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Differential Mortality of North Atlantic Bivalve Molluscs During Harmful Algal Blooms Caused by the Dinoflagellate, Cochlodinium (a.k.a. Margalefidinium) polykrikoides

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Abstract

Blooms of the dinoflagellate, *Cochlodinium* (*a.k.a. Margalefidinium*) *polykrikoides*, have had deleterious effects on marine life across the Northern Hemisphere and, since the early 1990s, have become more frequent and widespread. While the toxic effects of *C. polykrikoides* have been well-described for finfish, the effects on bivalve molluscs are poorly understood, particularly in ecosystem and aquaculture settings. The purpose of this study was to characterize the comparative effects of *C. polykrikoides* blooms on North Atlantic bivalves and to identify the environmental factors that influence its toxic effects. The growth and survival of two age-classes (first- and second-year) of the northern quahog (*Mercenaria mercenaria*), the bay scallop (*Argopecten irradians*), and the eastern oyster (*Crassostrea virginica*) were quantified in surface deployments and at depth during annual bloom events in multiple locations across eastern Long Island (NY, USA), capturing a natural gradient in *C. polykrikoides*. In two consecutive years, scallops deployed within surface locations experienced significant mortality (75–100%) during short-term (1–2 weeks) but intense ($> 1.5 \times 10^4$ cells mL^{-1}) *C. polykrikoides* blooms. Conversely, scallops deployed at depth and clams and oysters deployed at either the surface or at depth were more resistant to blooms. First-year oysters and scallops that survived blooms displayed significant reductions in growth rates, while clams and older scallops and oysters did not. Results suggest that blooms of *C. polykrikoides* pose significant age- and species-specific threats to native and cultured bivalve shellfish and that shellfish deployed in surface waters are at greater risk during blooms than those deployed at depth.

Keywords *Margalefidinium polykrikoides* · *Cochlodinium polykrikoides* · Harmful algae · *Mercenaria mercenaria* · *Argopecten irradians* · *Crassostrea virginica*

Introduction

Harmful algal blooms (HAB) pose a significant and growing threat to aquaculture (Shumway 1990; Landsberg 2010), and climate change is predicted to increase the distribution and severity of several HAB (Hallegraeff 2010; Glibert et al.

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2014; Gobler et al. 2017). At bloom-exposed aquaculture locations, HAB can cause widespread (Gobler et al. 2017) mortality among cultured organisms and sub-lethal impacts (i.e., reduced growth, physical damage, etc.; Shumway 1990; Landsberg 2010; Matsuyama and Shumway, 2009; Burkholder and Shumway 2011) can limit marketability of products (Shumway 1990; Anderson et al. 2000). Certain HAB are capable of producing potent neurotoxic or gastrointestinal biotoxins that can (bio)accumulate in the tissues of exposed shellfish, and when consumed by humans can result in severe intoxication (Shumway 1990; Hégaret et al. 2009) making shellfish aquaculture particularly vulnerable to these events. As aquaculture industries continue to expand and concurrent changes in climate stimulate the growth and proliferation of certain HAB (Gobler et al. 2017), identifying potential risks (i.e., vulnerable species) and mitigation strategies may limit losses.

Identified in 1895 (Schütt 1895), blooms of dinoflagellates within the genus *Cochlodinium* (*a.k.a Margalefidinium*) have

been reported along North American and East Asian coast-lines for decades (Kudela and Gobler 2012). Since the 1990s, however, reports have become more commonplace with blooms now occurring in areas previously void of these HAB (Kim et al. 1999; Gobler et al. 2008; Kudela et al. 2008; Kudela and Gobler 2012). Dense aggregations of *C. polykrikoides* also known as, 'rust tides,' can be associated with widespread marine animal mortality (Kim et al. 1999; Gobler et al. 2008; Mulholland et al. 2009; Richlen et al. 2010). The toxic effects of *C. polykrikoides* on finfish in both field and laboratory settings have been well-described (Kim et al. 1999, 2000; Tang and Gobler 2009a) being highly lethal (Gobler et al. 2008; Tang and Gobler 2009a), manifested acutely (Kim et al. 1999; Gobler et al. 2008), and causing significant economic damage (Kim 1997; Kim et al. 1999). Shellfish are more resistant than fish to *C. polykrikoides*, but are nonetheless susceptible (Ho and Zubkoff 1979; Gobler et al. 2008; Tang and Gobler 2009b). While the effects of *C. polykrikoides* on bivalve shellfish have been described (Ho and Zubkoff 1979; Gobler et al. 2008; Tang and Gobler 2009b), there is little comparative information (i.e., species- and size-specific) and few reports describing lethal or sub-lethal effects in ecosystem settings.

Blooms of *C. polykrikoides* are now annual occurrences in many temperate zones of the Northern Hemisphere (Gobler et al. 2008; Kudela et al. 2008; Kudela and Gobler 2012) and commonly occur in areas with widespread aquaculture within the northwest Atlantic (Gobler et al. 2008; Mulholland et al. 2009; Li et al. 2012) and Pacific (Kim et al. 1999, 2000). To date, approximately 50% of the global seafood production is aquaculture-sourced, with more than half of that production being attributed to shellfish (NMFS 2015; FAO 2016a). Within *C. polykrikoides*—afflicted regions of the northeastern US, bivalve shellfish represent a large and increasing portion of fisheries landings (Shumway et al. 2003; Ekstrom et al. 2015; NMFS 2015) and are a key economic resource in some coastal communities (Neiland et al. 1991; Shumway et al. 2003; Grabowski et al. 2012). In addition to their economic value, bivalve shellfish provide essential ecosystem services through the control of eutrophication (Officer et al. 1982; Dame 1996; Newell 2004; Burkholder and Shumway 2011), stabilization of coastlines (Coen et al. 2007; Grabowski and Peterson 2007), establishment of critical habitat (Tolley and Volety 2005; Coen et al. 2007; Abeels et al. 2012), and re-moval of particulates from the water column (Newell 2004; Wall et al. 2011).

Daily vertical movement of *C. polykrikoides* has been doc-umented in Korean coastal waters (Park et al. 2001; Kim et al. 2010), with high concentrations reported at the surface during daylight hours and greater abundances at depth (< 20 m) dur-ing the night. Diel vertical migration is common in many dinoflagellate species, enabling cells to exploit nutrient-rich bottom waters in areas where surface-nutrients are depleted

(Smayda and Reynolds 2003; Doblin et al. 2006). The ability of *C. polykrikoides* to form chains of two or more cells en-hances motility (Fraga et al. 1989; Smayda and Reynolds 2003), helps to maintain surface positions in warm, low-viscosity waters (Fraga et al. 1989), and deters grazers (Jiang et al. 2009, 2010). Fish kills associated with *C. polykrikoides* along the east coast of Korea have been reported at depth, at night, presumably as *C. polykrikoides* cells migrate deeper into the water column (Kim et al. 2010). While diel movements of *C. polykrikoides* have been partly char-acterized in Asia, they have never been described along the east coast of the USA. Nonetheless, movements are likely dependent upon the hydrographic conditions in bloom-exposed areas and/or strain-specific (Kudela et al. 2008) with the ribotype (e.g., East Asian) of *C. polykrikoides* forming blooms in Korea being distinct from the American/Malaysian ribotype (Iwataki et al. 2008). Regardless, vertical movement within the water column could influence impacts of *C. polykrikoides* on aquaculture in areas where blooms are present.

The purpose of this study was to identify species-, age-, and position-specific effects of *C. polykrikoides* on the growth and survival of three commercially and ecologically significant bivalve shellfish, the eastern oyster (*Crassostrea virginica*), the northern quahog (= hard clam; *Mercenaria mercenaria*), and the bay scallop (*Argopecten irradians*). Two age-classes of each species (first- and second-year) were deployed at bloom-prone locations in Long Island (NY, USA) estuaries at surface and bottom positions prior to and during annual bloom events in 2014 and 2015. Survival and growth of shell-fish were quantified weekly as blooms initiated, peaked, and waned. In addition to quantifying growth and survival of bi-valves, surface and bottom chlorophyll *a*, temperature, dis-solved oxygen, and *C. polykrikoides* densities were measured at each site.

Materials and Methods

### Shellfish Collection and Maintenance

To assess the age- and species-specific effects of *C. polykrikoides* exposure at varying vertical positions within the water column, multiple species of shellfish of different age classes (first- and second-year; all diploid) were deployed at multiple locations within Shinnecock and Peconic Bays during *C. polykrikoides* bloom events on Long Island (NY, USA). In 2014, responses among two size-classes of each shellfish species (*C. virginica*, *M. mercenaria*, and *A. irradians*) were examined. First-year shellfish (all species) were obtained from the East Hampton Town Shellfish Hatchery (EHTSH; Montauk, NY, USA). Second-year clams and oysters were obtained from EHTSH and second-year size-

class bay scallops were collected from eastern Shinnecock Bay (40.8647° N, 72.4913° W). In 2015, juvenile scallops (first-year only) were obtained from the Cornell University Cooperative Extension (Southold, NY). Prior to deployments, all shellfish were maintained in flow-through sea tables (~23 °C) for ~2 weeks at the Stony Brook—Southampton Marine Science Center which circulates water from eastern Shinnecock Bay.

Shellfish Deployments—2014

Shellfish were deployed August 13, prior to blooms, at surface and bottom positions (~2 m) in Old Fort Pond (OFP; within eastern Shinnecock Bay; 40.8688° N, 72.4468° W) and East Creek (EC; northern shore of Peconic Bay; 40.9439° N, 72.5702° W; Fig. 1), two locations prone to annual blooms of *C. polykrikoides*. In addition, shellfish were deployed at the northern shore of Shinnecock Bay (NS; control site within eastern Shinnecock Bay; 40.8827° N, 72.4893° W), a site typically void (personal observation, unpublished) of *C. polykrikoides*. Prior to deployments, each individual shellfish was measured. Larger size-class individuals were labeled with glue-on shellfish tags (Hall Print Fish Tags®). One hundred first-year clams (3.83 ± 0.18 mm; mean shell height ± S.D.)

and oysters (4.86 ± 0.19 mm; mean shell height ± S.D.) and 50 first-year scallops (5.71 ± 0.11 mm; mean shell height ± S.D.) were added to surface and bottom shellfish rafts (3 rafts species^{-1} depth^{-1}; e.g., 6 rafts location^{-1} species^{-1}; 18 rafts site^{-1}). For 2014 deployments, first-year shellfish were maintained within smaller mesh (1 mm opening) bags placed into larger (5 mm; see below) grow-out rafts. Each mesh bag was replaced weekly. Shellfish rafts (Go Deep International®) were approximately $1 \times 0.5 \times 0.05$ m ($l \times w \times h$) with 5 mm openings. As shellfish grew, individuals were transferred into 15 mm mesh size rafts (same dimensions as above) to increase water flow around shellfish and limit fouling. For second-year size-class individuals, 50 clams (13 ± 3.02 mm; mean shell height ± S.D.) and oysters (32 ± 4.25 mm; mean shell height), and 30 scallops (53 ± 3.60 mm; mean shell height ± S.D.) were within each raft (same dimensions and replication as above) at each site. Mean bottom depth at all sites was 2 m; all surface rafts were deployed just below the water surface using surface floats, whereas bottom bags were weighted and held ~10 cm above sediments. Care was taken to separate cohorts of shellfish within each raft using a permeable baffle. Bivalves were examined weekly at each location. During weekly monitoring, water samples were collected at surface and depth using horizontal Van Dorn bottles. Samples for *C.*
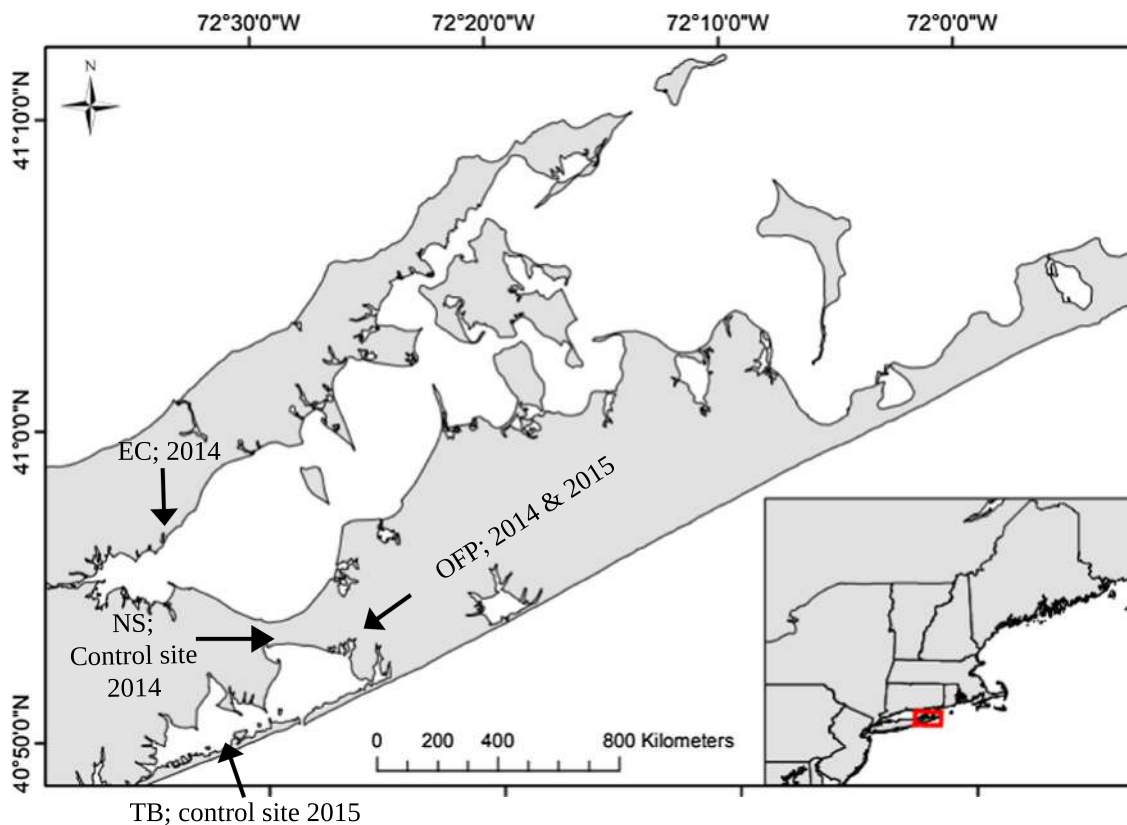
Fig. 1 Map of shellfish deployment locations (*EC* East Creek, *OFP* Old Fort Pond, *NS* northern shore of Shinnecock Bay, *TB* Tiana beach) on eastern Long Island (NY, USA) for 2014 and 2015

polykrikoides enumeration were preserved in a 1% Lugol's iodine solution and quantified microscopically using a Sedgewick-Rafter counting chamber. Chlorophyll *a* (5 μm) was analyzed fluorometrically according to Parsons et al. (1984). Other water quality measurements were made at surface and bottom (temperature, dissolved oxygen (DO), and salinity) using a multi-parameter handheld sonde (YSI®). In addition to weekly quantification of water quality parameters, temperature and DO loggers (Onset HOBO®) were placed in surface and bottom rafts at each locale to provide continuous data during the entire experiment at each site. Experiments ended when *C. polykrikoides* cells were no longer present at any of the locations (e.g., 26 Sept 2014). Final shell heights of each shellfish were determined upon the termination of the deployment and used to calculate final growth rates (mm day^{-1}) for each species and size-class.

Shellfish Deployments—2015

An additional series of experiments was conducted during the summer of 2015 with first-year scallops (~15 mm) only. Scallops, obtained from the Cornell University Cooperative Extension Marine Program (Southold, NY), were deployed within OFP and at Tiana Beach (TB; 40.8289° N, 72.5305° W; Fig. 1) within western Shinnecock Bay, a site historically void of *C. polykrikoides*. Shellfish were deployed in grow-out rafts (15 mm mesh size; *n* = 3 rafts site^{-1} position^{-1}; *n* = 100 scallops raft^{-1}; see above for description) at surface and at depth prior to the occurrence of *C. polykrikoides* blooms (e.g., 2 Sept 2015). Shellfish were monitored for survival and temperature and DO monitored as described for 2014. Experiments lasted ~1 week due to a mass mortality event associated with a *C. polykrikoides* bloom and thus growth was not quantified.

Assessment of Diel Vertical Migration

Multiple diurnal water collections were conducted over 72 h within OFP during the peak of the 2014 bloom (9–12 Sept 2014) to identify spatial and temporal patterns of cell densities among surface and bottom positions. At 2- and 3-h intervals, water samples were collected from the surface and bottom using a horizontal Van Dorn water sampler. Samples were preserved in Lugol's iodine and cell densities determined using a compound light microscope.

Data Analysis

All statistical analyses were conducted using R® (www.r-project.org,Version 3.4.4) software. To compare differences in the growth and survival of shellfish, a three-way analysis of variance (ANOVA) was performed for each age-class with 'species,' 'site,' and 'position' included as the main, fixed

effects. Surface and bottom bags, within each site, were maintained independent from one another and thus it was assumed that effects at one position did not carry-over to concurrently deployed shellfish at the same position or to individuals at other positions. Maximum cell densities between sites and positions were analyzed using a two-way ANOVA. All data was verified to conform to a normal distribution with equal variance using Kolmogorov-Smirnov Goodness-of-Fit and Levene's (http://cran.r-project/package=car) tests respectively. When significant differences were detected, a Tukey's honest significant difference (Tukey HSD) test was performed to identify the source of variance and to adjust *p* values for multiple comparisons. Differences in levels of environmental variables (e.g., mean temperature, dissolved oxygen, and chlorophyll *a*) between sites and among surface and bottom positions within each site during deployments were analyzed using a linear mixed effect model (LME; https://cran.r-project.org/package=nlme) with 'site' and 'position' included as fixed effects in addition to a random effect of 'time' to account for non-independence (i.e., repeated measures) of measurements over time. Assumptions of a normal distribution were confirmed using Kolmogorov-Smirnov's test. Unequal variances of environmental parameters between sites and among position within sites were observed and as such, site- and position-specific variances were included in model parameters. Pairwise comparisons of environmental conditions within and between shellfish deployment sites were analyzed using least-square means (http://cran.r-project.org/packag=lsmean) and *p* values adjusted as per Tukey's method. All results were deemed significant at $\alpha \leq 0.05$.

Results

Progression of Blooms During 2014 and 2015

Blooms of *C. polykrikoides* were present at both OFP and EC during the last week of August (2014) and persisted for ~3 weeks (Figs. 2 and 3). Maximum cell densities observed during the second week of September (11–19 Sept 2014) varied significantly by site ($p < 0.001$; two-way ANOVA) and by position within each site ($p < 0.001$; two-way ANOVA). Peak surface densities at each location were significantly ($p < 0.001$; Tukey HSD) greater than those observed within the bottom waters and, regardless of position, densities were the greatest at OFP, followed by EC, and then NS; of which, all were significantly different (all $p < 0.001$; Tukey HSD; Figs. 2, 3, and 4). Maximum densities were 34,950 ± 2404 and 2215 ± 98 cells mL^{-1} (mean ± S.D.) at the surface of OFP and EC, respectively. During the same period, densities within bottom positions at these locations were 4810 ± 240 and 275 ± 9 cells mL^{-1} respectively. Only low densities (18 ± 6 and 44

Fig. 2 Survival (mean ± S.D.; $n = 3$ species^{-1} size-class^{-1}) of first- (**a**, **c**) and second-year (**b**, **d**) shellfish deployed within Old Fort Pond during August and September (2014) and corresponding *C. polykrikoides* densities (secondary *y*-axis; shaded line)
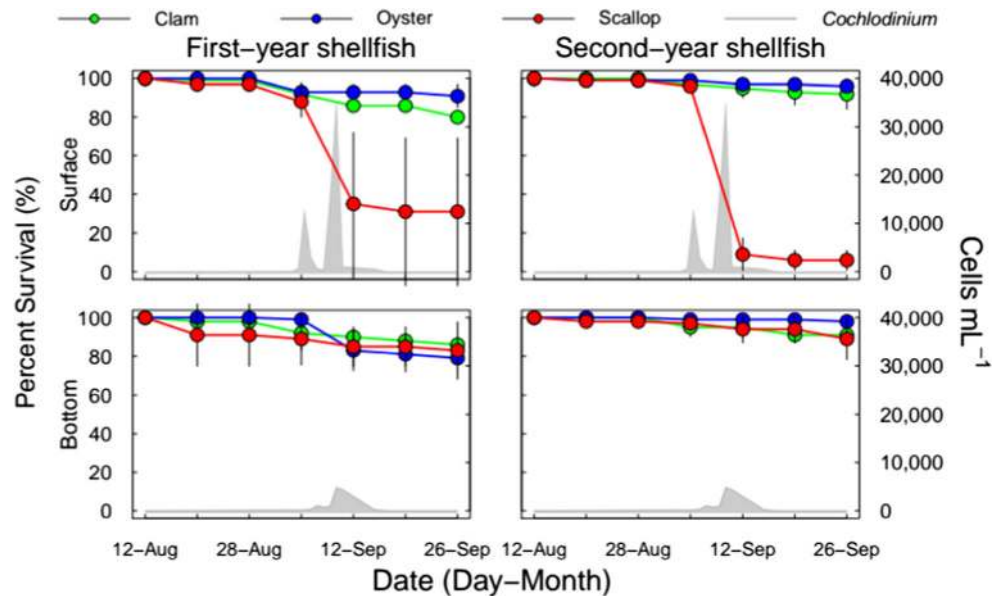
± 6 cells mL^{-1}; maximum surface and bottom densities respectively) of *C. polykrikoides* were observed at NS, making it an ideal control locale in 2014 (Fig. 4).

During 2015, *C. polykrikoides* was present in OFP throughout September (2–24 Sept 2014) and densities were found to differ between OFP and TB ($p < 0.001$; two-way ANOVA) and by position within each site ($p < 0.01$; two-way ANOVA). Two distinct peaks in cell density were observed in OFP (Fig. 5, inset) with a first maximum occurring on September 10th peaking at $13,350 \pm 438$ cells mL^{-1} and a second maximum (7800 ± 59 cells mL^{-1}) occurring on the 14th. In a manner similar to 2014, cell densities within bottom positions (212 ± 6 cells mL^{-1}; maximum density) of OFP were significantly lower ($p < 0.001$; two-way ANOVA) than

those observed at the surface (Fig. 5, inset). Densities at TB (surface and bottom positions; data not shown) never exceeded 200 cells mL^{-1} and were significantly ($p < 0.001$; Tukey HSD) lower than levels (both surface and bottom) observed at OFP.

## Shellfish Survival—Summer 2014

For first-year shellfish, significant ($p < 0.01$; three-way ANOVA; see Suppl. Table 1 for all pairwise comparisons) interactive effects between 'species,' 'site,' and 'position' were detected whereby survival of first-year scallops was significantly lower among surface positions of OFP only (Figs. 2 and 6a–c). Mortality of first-year scallops within

Fig. 3 Survival (mean ± S.D.; $n = 3$ species^{-1} size-class^{-1}) of first- (**a**, **c**) and second-year (**b**, **d**) shellfish deployed within East Creek during August and September (2014) and corresponding *C. polykrikoides* densities (secondary *y*-axis; shaded line)
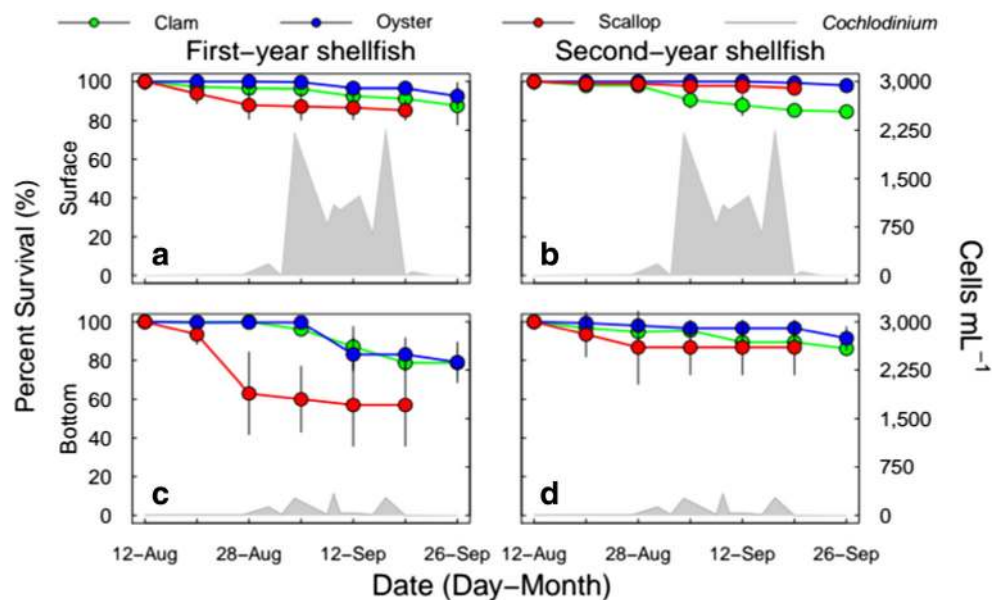
Fig. 4 Survival (mean ± S.D.; $n = 3$ species^{-1} size-class^{-1}) of first- (**a**, **c**) and second-year (**b**, **d**) shellfish deployed at the northern shore of Shinnecock Bay during August and September (2014) and corresponding *C. polykrikoides* densities (secondary *y*-axis; shaded line)
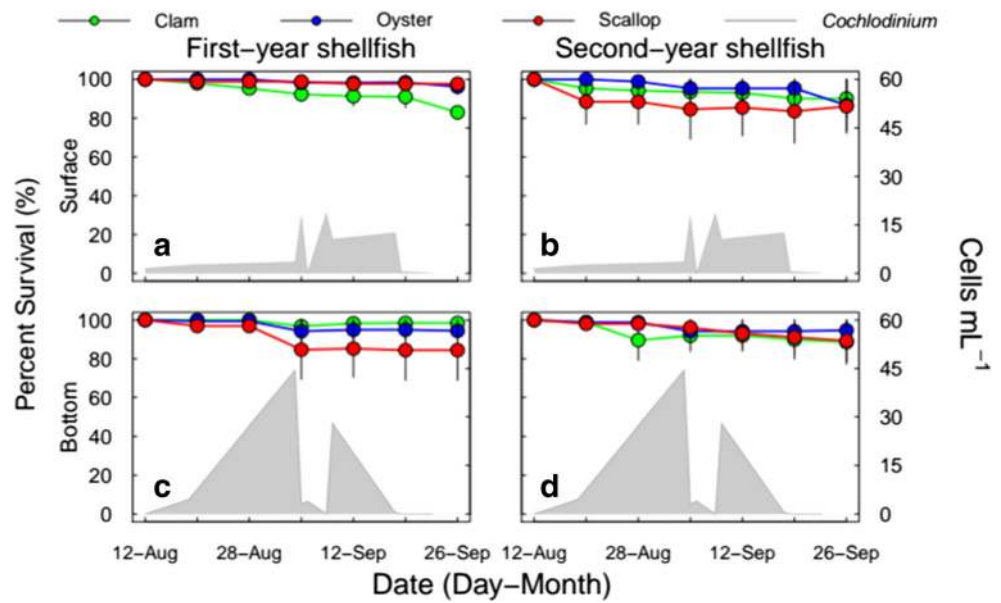

surface positions of OFP was $69 \pm 38\%$ (mean ± S.D.), significantly ($p < 0.01$; Tukey HSD) enhanced relative to those cultured at the bottom (e.g., $17 \pm 14\%$) and to any ($p < 0.05$; Tukey HSD) first-year shellfish cultured at any other site or position (Fig. 6c). No other differences in the survival of first-year shellfish were detected at any other site or position (Figs. 3, 4, and 6a–c). Similarly, for second-year shellfish, significant ($p < 0.001$; three-way ANOVA) interactive effects between 'species,' 'site,' and 'position' were detected with, again, scallops exhibiting significantly reduced survival within the surface waters of OFP only (Figs. 2 and 6d–f; see Suppl. Table 2 for all pairwise comparisons). The survival of second-year scallops within the surface of OFP was $5.6 \pm 5\%$ and significantly (all $p < 0.01$; Tukey HSD) reduced relative to the survival of all

other second-year shellfish at any other site or position (Figs. 2 and 6d).

Shellfish Survival—Summer 2015

For the 2015 experiment, surface mortality was observed again (Fig. 5). When the *C. polykrikoides* bloom emerged in OFP, significant ($p < 0.05$; two-way ANOVA; Fig. 5) scallop mortality followed at surface positions only, with 100% of scallops perishing. In contrast, scallops deployed at depth exhibited only 3% mortality. There was no effect of position or site on the survival of scallops deployed at TB where final survival was 97 and 93% at surface and bottom positions, respectively ($p > 0.05$; two-way ANOVA; Fig. 5). Growth

Fig. 5 Survival of bay scallops at OFP and TB during 2015 deployments ($n = 3$, error bars represent ± S.D.; asterisk denotes significant differences, $p < 0.05$; two-way ANOVA; inset depicts daily mean *C. polykrikoides* densities at OFP during deployments)
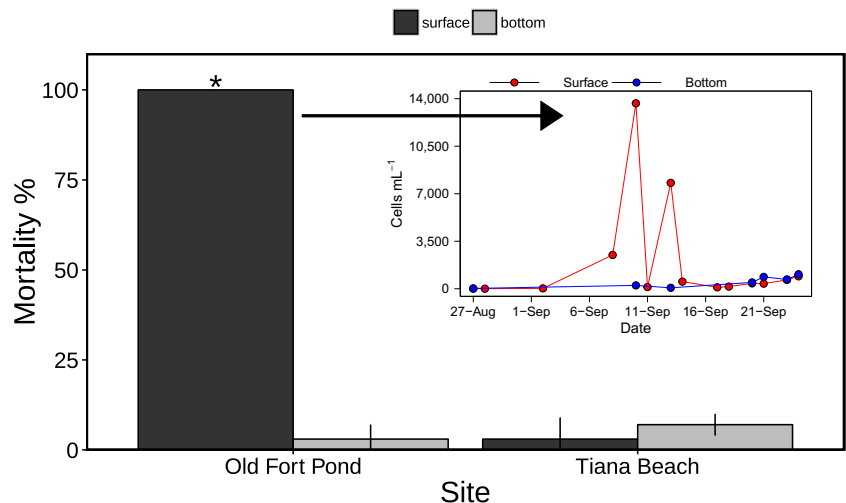
Table 1 Mean (± S.D) temperature (°C), dissolved oxygen (DO; mg L^{-1}), chlorophyll *a* (5 μm; μg L^{-1}), and peak *C. polykrikoides* cell densities (cells mL^{-1}) at deployments sites

Site	Position	Temperature	DO	Chlorophyll *a* 5 μm	Peak cell densities
OFP	Surface	22.71 ± 2.33	7.37 ± 2.08	26.10 ± 14.52	34,950 ± 2404
OFP	Bottom	22.99 ± 2.26	5.20 ± 2.17	19.26 ± 6.06	4810 ± 240
EC	Surface	22.63 ± 2.27	7.04 ± 1.79	28.31 ± 32.98	2215 ± 120
EC	Bottom	22.50 ± 2.28	5.80 ± 1.88	13.16 ± 13.82	267 ± 88
NS	Surface	22.64 ± 1.95	8.03 ± 1.03	3.14 ± 2.37	18 ± 3
NS	Bottom	22.53 ± 1.85	7.36 ± 1.45	4.11 ± 0.48	44 ± 6

rates for 2015 deployments were not quantified since mortality was 100% in surface positions after 1 week.

Shellfish Growth—First-Year—Summer 2014

Significant (all $p < 0.001$; three-way ANOVA) differences in growth rates between species were detected whereby first-year clams, regardless of site and/or position, grew slower than scallops and oysters (all $p < 0.001$; Tukey HSD; Fig. 7a–c). Additionally, significant ($p < 0.001$; three-way ANOVA) interactive effects between species, site, and position were observed (see Suppl. Table 3 for all pairwise comparisons). For first-year oysters, growth was the most rapid (0.56 mm day^{-1}) at the surface of NS and significantly (all $p < 0.01$; Tukey HSD) greater than growth observed among first-year oysters deployed at either (surface or bottom) bloom-exposed site (Fig. 7b). The growth of firs-year oysters was slowest at EC and significantly reduced relative to oysters at either position within NS and surface positions of OFP (all $p < 0.001$; Tukey HSD), but similar ($p > 0.05$; Tukey HSD) to rates observed among bottom positions of OFP (Fig. 7b). The growth of first-year bay scallops, regardless of position, was significantly reduced at both locations where moderate to high densities of *C. polykrikoides* was observed, OFP (~35,000 cells mL^{-1}) and EC (NS ~2500 cells mL^{-1}), relative to the control site (both positions; all $p < 0.01$; Tukey HSD; Fig. 7c).

Shellfish Growth—Second-Year—Summer 2014

For second-year shellfish, again, species-specific differences ($p < 0.001$; three-way ANOVA; see Suppl. Table 4 for all pairwise comparisons) were observed with hard clams and bay scallops, regardless of position and site, growing slower than oysters (Fig. 7d–f). Significant interactive effects between site and position ($p < 0.01$; three-way ANOVA) were observed whereby hard clams grown among bottom positions of NS grew significantly ($p = 0.0342$; Tukey HSD), albeit slightly (e.g., 0.053 mm day^{-1}), slower than those cultivated among bottom positions of OFP (Fig. 7d). For second-year oysters, growth rates among the surface of OFP were

Fig. 6 Final mortality (mean ± S.D.; $n = 3$ species^{-1} size-class^{-1}) of first- (**a–c**) and second-year (**d–f**) shellfish at deployment locations during the 2014 bloom (2014; * denote significant groupings; $p < 0.05$; three-way ANOVA)
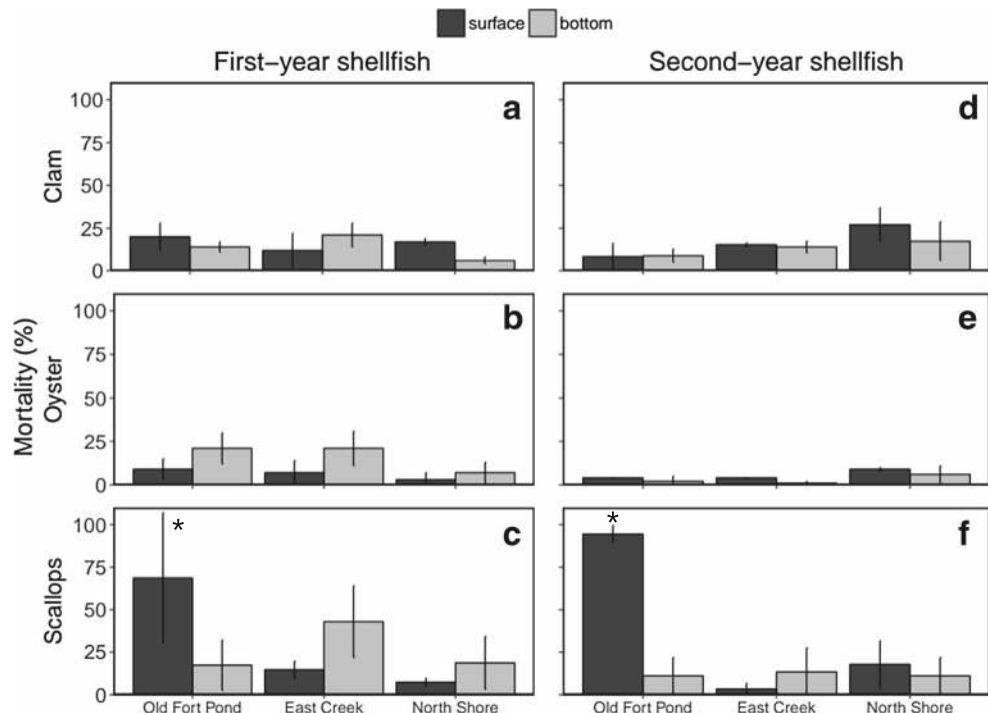
Fig. 7 Mean growth (mm day^{-1} ± S.D.; $n = 3$ species^{-1} size-class^{-1}) of first- (**a**–**c**) and second-year (**d**–**f**) shellfish at deployment locations during the 2014 bloom (2014; letters denote significant groupings by site and position; $p < 0.05$; three-way ANOVA)
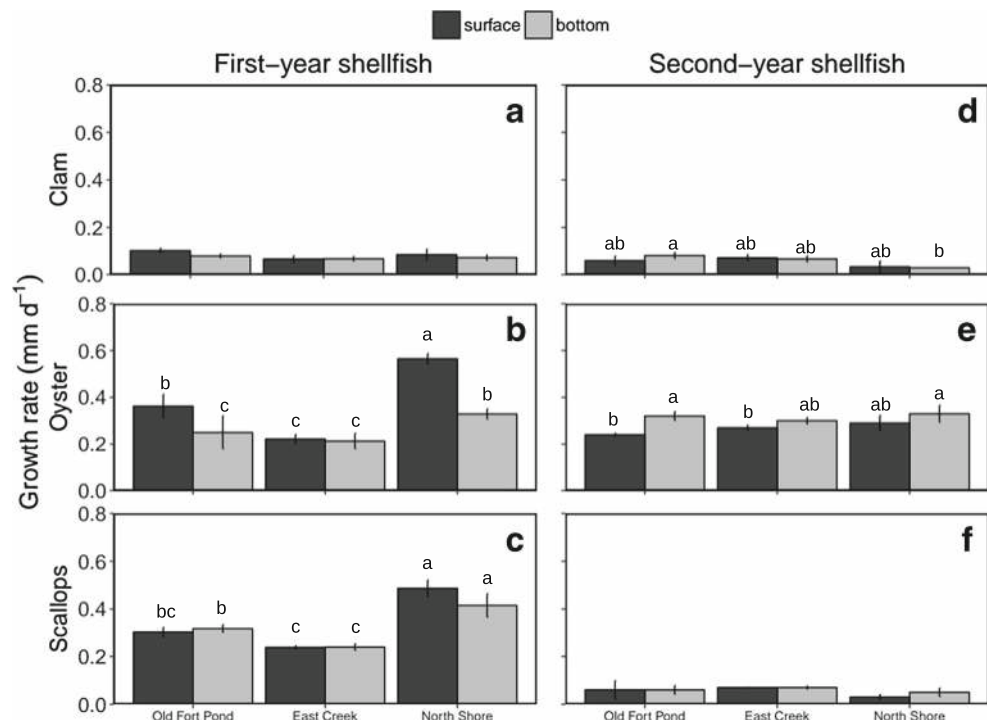
significantly (all $p < 0.01$; Tukey HSD) reduced relative to those cultivated at the surface of NS and among bottom positions of OFP, NS, and EC (Fig. 7e). Similarly, oysters among surface positions of EC grew slower relative to oysters among bottom positions of OFP and NS (Fig. 7e). There were no differences observed between the surviving scallops among any other sites or position within any site (Fig. 7f); however, survival of bay scallops was low (both age-classes, see "Shellfish Survival 2014—Summer 2014" section) at OFP; hence mean growth rates for this site were based upon the final lengths of the few surviving individuals within each raft.

Environmental Conditions During Bloom Events

Significant differences among environmental conditions were detected during 2014 shellfish deployments, but not during 2015. In 2014, temperatures during shellfish deployments (2014) were found to vary between site ($p < 0.05$; LME) and within each site ($p < 0.05$; LME; Table 1; Fig. 8). Surface temperatures at all sites were slightly, but significantly (all $p < 0.05$; Tukey HSD), warmer than at the bottom and among bottom positions, OFP was significantly ($p < 0.05$; Tukey HSD) warmer than NS and EC (Fig. 8a–c). There were no significant ($p > 0.05$; Tukey HSD) differences among surface temperatures at any deployment site. Levels of DO (Table 1) varied significantly (all $p < 0.05$; LME) within and between sites during deployments (Fig. 8). Within each site, DO levels at the bottom were significantly (all $p < 0.05$; Tukey HSD) lower than at the surface, and among surface-deployed shellfish,

DO levels were significantly (both $p < 0.05$; Tukey HSD) lower at OFP and EC compared to NS. Similarly, DO levels among bottom positions were significantly ($p < 0.05$; Tukey HSD) lower at OFP and EC relative to NS, but were not different ($p > 0.05$; Tukey HSD) from one another. Chlorophyll a concentrations were found to vary by site (all $p < 0.05$; LME) whereby surface and bottom concentrations were significantly lower at NS relative to EC. No detectable (all $p > 0.05$; Tukey HSD) differences in chlorophyll a were observed between surface and bottom positions at any site (Table 1). During the 2015 shellfish deployments, no differences among environmental parameters ($p > 0.05$; LME) were observed (Fig. 9).

Diel Vertical Migration—2014

Surface waters of OFP had consistently higher concentrations of *C. polykrikoides* compared to bottom samples (Fig. 10 and Table 1). During a 72-h period, cell densities within surface positions increased throughout the day while decreasing slightly at night. Peak cell densities (24,950 ± 2404 cells mL^{-1}) occurred at 22:30 (EST) on 11 Sept 2014 coinciding with a high tide (see Fig. 10) and decreased as the tide ebbed. Peak concentrations in bottom positions were significantly lower ($p < 0.05$; two-way ANOVA) at only ~4810 ± 240 cells mL^{-1}. Cell concentrations at bottom positions generally mirrored densities at the surface, but were, on average, ~10-fold lower during peak bloom activity.

Fig. 8 Surface and bottom temperatures (blue and red circles respectively), Chlorophyll *a* (5 μm; solid and dashed green lines respectively), and dissolved oxygen levels (light and dark great shaded areas respectively) within OFP (**a**), EC (**b**), and NS (**c**) during shellfish deployments (2014)
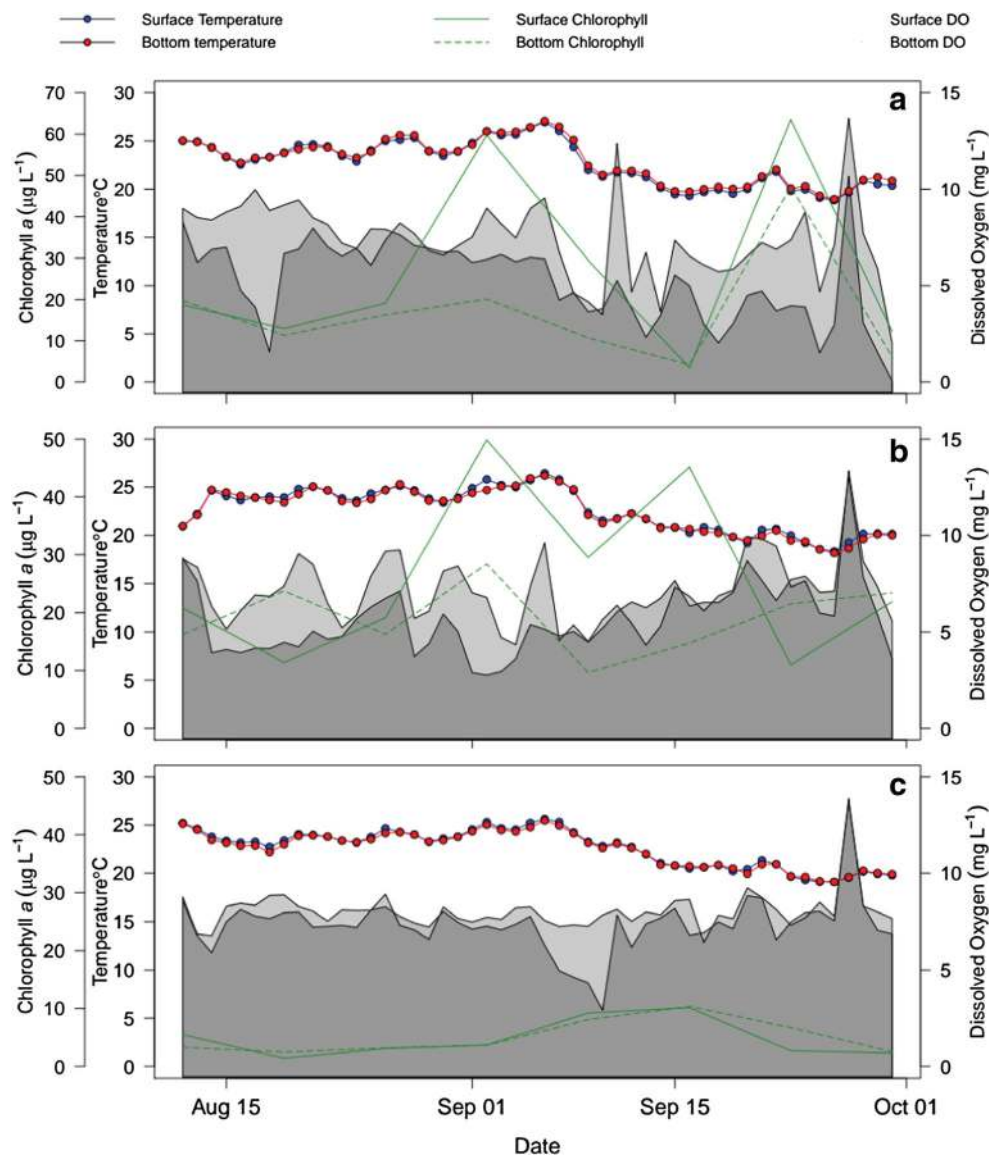
Fig. 9 Surface and bottom temperatures (blue and red circles respectively) and DO levels (light and dark gray shaded areas respectively) during shellfish deployments within OFP (**a**) and TB (**b**) during the 2015 bloom event
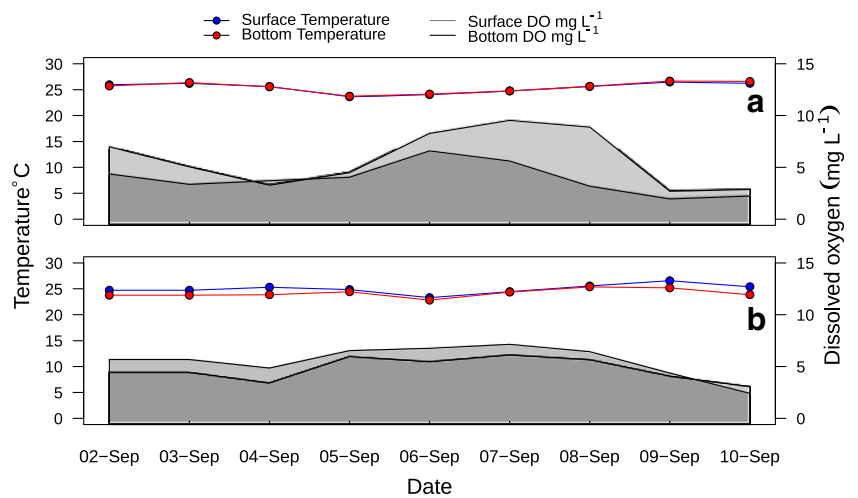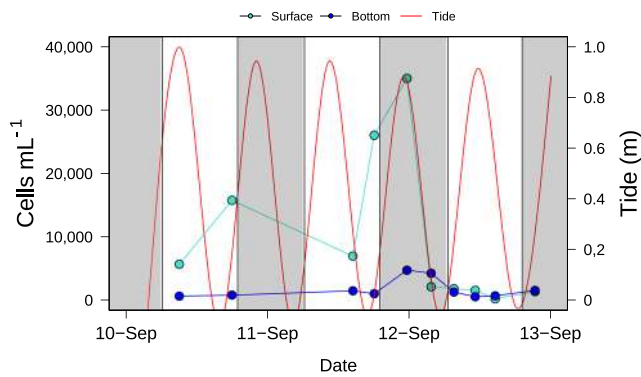
Fig. 10 Surface and bottom (turquoise and blue circles respectively) densities of *C. polykrikoides* within Old Fort Pond (09/10/14–09/12/14) during the 2014 bloom event and the corresponding tide (red line; secondary *y*-axis)

Discussion

Blooms of *C. polykrikoides* have long been known to be lethal to marine life, primarily cultured fish (Kim et al. 1999, 2000; Kudela and Gobler 2012). Results of this study demonstrate that blooms of *C. polykrikoides*, in addition to laboratory-based settings (Gobler et al. 2008; Tang and Gobler 2009a, 2009b), are lethal to shellfish in natural settings, posing a threat to multiple species and age-classes of bivalve molluscs. Differences in temperature were found to vary within and between deployment locations, but did not correspond directly with reduced survival or growth of shellfish. Effects were species-specific resulting in significantly reduced survival of bay scallops as well as the reduced growth of first-year scallops and oysters at bloom-prone sites. Scallop mortality, where present, was restricted to surface positions corresponding with maximum *C. polykrikoides* cell densities (Figs. 2a, b, 5, and 6e, f). Among commercially and ecologically significant North Atlantic bivalve shellfish, bay scallops appear to be at greater risk than oysters which appear more sensitive to blooms than clams and shellfish cultured at surface locations appear more vulnerable than those deployed at depth during *C. polykrikoides* blooms.

Implications for Shellfish Aquaculture

Aquaculture is a rapidly growing industry (FAO 2008, 2016b). Greater than half of the global seafood production now originates from cultured sources (FAO 2016b, a), supporting a growing demand for seafood that is an important source of protein and nutrition in many coastal communities (Mos et al. 2004; Hibbeln et al. 2007; Smith et al. 2010). Shellfish aquaculture in particular is growing in popularity due to its associated environmental benefits and its recognition as a 'sustainable' practice (Shumway et al. 2003; Burkholder and Shumway 2011). Results from this study, as well as others (see Ho and

Zubkoff 1979; Gobler et al. 2008; Mulholland et al. 2009; Tang and Gobler 2009a, 2009b; Li et al. 2012), suggest that *C. polykrikoides* blooms represent a threat to shellfish aquaculture and that the impacts are species-specific.

Beyond mortality, oysters and scallops displayed significant reductions in growth at sites where *C. polykrikoides* was present. Specifically, first-year oysters at surface positions displayed slower growth at bloom prone sites (OFP and EC) relative to the control location (NS), a finding consistent with prior studies of bivalves and *C. polykrikoides* in North America (Gobler et al. 2008; Li et al. 2012). Further reductions in first-year oysters were observed among bottom-deployed first-year oysters deployed at OFP and EC, possibly a result of low DO. Levels of DO at both OFP and EC were significantly lower than the control site (NS) with both sites exhibiting extended excursions below 5 mg L^{-1} (Fig. 9), levels that are known to slow the growth of shellfish (Vaquer-Sunyer and Duarte 2008; Levin et al. 2009; Gobler et al. 2014; Clark and Gobler 2016). Lower DO, however, at locations where elevated *C. polykrikoides* densities were observed may be linked, indirectly, to the presence of blooms (Bauman et al. 2010; Morse et al. 2011). For example, blooms occurring at the surface may limit light levels reaching the bottom and provide large quantities of organic matter, a scenario that would favor enhanced rates of microbial respiration that reduce DO levels and slow shellfish growth (Kim et al. 2010; Bauman et al. 2010; Morse et al. 2011). The concurrent effects of HAB and other environmental stressors have been poorly studied, but may yield interactions that inhibit the performance of shellfish. For example, Talmage and Gobler (2012) reported that bay scallop larvae concurrently exposed to the HAB-forming pelagophyte *Aureococcus anophagefferens* and low pH displayed synergistically low survival, i.e., mortality was greater than would have been predicted based upon individual exposures to each stressor. Hence, aquaculture locales where multiple additional stressors are present may be highly vulnerable to HAB.

Results presented here have implications regarding the species-specific management of commercially produced shellfish. Bay scallops and first-year oysters that are negatively affected by dense *C. polykrikoides* blooms may benefit from relocation to grow-out sites or facilities where blooms are less likely to occur or are less intense. Clams (both year-classes) and second-year oysters were resistant to *C. polykrikoides* and thus may withstand moderate bloom events at grow-out sites and culture facilities. At grow-out sites where relocation of shellfish is not feasible, shellfish deployed at depth may be exposed to lower densities of *C. polykrikoides* than shellfish deployed at the surface and thus would be less apt to suffer mortality due to blooms, but may experience slowed growth at locations prone to low levels of dissolved oxygen.

Recent investigations have demonstrated that increases in sea surface temperatures, since the early 1980s, have

contributed to increased growth and abundance of several HAB in areas where aquaculture is prominent (i.e., northwest Atlantic; Gobler et al. 2017). Additionally, warming can stimulate *C. polykrikoides* growth (Jeong et al. 2004; Lee and Lee 2006; Griffith and Gobler 2016) contributing to an increase in bloom intensities. Recently, such warming along the northeastern US has expanded the realized niche of *C. polykrikoides* (Griffith et al., in prep) with blooms now occurring annually in several locations including Chesapeake Bay (multiple tributaries; Marshall et al. 2006; Mulholland et al. 2009), Long Island (NY; Gobler et al. 2008, 2012), Rhode Island (Narragansett Bay; Hargraves and Maranda 2002), and Massachusetts (Buzzards Bay and Cap Cod; Kudela and Gobler 2012; Rheuban et al. 2016). Where present, blooms have been attributed to marine animal die-offs (Gobler et al. 2008; Mulholland et al. 2009; Morse et al. 2011) and in terms of shellfish mortality, there are reports of widespread mortality among shellfish populations following blooms of *Cochlodinium* (Curtiss et al. 2008; Gobler et al. 2008). Hence, as climate changes continue to expand within the Northern Hemisphere, the subsequent risk posed by these blooms will increase.

Species-Specific Effects of Exposure

The extreme sensitivity of bay scallops to *C. polykrikoides* is consistent with prior studies involving environmental stressors and these bivalves. Bay scallops are generally more sensitive to elevated temperatures (Tettelbach and Rhodes 1981; Brun et al. 2008; Talmage and Gobler 2011), acidification (Talmage and Gobler 2009), low dissolved oxygen (Bricelj et al. 1987; Chun-de and Fu-sui 1995; Clark and Gobler 2016), and exposure to other harmful algal species (Leverone et al. 2006, 2007) than other bivalves. Bay scallops rely upon carbohydrate reserves within adductor muscle tissue during periods of reduced food supplies (Barber and Blake 1981, 1983) and have a lower capacity for energy storage than other bivalves (Epp et al. 1988) making them more sensitive to stressors as food quality diminishes. Within the northwest Atlantic, bay scallop fisheries have been greatly diminished in recent decades due to over harvesting (Barber and Davis 1997; Oreska et al. 2017), habitat loss (Bowen and Valiela 2001; Serveiss et al. 2004; Orth et al. 2006), and recurrent harmful algal blooms (Cosper et al. 1987; Summerson and Peterson 1990). While some bay scallop restoration efforts have exhibited some success (Tettelbach et al. 2013), the current results indicate the annual recurrence of *C. polykrikoides* blooms may make restoration of bay scallops in bloom-exposed areas along the northeast US a significant challenge.

While the impacts of *C. polykrikoides* on oysters in the current study (slowed growth) were less severe than those exhibited by bay scallops (mortality), previous investigations from both the field and laboratory have described lethal effects of *C. polykrikoides* for oysters. Gobler et al. (2008) observed increased mortality among juvenile oysters and scallops following prolonged (9-day) laboratory exposures to bloom water. Similarly, Li et al. (2012) noted decreases in feeding activity, slow/no growth, and reduced survival of juvenile oysters following a prolonged (> 1 month) bloom of *C. polykrikoides* at a bloom-exposed oyster nursery. Differences between the sensitivities of oysters reported here and elsewhere may be due to the duration of bloom exposure. In the current study, oysters were exposed to short-term (< 9 days) but intense blooms (>30,000 cells mL^{-1}), whereas reports of oyster mortality reported elsewhere (Gobler et al. 2008; Li et al. 2012) followed a more prolonged exposure to bloom conditions ($\geq$ 9 days). To date, no study, including the present one, has reported on the harmful effects of *C. polykrikoides* for juvenile hard clams. Collectively, results presented here and elsewhere suggest that oysters and scallops are more vulnerable to *C. polykrikoides* blooms than clams and that the bay scallops are at greater risk than oysters.

Diel Vertical Migration

Previous investigations with East Asian ribotypes of *C. polykrikoides* from the field have indicated this alga undergoes diel movement throughout the water column over a 24-h period with greater cell densities quantified at the surface during daylight hours and dense subsurface maximums (e.g., 5–15 m) occurring at night (Park et al. 2001; Kim et al. 2010). In the current study, vertical movement was observed, but surface cell densities were consistently higher than bottom cell densities where levels were often an order of magnitude or more lower than surface concentrations. Differences in the magnitude of diel movements between this current study and observations elsewhere may be due to strain-specific variability or differences in hydrographic conditions among the study sites. In shallow well-mixed bays, cells may be more likely to aggregate at the surface during the daytime and simply disperse during the night or migrate onto or in sediments. Sites for the current study were shallower (~2 m) than those included in prior investigations (Park et al. 2001; Kim et al. 2010), and were in semi-enclosed bays rather than open seas. Nutrient levels, among shallow, tidally mixed, embayments studied here are similar at surface and at depth (Suffolk County Department of Health Services, suffolkcountyny.gov, 1976–2016) which may diminish diel movement of phytoplankton (Doblin et al. 2006) as vertical movement may not offer nutritional advantages. In larger, deeper, embayments where stratification of the water column is more pronounced, complete vertical migration of *C. polykrikoides* cells may be more pronounced.

Environmental Factors Influencing Toxicity

Environmental factors that influence the lethality of *C. polykrikoides* have yet to be fully investigated. For

example, the impacts of irradiance on toxicity are currently unknown. While some controversy regarding the toxic mechanism of this HAB remains, the majority of evidence suggests that the toxic effects are, at least in part, related to the production of reactive oxygen species (ROS; Kim et al. 1999; Tang and Gobler 2009a; Griffith and Gobler 2016). Production of ROS, a by-product of photosynthetic processes (Yu 1994; Wise 1995), would likely be greater during periods of adequate irradiance (i.e., surface positions during the daytime) and minimized during periods of low light (i.e., night or at depth). In addition to light effects, the effects of carbon dioxide (pCO_2) on the growth and toxicity of *C. polykrikoides* have yet to be studied. In many temperate, net-heterotrophic estuaries, microbial respiration in bottom waters at night can elevate pCO_2 levels (Wallace et al. 2014; Baumann et al. 2015). Such conditions may down-regulate photosynthetic machinery within phytoplankton and reduce ROS production (Sobrino et al. 2014), a phenomenon that may also diminish the toxicity of *C. polykrikoides*. Finally, while warmer temperatures are known to render *C. polykrikoides* less toxic (Griffith and Gobler 2016), there were no significant differences among surface temperatures during this study.

Conclusion

Blooms of the dinoflagellate *C. polykrikoides* pose a significant and growing threat to native and commercially produced shellfish within temperate regions of the Northern Hemisphere. During field experiments with three commercially and ecologically significant bivalves, species-specific reductions in growth and survival were observed. While hard clams were resistant to blooms, first-year oysters and scallops that survived blooms displayed significant reductions in growth and among the species deployed, only first- and second-year bay scallops exhibited significant declines in survivorship during blooms. Lethal effects, where observed, coincided with maximum *C. polykrikoides* cell densities and were restricted to surface positions only. Findings suggest that current restoration efforts and aquaculture involving bay scallops are vulnerable to recurring *C. polykrikoides* blooms and that risks posed to aquaculture may be greatest among surface-deployed shellfish where cell densities are likely to be greatest.

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