at the coolest site (Salt Pond, MA), respectively, during the 2020 field deployment; target DO levels were chosen to recreate DO conditions at sites commonly exhibiting hypoxic impairment or at sites typically saturated in air during the 2020 field deployment.

Replicate 2-L polypropylene experimental vessels ( $n = 64$ , 16 per treatment) filled with 0.2  $\mu\text{m}$  filtered seawater (salinity: 29.9) and covered with polycarbonate lids received gas mixtures of tanked N<sub>2</sub>, CO<sub>2</sub>, and air (tanked CO<sub>2</sub> prevents artificial basification under hypoxic conditions; Gobler et al., 2014), or solely air to enable the maintenance of hypoxic (22.2 ± 3.6%) or normoxic (96.0 ± 2.6%) conditions at 25 or 29°C in all combinations. Gas delivery rates were adjusted to ~500 mL min<sup>-1</sup> via proportioners (Cole-Parmer Flow Meter System) and allowed for a complete turnover of the volumes >200 times daily. Two target temperatures were maintained in two separate sea table recirculating water baths by custom-built aquaria temperature controllers that used digital thermostats with sensor relays (Elitech STC-1000), multiple heating wands, and an external water pump (Iwaki MD55RLT). Throughout the experiment, temperature and DO were measured daily in every vessel using a calibrated YSI Optical DO meter. Measurements of pH<sub>T</sub> (total scale) were made every other day with a Honeywell Durafet Ion Sensitive Field Effect Transistor (ISFET)-based pH sensor calibrated with Dr. Andrew Dickson's (Scripps Institute of Oceanography) seawater pH standard (Dickson, 1993).

On September 9, 2021, a total of 80 adult northern bay scallops were retrieved from lantern nets at the CCE Orient Harbor restoration site by staff scientists, transported to the Stony Brook—Southampton Marine Lab, and stored in a sea table as described above. A total of 64 comparably sized individuals (56.0 ± 3.6 mm SH) were selected for transfer into the experimental vessels ( $n = 16$  per treatment) which were split between two sea tables. Individuals were cleaned of all epibionts with bristle brushes and photographed atop a 1 mm gridded sheet for height measurements. Each individual was placed into a separate 2-L polypropylene vessel filled with 0.2- $\mu\text{m}$  filtered seawater, which functioned as the unit of replication throughout the experiment, and was fed a mixed algal diet (75% *Tetraselmis suecica* and 25%

*Tisochrysis lutea*) equivalent to 2% of their dry tissue weight per day (Helm, 2004); the mean dry weight was determined for a subset of scallops from the same cohort.

At the start of the preconditioning phase, all replicate vessels in all treatments were maintained at  $26 \pm 0.2^\circ\text{C}$  (to mimic the Shinnecock Bay temperatures scallops had been exposed to while at the Stony Brook–Southampton Marine Laboratory) and normoxic levels. On each successive day of preconditioning, the temperature was increased or decreased by  $1^\circ\text{C}$  until the “high temperature” or “ambient temperature” treatments reached the target temperature of 29 or  $25^\circ\text{C}$ , after which the temperature remained constant. Water changes were performed daily, whereby water was poured out and replaced with a combination of new  $0.2 \mu\text{m}$  filtered seawater and the mixed algal diet (2% of dry tissue weight) and brought back to temperature. Every other day, vessels were replaced during water changes with new vessels that had been previously washed and dried. Daily water changes and feedings continued throughout both the preconditioning and active phases of the experiment.

#### 2.4.2 | Survival and clearance rate analysis

After all treatments had reached the target temperatures the active phase of the experiment began, and gas mixtures of tanked  $\text{N}_2$ ,  $\text{CO}_2$ , and ambient air, or ambient air alone were delivered to the appropriate experimental vessels to establish contrasting hypoxic and normoxic conditions at the two temperatures (all experimental chemistry values can be found in Table S1). Over the 96-h active phase of the experiment, individual mortality was assessed and recorded every 12h. One of the multiple, complete water changes occurred 12h after the start of the active phase, after which feeding activity was quantified via a clearance rate assay (Riisgård, 2001).

To determine clearance rates, the mixed algal diet was added to the experimental vessels that had been brought to target temperatures and bubbled to target DO levels, and continued bubbling ensured the algae stayed in suspension. Initial 4.5 ml samples were withdrawn from all beakers and preserved with 0.5 ml of 10% glutaraldehyde solution for enumeration of algal cell densities. Preserved samples were stored at  $-20^\circ\text{C}$  until processing. After the retrieval of initial samples, all scallops were placed into their corresponding vessel (similar to after a daily water change) and were given 2 h to feed before samples were again withdrawn from all beakers and preserved. Cell densities were quantified using a flow cytometer with a 50mm aperture (Beckman Coulter Cytoflex) allowing quantification for both algal species by resolving distinct peaks that differed by cell size (Bricelj et al., 2001). The total algal cell density before and after feeding was used to calculate clearance rates according to the equation:  $\text{CR} = (V/t) \ln(C_0/C_t)$ , where CR = clearance rate, V = vessel volume, t = time,  $C_0$  = initial cell concentration, and  $C_t$  = cell concentration after time t (Riisgård, 2001). A linear relationship between individual heights and dry tissue masses ( $r^2 = .95$ ;  $p = .001$ ) from a previously measured scallop subset (described

above) was used to estimate biomasses and determine biomass-based clearance rates.

## 2.5 | Statistical analyses

Trend significance in the regional rates of summer water temperature change from 2003 to 2020 was assessed by Mann–Kendall tests and differences in the average number of days year<sup>-1</sup> over high-temperature thresholds between the first half and the second half of the 18-year temperature record were compared via Wilcoxon signed-rank tests. Differences in the average daily mean, minimum, and maximum temperatures and DO levels between field deployment sites were identified via Kruskal–Wallis ANOVAs followed by Dunn's multiple-comparisons tests. Correlations between individual heartbeat rates and environmental parameters at East Harbor were assessed over 15-min time intervals via Spearman's rank order correlation tests, and average daily heartbeat rate was evaluated for correlation with daily mean temperature, DO concentrations, pH, and chlorophyll in the same way. Differences in experimental algal clearance rates were assessed by Kruskal–Wallis ANOVAs followed by Dunn's multiple-comparisons tests with treatment as the explanatory variable. Cox proportional hazard regression models were used to assess differences in survival.

Graphics and statistical analyses were completed with R studio (v 4.1.2) using the *ncdf4*, *raster*, *rgdal*, *sp*, *fields*, *rasterVis*, *lattice*, and *rgeos* packages to load, analyze, and plot netcdf/raster spatial data. The *Kendall* package in combination with a custom function (Abdi et al., 2019) was used to test for trend significance in the regional rates of temperature increase across the  $0.01^\circ$  grid. To detect, categorize, and visualize estuarine heatwaves the *heatwaveR* package was used (Hobday et al., 2016, 2018). Statistical tests with in situ and laboratory experimental data were performed using *corr* (Spearman's rank order correlation tests), *FSA* (Dunn's Kruskal–Wallis multiple comparisons), and *survival* (Cox proportional hazard regression models) packages.

## 3 | RESULTS

### 3.1 | Multi-year temperature and dissolved oxygen record analyses

Analysis of SST at a  $0.01^\circ$  ( $\sim 1$  km) resolution revealed significant increases in summer temperature (Mann–Kendall tests,  $p < .05$ ) across much of the Peconic Estuary (Figure 2a) and the entire Cape Cod region (Figure 2b) from 2003 to 2020. In the northern and western regions of the Peconic Estuary at Orient Harbor and Flanders Bay, summer temperatures have significantly increased by  $1.25^\circ\text{C}$  ( $0.069^\circ\text{C year}^{-1}$ ) and  $1.40^\circ\text{C}$  ( $0.078^\circ\text{C year}^{-1}$ ), respectively (Mann–Kendall tests,  $p < .05$ ; Figure 2a). Increases in summer temperature in the Cape Cod region were consistently greater than in the Peconic Estuary (Figure 2b), particularly in parts of the Nantucket Sound where average summer temperatures increased by  $>3.42^\circ\text{C}$

( $0.190^{\circ}\text{C year}^{-1}$ ). In Nantucket Harbor, the fulcrum of Massachusetts' commercial bay scallop fishery, summer temperatures increased significantly by  $2.48^{\circ}\text{C}$  ( $0.138^{\circ}\text{C year}^{-1}$ ) from 2003 to 2020, 1.76–2x the rate of increase at Orient Harbor and Flanders Bay respectively (Mann–Kendall,  $p < .05$ ; Figure 2b).

Mean summer temperatures in Flanders Bay consistently exceeded  $25^{\circ}\text{C}$ , contrasting from Orient Harbor and Nantucket Harbor where they seldom exceeded and have yet to exceed  $25^{\circ}\text{C}$ , respectively (Figure 2c). Generally, mean summer temperatures at the two sites in the Peconic Estuary changed in synchrony with temperatures in Block Island Sound where mean summer temperatures increased by  $0.065^{\circ}\text{C year}^{-1}$  from 1982 to 2020 (Figure 2c). In Nantucket Harbor, more rapid warming caused average summer temperatures to occasionally rise to within  $0.3^{\circ}\text{C}$  of those measured in the Peconic Estuary at Orient Harbor (Figure 2c) reducing the temperature difference between the two regions. Likewise, the 1982–2020 temperature record of the Nantucket Sound indicated an abrupt period of accelerated temperature increase beginning in 2004 ( $0.188^{\circ}\text{C year}^{-1}$ ) whereby summer temperatures rapidly rose and even matched those of Block Island Sound (Figure 2c). In the Peconic Estuary, Flanders Bay daily temperatures were consistently elevated relative to Orient Harbor (Figure 2d). The mean number of warm days ( $>25^{\circ}\text{C}$ )  $\text{year}^{-1}$  was significantly greater in the second 9 years of the 18-year record relative to the first 9 years by 9.9 days (120%), and 7.4 days (770%) in Flanders Bay and Nantucket Harbor, respectively ( $p < .05$  for both, Wilcoxon rank sum tests; Figure 2d, Table S2). The mean number of warm days  $\text{year}^{-1}$  in Orient Harbor increased by 4.0 days (138%) in the second half of the 18-year record but the difference was not significant (Table S2). Hot days ( $>28^{\circ}\text{C}$ ) were only observed in Flanders Bay, and the mean number of hot days  $\text{year}^{-1}$  was  $\sim 3.5$  times greater in the second half of the 18-year record, but the difference was not significant because of the substantial variability from year to year (Figure 2d, Table S2). Average summer DO records (as indicated by averages of daily mean DO) in Flanders Bay and Orient Harbor of the Peconic Estuary indicated no significant trends over the 8 years of USGS observations.

### 3.2 | 2020 Northern bay scallop deployment at sites along a temperature and dissolved oxygen gradient

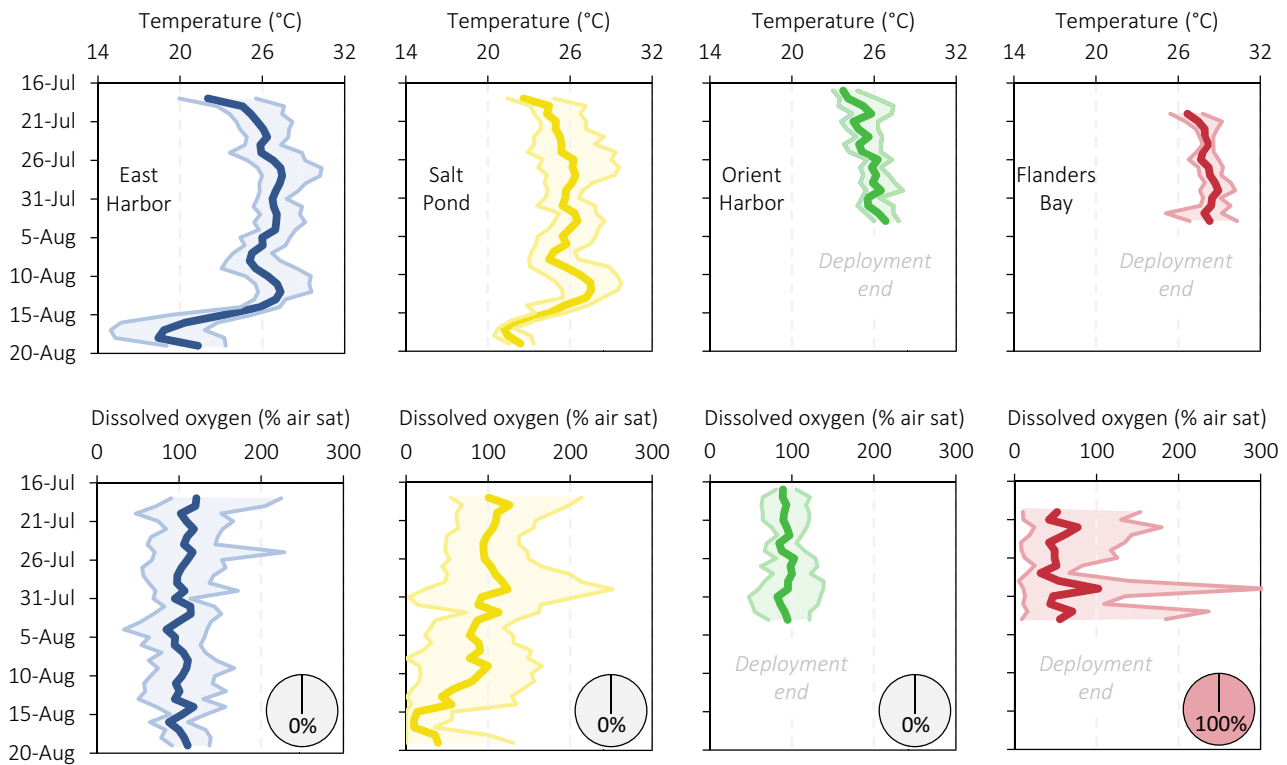
All four field deployment sites exhibited contrasting ranges of temperature and DO dynamics throughout the deployment periods

(Table 1, Figure 3). Patterns of diel-cycling DO that typify shallow coastal environments were evident at all sites, although the magnitude of the diel fluctuations varied and sometimes led to episodes of hypoxia, particularly at Salt Pond and Flanders Bay (Figure 3). These locations also displayed the largest DO ranges (max–min) with levels varying between  $>200\%$  air sat. and  $<10\%$  air sat. ( $>14$  and  $<0.7\text{ mg L}^{-1}$  at temperature of  $25^{\circ}\text{C}$  and salinity of 29; Figure 3).

In Flanders Bay, complete mortality of all bay scallops occurred within the first 11 days of the deployment, while no mortality occurred at any other site during their respective deployments (Figure 3). Comparing the environmental levels from the deployment start to the deployment midpoint when the mass mortality was observed, the daily mean temperatures observed at Flanders Bay ( $28.0 \pm 0.6^{\circ}\text{C}$ ) were significantly higher than at all other sites (Orient Harbor:  $25.3 \pm 0.8^{\circ}\text{C}$ , Salt Pond:  $25.3 \pm 1.0^{\circ}\text{C}$ , East Harbor:  $26.0 \pm 1.4^{\circ}\text{C}$ ;  $p < .05$ , Kruskal–Wallis ANOVA followed by Dunn's test; Figure S4, Tables S3 and S4). In addition, daily maximum temperatures at Flanders Bay ( $29.0 \pm 0.6^{\circ}\text{C}$ ) over that time were significantly higher than at Salt Pond ( $27.7 \pm 1.3^{\circ}\text{C}$ ) and Orient Harbor ( $26.7 \pm 0.8^{\circ}\text{C}$ ;  $p < .05$ , Kruskal–Wallis ANOVA followed by Dunn's test; Figure S4, Tables S3 and S4), but not East Harbor ( $28.3 \pm 1.2^{\circ}\text{C}$ ). Daily mean DO levels at the Cape Cod sites (Salt Pond:  $105 \pm 12\%$  air sat., East Harbor:  $108 \pm 8\%$  air sat.) were both significantly higher ( $p < .005$ , Kruskal–Wallis ANOVA followed by Dunn's test; Figure S4, Tables S3 and S4) than Flanders Bay (Flanders Bay:  $55 \pm 19\%$  air sat.), while the daily mean DO levels of Orient Harbor ( $93 \pm 5\%$  air sat.) did not differ from Flanders Bay or Salt Pond but were significantly lower than East Harbor ( $p < .005$ , Kruskal–Wallis ANOVA followed by Dunn's test; Figure S4, Tables S3 and S4). Daily minimum DO levels were significantly lower at Flanders Bay ( $13 \pm 6\%$  air sat.) relative to Orient Harbor and East Harbor (Orient Harbor:  $70 \pm 8\%$  air sat., East Harbor:  $69 \pm 11\%$  air sat.;  $p < .00001$ , Kruskal–Wallis ANOVA followed by Dunn's test; Figure S4; Tables S3 and S4) but not Salt Pond (Salt Pond:  $46 \pm 19\%$  air sat.), with 75% of observations  $<20\%$  air sat., or  $\sim 1.35\text{ mg L}^{-1}$  at the average temperature and salinity (Table 1) observed in Flanders Bay. At Salt Pond, extensive and often severe hypoxia occurred between the midpoint and conclusion of the deployment with observations of daily mean DO  $<15\%$  air sat. ( $\sim 1.05\text{ mg L}^{-1}$ ) for two successive days, for example (Figure 3). The average temperatures on days with episodic hypoxia, however, were significantly higher at Flanders Bay ( $26.7$ – $29.0^{\circ}\text{C}$ ) relative to Salt Pond ( $p < .005$ ; Kruskal–Wallis ANOVA; Figure 4a, Table S5). Analysis of the 18 years of NASA MUR SST data at Flanders Bay indicated that the field deployment overlapped with 8 days of mean

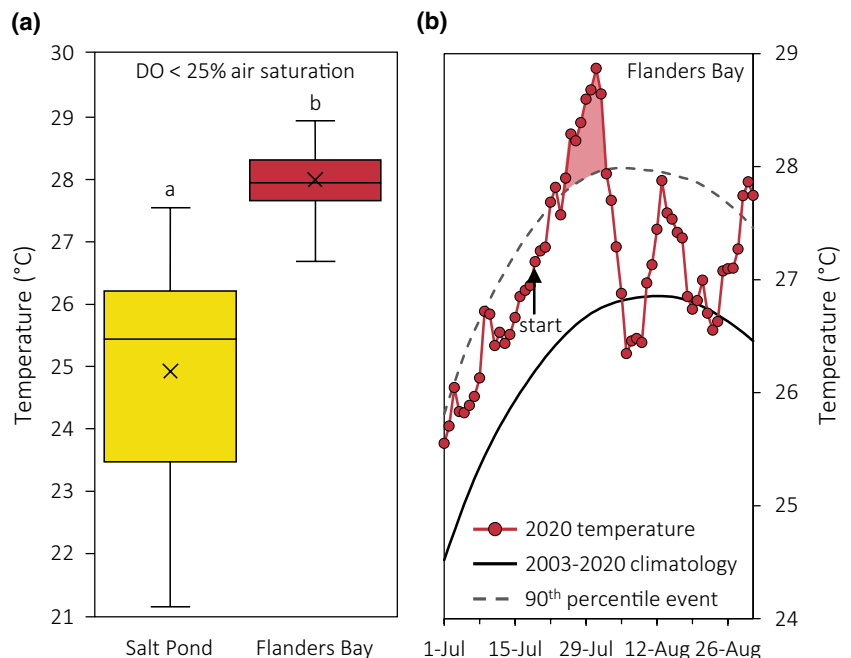
TABLE 1 Mean ( $\pm 1$  SD) temperature, salinity, and dissolved oxygen (DO) at each field site during the deployment periods

	Temperature ( $^{\circ}\text{C}$ )	Salinity (PSU)	DO ( $\text{mg L}^{-1}$ )	DO (% air sat)	Night DO (% air sat)	Day DO (% air sat)
East Harbor	$25.2 \pm 2.76$	$29.1 \pm 1.09$	$7.31 \pm 1.46$	$104.8 \pm 21.9$	$98.1 \pm 18.5$	$109.7 \pm 23.7$
Salt Pond	$25.1 \pm 1.97$	$29.7 \pm 1.70$	$5.65 \pm 3.22$	$81.6 \pm 47.1$	$60.6 \pm 39.1$	$96.1 \pm 46.8$
Orient Harbor	$25.4 \pm 1.03$	$29.0 \pm 0.02$	$6.42 \pm 1.00$	$92.5 \pm 15.3$	$88.5 \pm 13.9$	$95.0 \pm 15.5$
Flanders Bay	$28.1 \pm 0.77$	$25.0 \pm 1.36$	$3.73 \pm 2.89$	$55.1 \pm 43.1$	$45.3 \pm 29.6$	$61.4 \pm 48.9$



**FIGURE 3** Daily temperature and dissolved oxygen means (solid lines) and ranges (max-min; shading) during the northern bay scallop deployment in the Cape Cod National Seashore (East Harbor, Salt Pond) and Peconic Estuary (Orient Harbor, Flanders Bay). Pie charts indicate total mortality experienced at each site during the deployment ( $n = 7$ – $16$  scallops).

**FIGURE 4** Average daily temperatures at sites experiencing hypoxia during the northern bay scallop deployment. (a) Average daily temperature of days when there were observations of  $\text{DO} < 25\%$  air saturation. Letters indicate statistically significant temperature differences. The box and whiskers denote the median, 25th and 75th percentiles, and ranges of average temperatures observed. (b) Average daily temperature in Flanders Bay, NY during summer of 2020, in which the deployment of northern bay scallops coincided with an 8-day estuarine heatwave. The arrow denotes the start of the bay scallop deployment.



temperatures (8-day mean:  $28.4 \pm 0.3^\circ\text{C}$ ) that exceeded the 90th percentile of the long-term (2003–2020) climatology, meeting the criteria of an estuarine summer heatwave (Hobday et al., 2016), and coincided with 8 days of daily minimum  $\text{DO} < 25\%$  air sat. ( $13 \pm 6\%$  air sat.), revealing concomitant extremes in oxygen and temperature (Figure 4b).

### 3.3 | High-frequency observations of cardiac activity and environmental parameters

During the East Harbor field deployment, continuous logging of cardiac activity every 15 min allowed for the characterization of the bay scallop response to environmental fluctuations over



instantaneous and daily temporal scales (Figure 5). Throughout the deployment, cardiac activity was highly synchronous between scallops (0.57–0.86  $\rho$ ; Figure 5 inset, Table S6), and the mean heartbeat rates of each individual were within 5 beats per minute (bpm) of each other—measuring  $39 \pm 7$  bpm,  $37 \pm 7$  bpm,  $39 \pm 7$  bpm,  $36 \pm 5$  bpm, and  $40 \pm 7$  bpm for the five individual scallops over the 1-month field deployment. These data indicate a consistent physiological response to environmental fluctuations among individuals. Across the high-frequency measures, DO was inversely correlated most with heartbeat rates ( $-0.32$  to  $-0.51$   $\rho$ ,  $p < .0005$ , Spearman's rank correlation; Figure 5 inset, Table S6), indicating that as DO decreased, heartbeat rates increased and vice versa (Figure 5 inset). This contrasted with the results over daily temporal scales, where average daily temperature correlated most with cardiac activity (0.60  $s$ ;  $p < .005$ , Spearman's rank correlation; Figure 5, Table S7). At 15-min intervals, correlation coefficients for temperature and scallop heartbeat rates were always  $\leq 0.2$ , indicating suppressed temperature dependency of cardiac activity over that temporal scale (Figure 5 inset, Table S6).

### 3.4 | Laboratory experiment assessing impacts of temperature and dissolved oxygen on survival and feeding

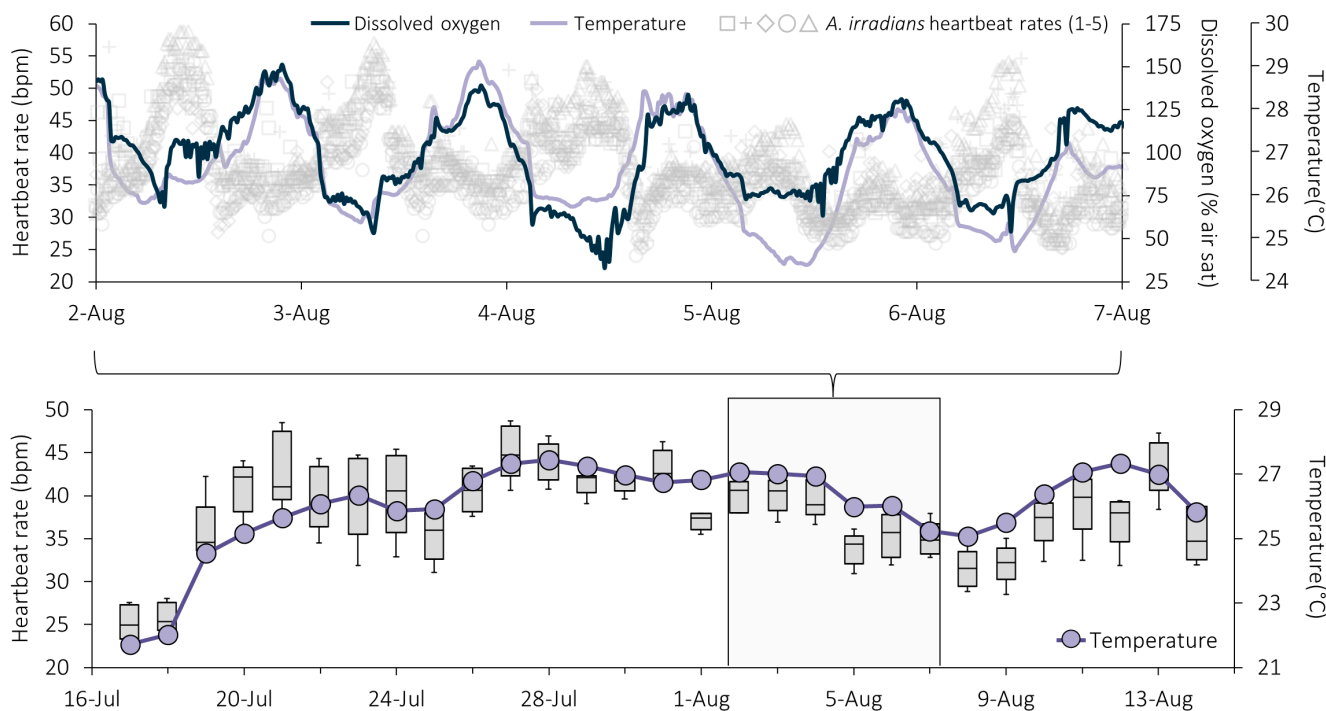
The combination of high temperatures ( $29.0 \pm 0.3^\circ\text{C}$ ) and low DO ( $21.6 \pm 1.7\%$  air sat. or  $1.41 \pm 0.11 \text{mgL}^{-1}$ ) significantly reduced adult northern bay scallop survival relative to all other treatments ( $p < .0005$ ,

Cox proportional hazard regression model; Table S8), and 100% cumulative mortality occurred within the first 3 days of exposure (Figure 6a). The hazard ratios—a measure of the likelihood of individual death under the experimental conditions—revealed that an individual in the  $29^\circ\text{C}$ -hypoxic treatment was 9.4 $\times$ , 57.4 $\times$ , and 119.7 $\times$  more likely to perish than one in the  $25^\circ\text{C}$ -hypoxic,  $29^\circ\text{C}$ -normoxic, and  $25^\circ\text{C}$ -normoxic treatments, respectively ( $p < .0005$ , Cox proportional hazard regression model; see Table S8 for CIs). Survival in the  $25^\circ\text{C}$ -hypoxic treatment was also significantly reduced relative to the  $25^\circ\text{C}$ -normoxic treatment (hazard ratio: 12.79,  $p < .05$ , Cox proportional hazard regression model) but was not statistically distinguishable from the  $29^\circ\text{C}$ -normoxic treatment (Figure 6a; Table S8). Similarly, there were no significant differences between survival in  $29^\circ\text{C}$ - and  $25^\circ\text{C}$ -normoxic treatments (Figure 6a; Table S7). At both temperatures, hypoxia significantly reduced northern bay scallop algal clearance rates relative to normoxic treatments ( $p < .005$ , Kruskal–Wallis ANOVA followed by Dunn's test; Figure 6b; Table S9). From largest to smallest, median clearance rates were 1.26, 0.89, 0.14, and  $0.01 \text{Lg}^{-1} \text{h}^{-1}$ , in the  $25^\circ\text{C}$ -normoxic,  $29^\circ\text{C}$ -normoxic,  $25^\circ\text{C}$ -hypoxic, and  $29^\circ\text{C}$ -hypoxic treatments respectively.

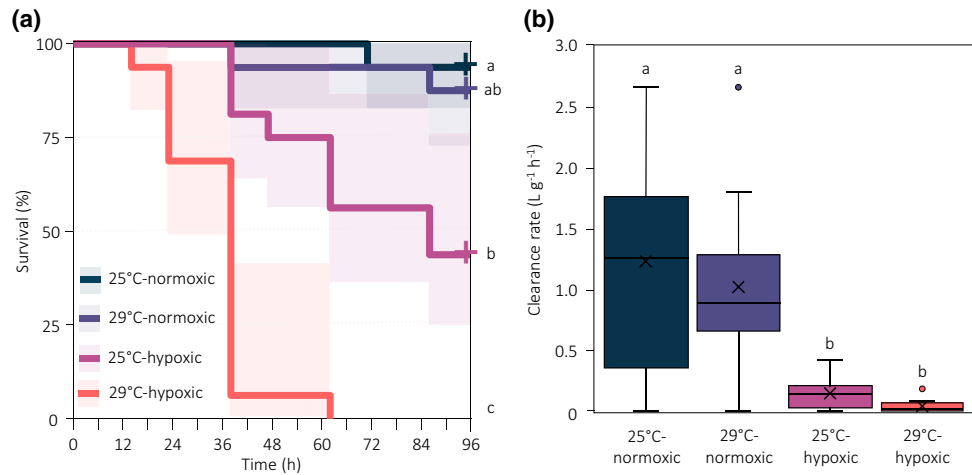
## 4 | DISCUSSION

### 4.1 | Warming and hypoxia

Among the anthropogenic impacts on coastal ecosystems, warming temperatures and diminished DO concentrations are recognized as some of the most widespread and influential factors (Breitburg



**FIGURE 5** Observations of the cardiac activity of five northern bay scallops and environmental parameters from July 17 to August 14 in East Harbor, MA over daily (bottom) and 15-min (inset, top) temporal frequencies. Box and whiskers denote the range of five mean daily heartbeat rates (from lowest to highest values) observed among the bay scallops.



**FIGURE 6** Lab experiment assessing impacts of temperature and DO on the survival and clearance rate of adult northern bay scallops. (a) The survival probability of the bay scallops ( $n = 16$  independent scallops per treatment) during 96 h of exposure to a combination of one of two temperatures and one of two dissolved oxygen levels. (b) The algal clearance rates of individual northern bay scallops ( $n = 14$ – $16$  independent scallops per treatment) exposed to two different temperatures and dissolved oxygen levels. Letters indicate statistically significant differences.

et al., 2018; Halpern et al., 2008). Our analysis of satellite-based temperature records and long-term temperature monitoring data shows that the biogeographic habitat of the northern bay scallop has undergone rapid summer warming during this century. Furthermore, a combination of environmental observations and field/laboratory experiments revealed the detrimental impacts of concomitant thermal and hypoxic stress, with acute consequences on individual performance and survival that could potentially disrupt entire fisheries.

Given the relationship between temperature and oxygen solubility, hypoxic impairment will likely be exacerbated by warming in already stressed systems such that extremes will become more frequent, persistent, or severe. The rate of annual summer temperature increase ( $0.078^{\circ}\text{C year}^{-1}$ ) observed in Flanders Bay over the 18-year NASA MUR temperature record, for example, equates to a 2.8% decrease in average summer DO saturation ( $-0.21 \text{ mg L}^{-1}$ ) from 2003 to 2020, at the mean summer salinity (26.2) from the USGS records. This is without accounting for warming-induced DO decreases associated with increased stratification or increased net-respiration rates and the enhanced physiological oxygen demands induced by higher temperatures (Harris et al., 2006; Shepherd et al., 2017; Tian et al., 2021). For Nantucket Harbor, where the rate of summer warming was more than twice as rapid ( $0.190^{\circ}\text{C year}^{-1}$ ), at a salinity of 30 (Conant, 2007) the gas solubility-related summer DO saturation declined by 6.1% ( $-0.48 \text{ mg L}^{-1}$ ) between 2003 and 2020.

DO reductions can force ectotherms to endure a greater than usual magnitude of physiological disturbance, especially if intensified hypoxic conditions coincide with temperature extremes (Pörtner, 2010). This was clear in Flanders Bay where scallops were exposed to severe diel-cycling hypoxia during an 8-day estuarine heatwave and all individuals perished. The survival results from the laboratory experiment that recreated the extreme daily temperature of Flanders Bay along with normoxic or hypoxic conditions affirmed that the combination of high temperature and low DO stress was

lethal to the adult bay scallops, as all individuals died within 72 h. These findings were consistent with a previous laboratory study on juvenile bay scallops ( $13.7 \pm 0.8 \text{ mm SH}$ ) where the combination of chronic low DO ( $2.41 \pm 0.54 \text{ mg L}^{-1}$ ) and high temperature ( $30^{\circ}\text{C}$ ) significantly increased mortality 10-fold relative to the comparable hypoxic treatment at ambient temperatures of  $24^{\circ}\text{C}$  (Stevens & Gobler, 2018).

Temperature extremes alone, absent of hypoxia, have also been demonstrated to induce negative consequences for northern bay scallops. A mariculture suitability study in Georgia (outside of the subspecies' natural geographic distribution), where bay scallops were grown 0.3 m below the surface, reported mass mortality (size: 43.3–49.0 mm) associated with a 7-day increase in temperature from 26 to  $29.6^{\circ}\text{C}$ , suggesting lethal temperatures between those bounds (Heffernan et al., 1988). The study by Stevens and Gobler (2018) also reported a significant, negative effect of elevated temperature on juvenile survival during a 4-week exposure. While our 4-day laboratory experiment revealed a slightly elevated likelihood of individual mortality in the  $29^{\circ}\text{C}$ -normoxic treatment relative to the  $25^{\circ}\text{C}$ -normoxic treatment, the difference was not significant (hazard ratio: 2.086, CI: 0.19–23.01); however, the exposure duration was nearly 45% and 86% shorter than those reported by Heffernan et al. (1988) and Stevens and Gobler (2018), respectively, and 50% shorter than the estuarine heatwave in Flanders Bay.

Hypoxia alone (at  $25^{\circ}\text{C}$ ) also significantly increased the likelihood of individual bay scallop mortality (hazard ratio: 12.79) in the laboratory experiment, contrasting with the field results at Salt Pond where no scallop mortality occurred despite repeated episodes of hypoxia at daily mean temperatures of  $\sim 25^{\circ}\text{C}$ . It is possible that the diel cycling of DO at Salt Pond provided a physiological refuge from hypoxic stress under average temperatures ( $24.9 \pm 2.0^{\circ}\text{C}$ ) that was not afforded under the temperature extremes in Flanders Bay ( $28.0 \pm 0.6^{\circ}\text{C}$ ). Although little is known about sensitivities of adult

bay scallops to diel-cycling hypoxia, results from two separate field studies suggest resilience to mild diel-cycling hypoxia (Gurr et al., 2018, 2021). A study on larvae indicated that diel-cycling hypoxia failed to alleviate mortality from hypoxic stress at 23°C (Clark & Gobler, 2016), but planktonic larval stages are generally considered more sensitive to hypoxia than benthic post-larval stages of invertebrates (Alter et al., 2015; Baker & Mann, 1992; Tomasetti et al., 2021). Future experiments simulating diel-cycling hypoxia across a temperature gradient are needed to clarify the extent to which periods of DO saturation and supersaturation under diel-cycling hypoxic conditions may influence adult bay scallops and other bivalves relative to chronic hypoxic conditions.

## 4.2 | Ecophysiology

During a field deployment, the negative correlation of scallop heart-beat rates with DO at 15-min intervals indicated that scallops responded quickly to decreases in DO, initially increasing cardiac output to maintain oxygen to the tissues, a common first response among mollusks under declining DO concentrations (Grieshaber et al., 1994; Herreid, 1980). This oxyregulation strategy persists only until a critical hypoxic threshold ( $P_c$ ) is reached, ~2–3 mg O<sub>2</sub> L<sup>-1</sup> for bay scallops (Gurr et al., 2018; Voyer, 1992), after which heart-beat rates and oxygen consumption are dramatically reduced to conserve energy, coinciding with a switch to anaerobic metabolism (Grieshaber et al., 1994; Herreid, 1980). Beyond DO, metabolic regulation also depends on temperature. Energy expenditure increases with increasing environmental temperature, and predictably, the  $P_c$  generally increases under elevated temperatures (Herreid, 1980). To that end, the strong significant correlation ( $\rho = 0.6$ ) of in situ heart-beat rate with temperature over daily temporal scales depicted the influence of background temperatures on oxygen consumption rates. Accelerated depletion of energy reserves under elevated temperatures forces individuals to cope with longer durations of energy limitation and increased energetic costs under hypoxic stress, further diminishing their aerobic scope (Sokolova, 2013), a potential precursor to the mortality observed under temperature and oxygen extremes in the field and laboratory experiments.

Rapid temperature increase in late spring or early summer serves as a spawning cue for bay scallops, with gamete release sometimes coinciding with temperature peaks (Tettelbach & Weinstock, 2008). The gonad indexes measured on bay scallops from Orient Harbor suggested that spawning occurred just before the scallop deployment and was followed by the estuarine heatwave and severe hypoxia in Flanders Bay. Energetic costs associated with reproduction may have compromised tolerance to extremes in temperature and/or DO, as has been shown for mussels (Cheung, 1993) and oysters (Li et al., 2007). A study by Li et al. (2007) found decreased glycogen stores and heat shock protein (HSP) levels in the tissues of post-spawning adults, resulting in an 8x increase in mortality among oysters exposed to thermal stress relative to pre-spawning individuals. The ability of bay scallops to withstand short periods of

30°C temperatures is predicated upon the synthesis of HSPs (Brun et al., 2008), a process requiring energy from glycogen stores that may be exhausted postspawning (Li et al., 2007). Efforts to quantify these metrics will be critical to assess the impact of the spawning event on the aerobic scope and stressor tolerance of this mostly semelparous species.

In some cases, food availability can enhance bivalve performance and aerobic scope during stress exposure (Norkko et al., 2005; Ramajo et al., 2016; Thomsen et al., 2013), although food limitation for suspension-feeders may be rare in hypoxic, eutrophic systems. Filtration rates measured during the laboratory experiment, however, revealed significant reductions in algal clearance for bay scallops exposed to hypoxia (88% reduction) or the combination of hypoxia and high temperatures (97% reduction). These findings are consistent with reports of reduced feeding rates among bivalves (Sanders et al., 2014; Sobral & Widdows, 1997; Wang et al., 2011) and other invertebrates (Cheung et al., 2008; Young & Gobler, 2020) during environmental hypoxia. Dramatic reductions in filtration rates may not always indicate negative aerobic scope (energetic supply < energetic demand), as both energy acquisition (via feeding) and energy expenditure (via metabolism) can be greatly reduced. However, the significant mortality over the 82 h following the clearance rate assay pointed toward energy-limited tolerance to chronic hypoxic- or combined thermal and hypoxic stress as a potential driver. Moreover, a previously undescribed parasite recently discovered in bay scallops was shown to increase scallop susceptibility to environmental stressors, including high temperature and low oxygen levels (Allam et al., 2022). Similarly, salinity dynamics at Flanders Bay may have influenced parasite loads and stressor tolerance, as the mean salinity was reduced at Flanders Bay relative to the other sites (Table 1) but within the range of tolerable levels for bay scallops (Marshall, 1960; Rhodes & Widman, 1984).

## 4.3 | Climate change biogeography and implications for fisheries

Distribution shifts toward higher latitudes and/or deeper depths are characteristic species-level responses to increasing water temperatures encompassed within current climate change (Nye et al., 2009; Perry et al., 2005; Pinsky et al., 2013). Where possible, marine species generally follow the movement of isotherms in time and space (Pinsky et al., 2013) to match their physiological tolerances but are also likely influenced by additional factors such as community interactions (Wisiz et al., 2013) and fishing effort (Lucey & Nye, 2010). Shifts in the distribution of many important fishery species have been documented in tandem with rapid warming of the northwest Atlantic Ocean (Nye et al., 2009; Pinsky & Fogarty, 2012; Weinberg, 2005). The centers of biomass of North Atlantic fish stocks have shifted poleward (Nye et al., 2009), and bottom trawl survey data indicate that the preferred temperature of fish assemblages in each subregion has increased as individual species shift northward (Lucey & Nye, 2010). Warming bottom temperatures have also displaced

Atlantic surf clam, *Spisula solidissima*, populations poleward and further offshore (Narváez et al., 2015; Weinberg, 2005). Warming trends are punctuated by episodic thermal events that result in the mortality of larger individuals and potentially explain overall declines in surf clam abundance (Narváez et al., 2015).

Fishery collapse and/or mass mortality events linked to summer temperature increases have been reported for blue mussels (*Mytilus edulis*) in multiple estuaries south of Delaware Bay (Jones et al., 2009, 2010), American lobsters (*Homarus americanus*) in Long Island Sound (Pearce & Balcom, 2005), and cod (*Gadus morrhua*) in the Gulf of Maine (Pershing et al., 2015) over the past two decades. In all cases, fishery collapses occurred at or near the southern margins of the species' ranges. Similarly, while northern bay scallops can inhabit areas of NJ, the Peconic Estuary marks the southernmost edge of significant, commercially viable populations (MacKenzie Jr., 2008). If the thermal tolerances of NY populations are exceeded more frequently, continuing summer warming may constrain the *A. i. irradians* fishery solely to coastal MA waters. Alternatively, shifting isotherms may help to strengthen or establish *A. i. irradians* fishery regions north of Cape Cod, as has been observed for other species in the North Atlantic (Pinsky & Fogarty, 2012). For instance, the mean latitude of American lobster landings in the northeast United States increased in parallel with poleward range shifts from 1970 to 2010 (Pinsky & Fogarty, 2012). In 1999, sustained anomalously warm bottom waters in Long Island Sound (NY-CT) were associated with mass mortality and collapse (98% reduction in landings) of its lobster fishery (Pearce & Balcom, 2005; Wilson & Swanson, 2005), but in Maine record-breaking landings occurred that year and continued into the decade that followed (Steneck & Wahle, 2013). Modeling efforts indicated that the success of the fishery in the Gulf of Maine during that time was also aided by proactive management and conservation measures (Le Bris et al., 2018), suggesting that fishing pressure and social responses to range shifts and climate impacts are critical determinants for sustainable fisheries. This was further illustrated by the collapse of cod stocks in the Gulf of Maine where mortality associated with record warming and sustained fishing pressure collectively led to severe declines in biomass (Pershing et al., 2015).

Rapid regional warming is expected to continue throughout the century. High-resolution climate models project North Atlantic warming rates that are nearly 3× the global average under a doubling of atmospheric CO<sub>2</sub>, associated with a combination of external CO<sub>2</sub> forcing, the continued northern migration of the Gulf Stream, and lessened influence of the Labrador current (Saba et al., 2016). These forcing mechanisms interact with smaller-scale physical and/or geographic features that may partially mitigate or exacerbate warming patterns and produce spatial heterogeneity in temperature trends. For example, for Nantucket Sound, the bathymetry and sheltered geography (via the islands of Martha's Vineyard and Nantucket) in tandem with the shifting circulation patterns of the Northwest Atlantic jointly led to the rapid summer warming trend observed in that location (Yu & Tang, 2022).

Projected warming and O<sub>2</sub> loss throughout the temperate northern hemisphere are predicted to substantially decrease (~50%) the ratio of

O<sub>2</sub> supply to O<sub>2</sub> demand for marine species, constraining the availability of metabolically viable habitat (Deutsch et al., 2015). Particularly relevant to coastal benthic shellfish, factors such as dispersal capacity and availability of tolerable habitat may either grant or prevent expansion (Doney et al., 2012). The persistence of the *A. i. irradians* fishery throughout the Northeast will likely depend in part on the extent of summer temperature change under climate change and the availability of habitat with tolerable temperature and DO conditions.

The northward migration of the Gulf Stream, in addition to delivering warmer waters to the region, also results in a relative increase in saltier, more buffered Gulf Stream seawater (Cai et al., 2020; Salisbury & Jönsson, 2018). While these shifts could mask or partially mitigate ongoing ocean acidification (Salisbury & Jönsson, 2018; Xu et al., 2020), the enhanced respiration that drives hypoxia can lead to the production of CO<sub>2</sub> and temporary extremes in low pH (Tomasetti & Gobler, 2020; Wallace et al., 2014). Accordingly, bay scallops exposed to low DO are simultaneously exposed to low pH which has been shown to negatively impact the survival of larval-stage individuals in an additive manner (Gobler et al., 2014). Larval bay scallop survival is particularly sensitive to acidification (Gear et al., 2020), while juvenile stage sensitivities can vary by size and exposure duration (Stevens & Gobler, 2018). This additional acidification stressor may further strain adult bay scallops exposed to hypoxia. To that end, a recent meta-analysis determined that the impacts of hypoxia and acidification co-stressors on mollusk survival and performance are predominately additive (Steckbauer et al., 2020).

#### 4.4 | Conclusion

During 2019–2021, the *A. i. irradians* fishery in NY collapsed with a decline in landings of >98%, resulting in estimated dockside losses of >\$6 M in 2019–2020 (NOAA, 2021). The results presented here suggest that a combination of thermal and hypoxic stress, potentially in conjunction with other stressors (e.g., disease or acidification), contributed to the widespread summer mortality. In the US Northeast and Mid-Atlantic, shellfisheries account for >75% of the nearly \$1.8B annual value of fisheries over the last decade (NOAA, 2021). Whether other economically important bivalve populations will be susceptible to the combination of warming and hypoxia under continued climate change is unknown, as bay scallops are considered among the more sensitive of the regional bivalve fishery species to global change stressors (Gear et al., 2020; Stevens & Gobler, 2018). These drivers, however, can also transform habitats and ecosystems in ways that harm fisheries, even if not as direct “stressors,” for instance via the promotion of harmful algal blooms (Díaz et al., 2019; Gobler et al., 2017; Griffith et al., 2019), the loss of seagrass habitat (Nyström et al., 2012; Strydom et al., 2020), or increased impacts of disease (Ford & Chintala, 2006; Pearce & Balcom, 2005). While climate change mitigation will require a global effort, identifying pathways toward the recovery of highly impacted hypoxic systems (Conley et al., 2009; Gobler et al., 2022; Steckbauer et al., 2011) may benefit vulnerable fisheries.



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## CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Dryad at <https://doi.org/10.5061/dryad.j0zpc86jj> and in the Physical Oceanography Distributed Active Archive Center (podaac) at <https://doi.org/10.5067/GHGMR-4FJ04>. These data were derived from the following resources available in the public domain: NOAA Commercial Fisheries Landings data at <https://www.fisheries.noaa.gov/foss>; NOAA National Data Buoy Center data at [https://www.ndbc.noaa.gov/station\\_page.php?station=ntkm3](https://www.ndbc.noaa.gov/station_page.php?station=ntkm3); USGS Water-Quality Data for the Nation at <https://waterdata.usgs.gov/nwis/qw>; NOAA Optimum Interpolation (OI) Sea Surface Temperature (SST) V2 data at <https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html>; and Multi-scale Ultra-high Resolution (MUR) Sea Surface Temperature (SST) Analyses data available in the Physical Oceanography Distributed Active Archive Center (podaac) at <https://doi.org/10.5067/GHGMR-4FJ04>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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