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Effects of the environment and culture depth on growth and mortality in juvenile Pacific oysters in the Strait of Georgia, British Columbia

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ABSTRACT: The effects of environmental variables, culture depth, and phytoplankton abundance and composition on juvenile Pacific oyster *Crassostrea gigas* growth and mortality were studied between June and October of 2008 at 4 sites in the Strait of Georgia, British Columbia, Canada. In addition, the effects of temperature-triggered depth manipulation on growth and mortality of oysters were examined in order to assess potential control measures for mitigating high summer mortalities associated with high temperature, harmful algal blooms (HABs), and other environmental stressors. Control oysters were held at constant depths of 3, 10, and 15 m, while experimental oysters were kept at 3 m depth and lowered to 10 or 15 m when the surface water temperature reached 14, 16, or 18°C. Site and Depth significantly affected the growth and mortality of control oysters. At the site with the best growth, cumulative mortality was low (range: 6.4 to 19%) and negatively correlated with temperature and positively with transparency. At the high-mortality site (range: 64 to 98%), mortality was positively correlated with temperature, chlorophyll concentration, and the biomass of diatoms and potentially harmful algae. Cumulative mortality was generally higher at 3 m than at 15 m depth. Significantly larger oyster volume was obtained with the oyster controls at 3 m than with those held at 10 or 15 m at most sites. Temperature-trigger treatments did not significantly affect oyster volume or cumulative mortality, and oysters moved to 10 and 15 m had final volumes similar to the 10 and 15 m controls, independent of trigger temperature. Oyster growers could select their sites for maximal growth and minimal mortality based on temperature profile, freshwater input, and phytoplankton abundance and composition.

KEY WORDS: Pacific oyster · *Crassostrea gigas* · Summer mortality · Harmful algae · HABs · *Heterosigma akashiwo* · Depth manipulation

INTRODUCTION

Globally, the Pacific oyster *Crassostrea gigas* Thunberg is the most common bivalve in aquaculture, owing to its handling ease, fast growth, euryhaline/eurythermal tolerance, and the variety of culture techniques available (FAO 2006). In British Columbia (BC), Canada, the Pacific oyster is the largest cultured crop in terms of tonnage, the main areas of production being in the Strait of Georgia (Fig. 1) in Baynes Sound and Okeover Inlet. Nursery systems are often used for both wild-collected and hatchery-produced seed before grow-out. The oysters are then grown using a variety of methods, but generally suspended in the water column (Quayle 1988).

Pacific oysters grow rapidly during their first year and more slowly thereafter (Gangnery et al. 2003). Their growth rate is dependent on seawater temperature (reaching a metabolic optimum at 19°C; Bougrier et al. 1995), food availability, and food quality (Brown & Hartwick 1988a,b, Hyun et al. 2001, King et al. 2006). These variables can, in turn, be linked to culture depth

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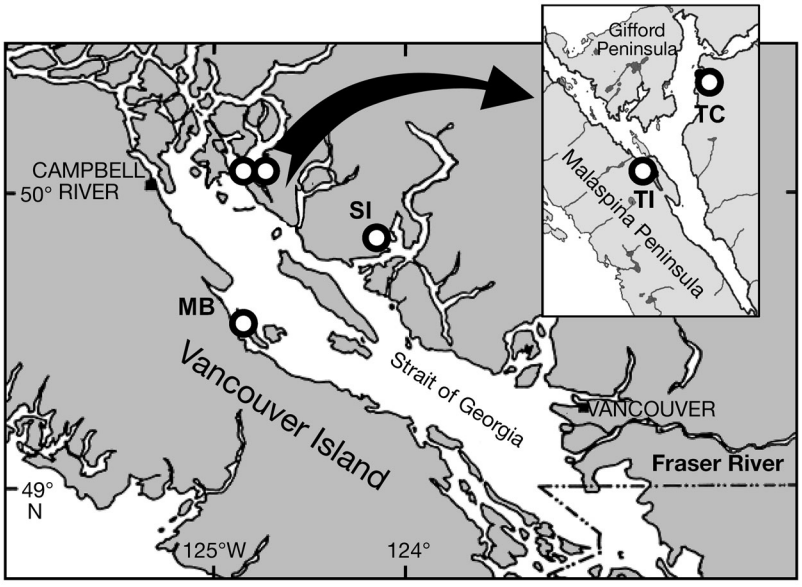

Fig. 1. Study site locations in the Strait of Georgia, British Columbia, Canada: Metcalf Bay (MB), Sykes Island (SI), Thor's Cove (TC), and Trevenen Inlet (TI)

(Ngo et al. 2006), water-column stratification, and nutrient abundance (Harrison & Yin 1998).

Oysters are suspensivores that prefer seston rich in small diatoms and flagellates and poor in harmful algae and detritus (Baldwin & Newell 1995, Chu et al. 2002). Oysters use their gills for particle selection, complemented by clapping of valves and other rejection reactions (Wildish et al. 1998, Cassis & Taylor 2006). Pacific oysters develop particle-processing capabilities as they grow, reaching the adult level of selectivity at approximately 2.4 cm shell length (Cannuel & Beninger 2007). This selectivity may have implications for their feeding capacity and the effects of blooms of harmful and noxious algae on growth and mortality (Cannuel & Beninger 2007).

Mortalities of Pacific oysters during the summer months have been documented throughout the world and can affect between 10 and 50% of the juveniles (Samain & McCombie 2007), with extreme cases involving >90% mortality (Pauley et al. 1988, FAO 2006, Burge et al. 2007). Mortality rates are typically higher in smaller oysters than in larger ones and this may be associated with the physiological stress of fast growth (García-Esquivel et al. 2000). Larger oysters, however, can also suffer mortalities during the summer, mostly due to physiological stress and exertion during the reproductive period (Moal et al. 2007). Extreme mortality rates have been observed during periods of high seawater temperature, low salinity close to the surface, or phytoplankton blooms (Shumway et al. 1990, Cheney et al. 2000, Landsberg 2002). Temperatures above 19°C can stress oysters and increase their metabolism during periods of low food availability, possibly causing an energetic deficit (Moal et al. 2007). Harmful algal blooms (HABs) can cause shellfish mortalities by means of oxygen depletion and/or toxin production (Shumway et al. 1990, Landsberg 2002). HABs can also reduce shellfish growth rates (Alexander et al. 2006) and filtration efficiencies (Gainey & Shumway 1988, Cassis & Taylor 2006), as well as damaging their digestive systems (Keppler et al. 2005, Galimany et al. 2008). Oysters may succumb to opportunistic viral and bacterial infections during or after periods of heightened environmental and/or physiological stress (Friedman et al. 1991, Cheney et al. 2000, Burge et al. 2007).

Growth and mortality of oysters have been investigated in large-scale (Brown & Hartwick 1988a,b, Samain & McCombie 2007) and local (Toro et al. 1999, García-Esquivel et al. 2000, King et al. 2006) studies. Salinity was the determining factor for oyster growth in the Strait of Georgia (Brown & Hartwick 1988a), while phytoplankton composition had a significant effect on oysters grown in Wales, UK (King et al. 2006). A number of studies (e.g. Sumner 1981, Gagnaire et al. 2006, King et al. 2006) have indicated that oysters typically grow faster closer to the surface, where food supply is abundant, although others have reported lower growth for oysters held close to the surface (Toro et al. 1999).

Salinity in the Strait of Georgia is typically around 32, but can reach values of 15 and lower in the vicinity of local sources of freshwater, producing a strong density-driven stratification in the top 10 to 15 m of the water column (Thomson 1981). During the summer, the surface seawater temperature generally ranges between 15 and 24°C (Thomson 1981, Masson & Cummins 2007), but summer temperature peaks of 25°C and greater can be observed close to the surface in some areas (Thomson 1981, this study). The water below the pycnocline generally maintains winter values of 6 to 8°C (Masson & Cummins 2007). These temperature and salinity values are in the ranges considered acceptable for Pacific oysters (Pauley et al. 1988). Nonetheless, large oyster mortality events have been correlated with periods of extreme values and/or strong fluctuations of temperature (Cardwell et al. 1979, Pauley et al. 1988). The phytoplankton community in the Strait of Georgia follows typical annual cycles and successions of temperate estuaries: spring and fall blooms of diatoms and dominance of flagellates in sum-

mer. The main species present are generally determined by the availability of nutrients and the water-column structure (Harrison & Yin 1998).

Due to intense summer stratification, high temperature spikes and HABs in the Strait of Georgia normally occur in the upper 10 m of the water column (Taylor & Harrison 2002), causing oyster mortalities and reducing oyster growth (Brown & Hartwick 1988a,b). The objectives of the current study were to: (1) assess the effects of various environmental variables on oyster growth and mortality at 3 m, the shallowest depth typically used by oyster growers in the Strait of Georgia; (2) determine the optimum depth for oyster culture (3, 10, or 15 m); and (3) establish if the manipulation of culture depth could be used to reduce exposure of oysters to damaging environmental conditions (e.g. high temperatures, large temperature fluctuations, HABs) and thus improve oyster growth and survival. Temperature, previously identified as one of the main variables involved in summer mortalities (Brown & Hartwick 1988a,b, Burge et al. 2007), was selected as the trigger for depth manipulation in our experiment. A possible drawback of this approach is that moving oysters to deeper waters could result in lower food intake and reduced growth, since the abundance of beneficial phytoplankton is also highest near the water surface. We had 2 main hypotheses: (1) oyster growth rate would be highest at the shallowest depth tested (3 m) where temperatures and food levels would typically be greatest, and (2) oyster mortality rate would decrease with increasing depth (due to reduced spikes in high temperatures and concentration of harmful algae). The results of this research may allow oyster growers to reduce oyster mortalities and to optimize the distribution of their stock based on environmental monitoring.

MATERIALS AND METHODS

The depth-manipulation experiment was conducted from June to October 2008 at 4 commercial oyster farms within 3 of the main oyster-producing areas in the Strait of Georgia: Metcalf Bay (MB) in Baynes Sound; Sykes Island (SI) in Jervis Inlet; and Thor's Cove (TC) and Trevenen Inlet (TI) in Okeover Inlet (Fig. 1). At each of these sites, 27 oyster culture trays (L × W × H: 56.25 × 56.25 × 21.25 cm) were stocked with hatchery-produced, diploid seed oysters. As no BC-wide industry standard exists, seed sizes and stocking densities particular to the companies that operate these commercial aquaculture leases were used for the experiment. Each individual tray at TC and TI was seeded with 1000 juvenile oysters (mean ± SE shell height: 27.6 ± 4.3 mm; n = 10), while each tray at MB and SI was stocked with ~2500 juvenile oysters (shell height: 5.3 ± 0.4 mm; n = 10). Shell height was the longest distance from the umbo to the ventral margin of the shell. The seeded trays were distributed randomly on 2 rafts (MB, TC, and TI) or 2 sets of long lines (SI) at each site, again depending on company protocol. During the study, the experimental oysters were managed in the same manner as the other oysters at each site, which included thinning to avoid density-related growth problems. This was normally done by placing half of the oysters of the original tray into a new one, which was kept along with the old tray in the same tray stack. During sampling, both trays were counted and the data averaged across trays.

All treatments were conducted in triplicate, with 3 random trays being assigned to each treatment; 3 sets of triplicate trays were kept at fixed depths (3, 10, and 15 m) throughout the experiment, while the rest of the trays were divided into 3 sets of 6 trays each and assigned a trigger temperature (14, 16, or 18°C) (Fig. 2). The 6 trays assigned to each temperature trigger were divided into 2 groups, one to be lowered to 10 m and the other to 15 m. The temperature-triggered trays were kept at 3 m depth until the seawater temperature at 3 m reached their temperature trigger. Once each particular temperature trigger was reached, the trays of oysters were lowered to their predetermined depths (10 and 15 m). These lowered trays were then brought

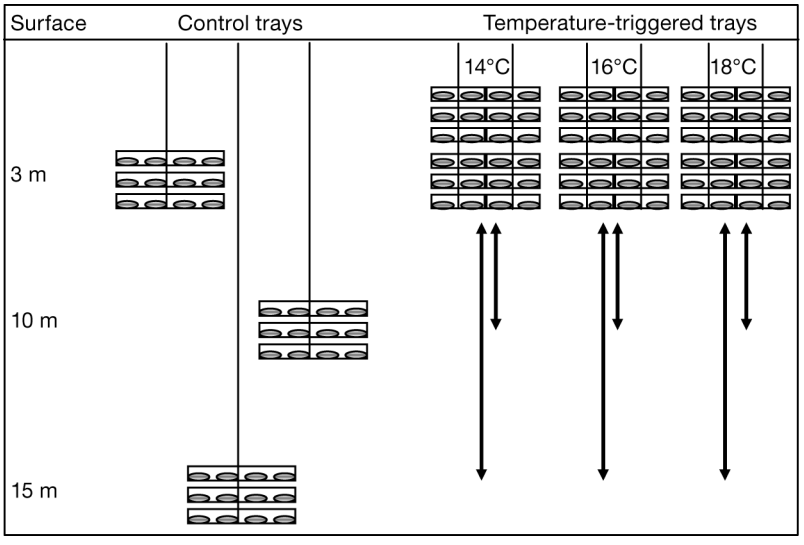

Fig. 2. Experimental design for depth manipulation trial. Control trays (n = 3) were kept at 3, 10, and 15 m depth throughout the study, whereas the temperature-triggered trays (n = 3 per trigger temperature and target depth) were held at 3 m and dropped to either 10 or 15 m when the seawater at 3 m reached the trigger temperature

back to 3 m depth when the seawater temperature at 3 m dropped below the temperature trigger. The depths chosen represented the upper depth normally used by oyster farmers (3 m), the depth of the pycnocline, which was also the lower depth typically used by the growers (10 m), and the deeper and colder water layer below the pycnocline (15 m).

Every 2 wk, the experimental and control trays were lifted out of the water and the shell heights of 5 randomly chosen oysters from each tray were measured with digital callipers. Oyster volume was estimated by measuring the water volume displaced by a random sample of oysters from each replicate tray. The sample sizes used during this experiment (>60 oysters per tray at MB and SI and >20 oysters per tray at TC and TI) are similar to other oyster growth studies (Toro et al. 1999, King et al. 2006) and were the highest number possible under the commercial farm conditions. Instant growth and mortality rates were calculated using the difference between one sample and the next, divided by the number of days between measurements. Oyster mortality was only determined at MB and SI during the volume measurements, as the sample size used for volume estimation at TC and TI was too small to accurately gauge mortalities.

Temperature was monitored daily at 3 m with a Clinefinder digital probe (Catalina Technologies). Temperature at 3, 10, and 15 m depth was recorded at each site every 3 h for the duration of the experiment by duplicate automatic data loggers (Tidbit V.2, Onset). Water samples were obtained every 2 wk at 3, 10, and 15 m for salinity measurement (STX-3 refractometer, Vee Gee Scientific) and quantitative evaluation of phytoplankton abundance. Secchi depth measurements and vertical tows of a plankton net (20 µm mesh) from 15 m depth were also conducted every 2 wk at each site. Seawater density was calculated using UNESCO's Equation of State for Seawater (Gill 1982). The stratification intensity of the water column was defined as the difference in density between 3 and 15 m.

Water mounts were analyzed quantitatively for microphytoplankton and small zooplankton by the Utermöhl method with modifications described in Hasle (1978). Gently homogenized water samples were placed in 5, 10, or 25 ml settling chambers for 24 to 48 h. The detailed composition of these samples was obtained under an Axiovert 10 inverted microscope (Carl Zeiss). Once the phytoplankton were counted and identified, the biovolumes were estimated using previously determined bio-volumes of local species (Haigh et al. 1992). These estimates were then used to calculate phytoplankton carbon biomass using equations from Strathmann (1967) and Montagnes & Franklin (2001). The phytoplankton counts were converted to carbon biomass to avoid problems associated with quantitative phytoplankton estimates based solely on cell counts. Usually phytoplankton cell counts, without estimates of carbon or bio-volume, overestimate the importance of small species that are present in large numbers and underestimate large species at low abundances. Chlorophyll samples were taken monthly from 3, 10, and 15 m depth. Seawater samples (250 ml) were GF/F filtered (0.7 µm), and the filters were frozen at –20°C until analysis by chlorophyll extraction in 90% acetone and fluorescence measurement in a 10AU fluorometer (Turner Designs).

We conducted 2- and 3-way ANOVAs on oyster volume and mortality per pair of sites that shared the same initial seed size (i.e. MB and SI, and TC and TI). Tukey's multiple comparison *post hoc* tests were used to determine significant ($p < 0.05$) differences among 3 or more treatment means. Prior to the ANOVAs, the data sets were tested for normality using the Kolmogorov-Smirnov test and for homoscedasticity using Bartlett's test. All data sets were normally distributed and homogeneous. Two-tailed Dunnett's tests were used to compare the 6 experimental treatments against the 10 m control within sites (comparisons with 15 m controls were also tried, with similar results). Correlations between environmental variables and instant oyster mortality and growth were examined using Pearson correlation coefficients with $\alpha < 0.05$. The statistical analyses were performed with XLStat for Windows (Addinsoft). The data analysis was tried with several different time lags, but the best results and most significant correlations were obtained with data of the same time period (i.e. no lag).

RESULTS

Environmental variables

Seawater temperature varied between 26.2°C during August at SI at 3 m, and 6.0°C in October at TC at 15 m. The average temperature was highest at SI (mean ± SE: 16.3 ± 2.2°C) and lowest at MB (14.9 ± 2.2°C), whereas TC (15.2 ± 1.8°C) and TI (15.3 ± 2.0°C) were intermediate and shared a very similar temperature regime. Several short periods of increased temperature throughout the water column were detected at all sites, with the longest periods occurring during July and August (Fig. 3). Seawater temperature rapidly decreased in September and October. In terms of the percentage of days on which the temperature at 3 m depth was above the trigger temperature, oysters in the 14°C group remained dropped to lower depths for the longest time at SI and for the shortest time at MB (Table 1). The oysters in the 16 and 18°C treatments spent the least amount of time at lower depths at TC and the most at SI (Table 1).

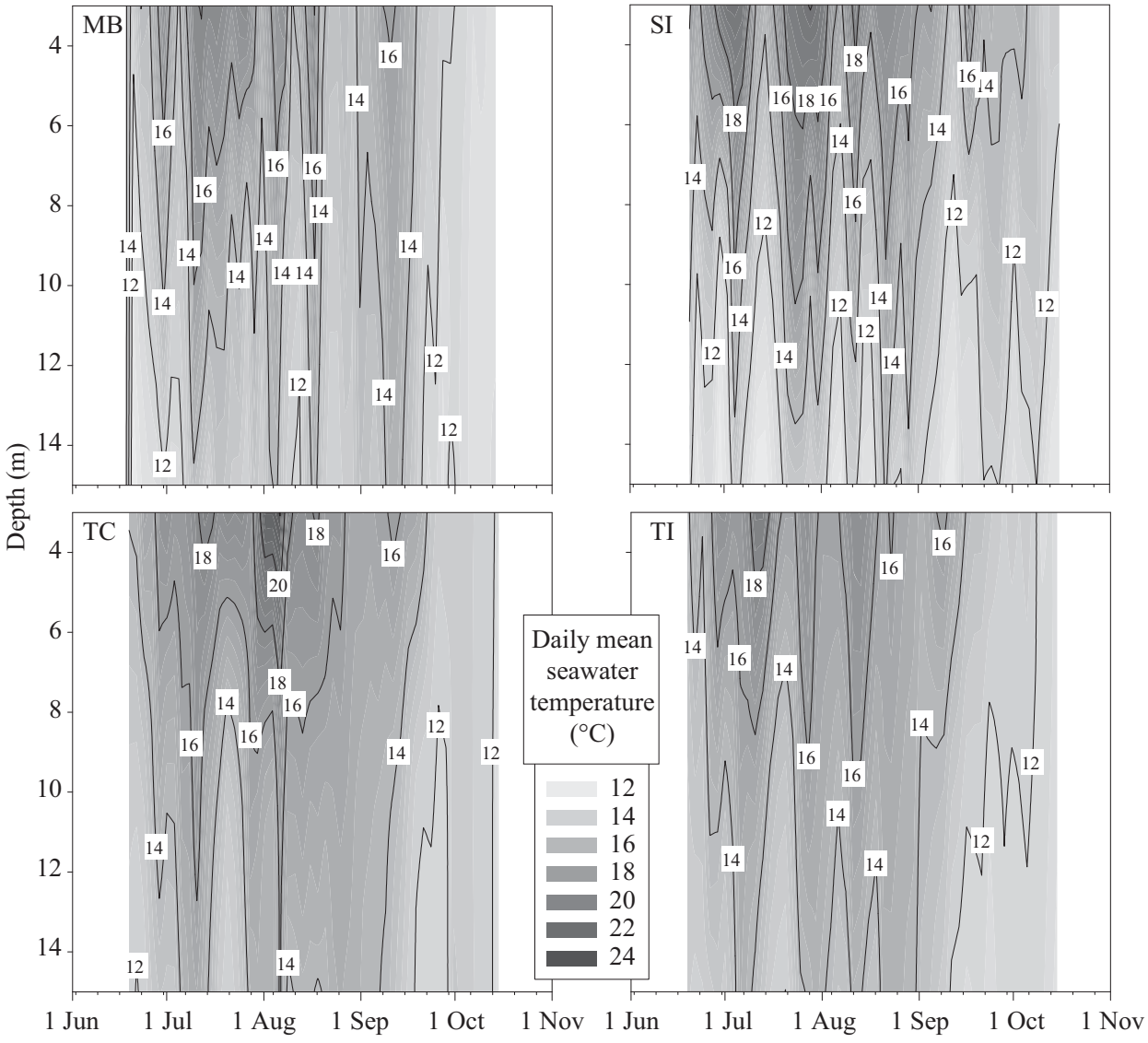

Fig. 3. Daily average (n = 8) seawater temperature (°C) at each study site (see Fig. 1 for abbreviations)

Salinity varied from 19 at SI during early July, to 30 in October at MB. Low values of salinity, ~20 to 24, were observed close to the surface at most sites during June and July (Fig. 4). Higher salinities were common at greater depth and throughout the water column from August onwards. Among all sites, SI presented the lowest values of salinity and for the longest period. Salinity-driven stratification was high at all sites during June and July, and especially strong at SI, which continued with high to moderate stratification until the fall (Fig. 4).

Chlorophyll concentrations ranged from 15.92 mg m^{-3} (3 m in June at TI) to 0.34 mg m^{-3} (15 m in July at TC). A 3-way ANOVA indicated that Site ($F = 5.41$, df = 3,24, $p = 0.005$), Depth ($F = 14.63$, df = 2,24, $p < 0.0001$), and Date ($F = 7.04$, df = 4,24, $p = 0.001$) all had significant effects on chlorophyll concentration. The TC site had the lowest chlorophyll values, while TI and SI had relatively high chlorophyll peaks during June and August (Table 2). The chlorophyll values observed at MB were intermediate. During the summer months, the average chlorophyll concentrations were normally higher at 3 and 10 m depth than at 15 m at all sites, with a large

Table 1. Percentage of days with water temperatures at 3 m depth above the trigger temperatures at each study site (see Fig. 1 for abbreviations)

Site	Trigger temperature (°C)		
	14	16	18
MB	64.5	37.0	11.0
SI	86.9	54.4	25.0
TC	79.7	31.7	9.5
TI	73.2	43.3	10.2

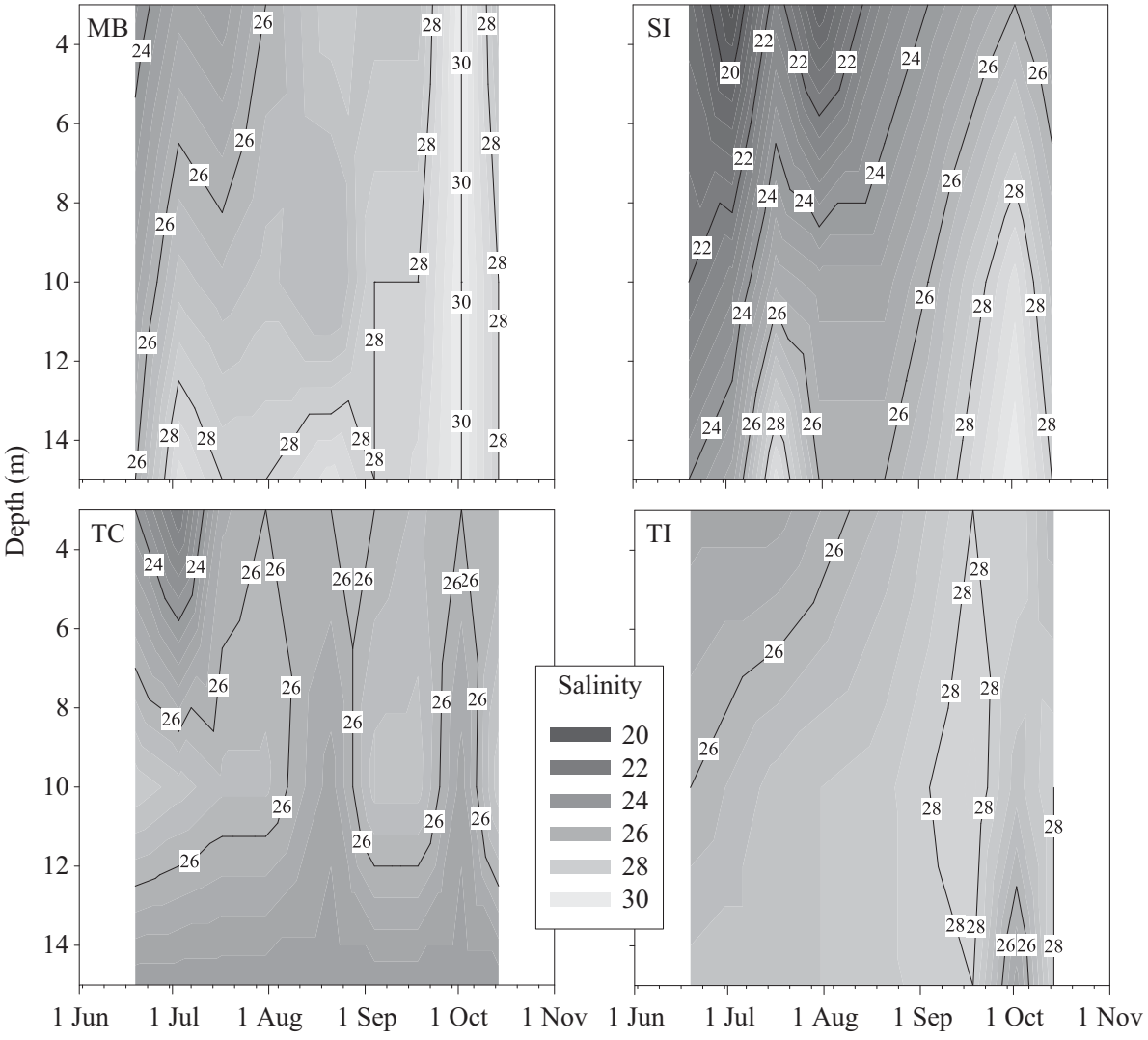

Fig. 4. Salinity at each study site, sampled every 2 wk (n = 1) (see Fig. 1 for abbreviations)

variation among months. The average difference between values at 3 and 15 m was lowest at MB with 2.7 times more chlorophyll at the surface than at 15 m depth. TC had the largest average depth difference in chlorophyll with around 7.1 times higher values at the surface than at 15 m, while SI and TI averaged 4.2 and 5.3 times more chlorophyll, respectively, at the shallowest depth than at 15 m.

The total phytoplankton biomass varied widely throughout the experimental period and among sites, generally being concentrated towards the surface with much lower values at depth (Fig. 5). This pattern was broken several times by blooms of different species during the summer and by the fall bloom of diatoms. The fall bloom was barely noticeable in the biomass profiles at most sites, but it was easily recognizable due to a sudden increase in the population of *Skeletonema costatum* (Greville) Cleve. The phytoplankton community at MB had a high abundance of mainly diatoms (mean of 95% of total carbon biomass across all sample dates) at all depths and months except for August. TI and TC had similar average proportions for various phytoplankton types with dinoflagellates comprising about 45% of the biomass, while equal proportions of diatoms and other phytoplankton species accounted for the remaining 55%. SI was the site with the lowest overall diatom abundance (6%), with dinoflagellates and other phytoplankton species dominating.

HABs, which were detected at all sites, were divided into 2 groups: (1) species potentially harmful to shellfish (potentially harmful algal blooms or pHABs) due to spiny projections, associated harmful bacteria, and/or the production of irritants or other harmful chemicals (i.e. *Heterosigma akashiwo* (Y. Hada) Y. Hada ex Y. Hara & M. Chihara), *Dictyocha speculum* Ehrenberg, *Ceratium fusus* (Ehrenberg) Dujardin, *Protoceratium*

Table 2. Monthly (n = 1) chlorophyll concentrations (mg m^{-3}) (see Fig. 1 for abbreviations)

Month	Depth (m)	MB	SI	TC	TI
June	3	1.82	5.29	4.25	15.92
	10	1.26	6.40	0.92	2.07
	15	0.78	1.78	0.44	1.02
July	3	3.95	1.82	3.14	6.48
	10	1.56	2.29	0.61	1.79
	15	0.65	0.67	0.34	1.05
August	3	3.12	13.08	4.28	13.30
	10	3.31	12.72	0.71	9.77
	15	1.42	1.79	0.41	4.29
September	3	5.20	7.25	3.22	1.96
	10	5.28	3.74	0.75	1.77
	15	2.65	0.94	0.71	2.01
October	3	3.45	0.73	0.84	0.63
	10	3.20	0.76	1.16	0.88
	15	2.55	1.32	0.49	0.91

reticulatum (Claparède et Lachmann) Bütschli, and *Rhizosolenia setigera* Brightwell), and (2) species that potentially cause toxicity in shellfish (toxic HABs or tHABs) (i.e. *Alexandrium* spp. Halim, *Dinophysis* spp. Ehrenberg, and *Pseudo-nitzschia* spp. H. Peragallo in H. & M. Peragallo). Most HABs were produced by pHABs, with tHABs only appearing in medium to low abundances and mostly during short periods of time.

Potentially harmful algae comprised 16 to 34% of the total phytoplankton biomass per site across all sample dates, with the highest proportion occurring at SI and TI (34% at both sites) and the lowest occurring at TC and MB (16 and 20%, respectively). Throughout the sites studied, pHABs were normally more abundant towards the surface, with some blooms affecting the whole water column (Fig. 6). The intensity of the blooms was highest at SI, where up to 93% of the total phytoplankton biomass was made up of pHABs during 2 large blooms in June and August (Fig. 6). TC and TI had a small bloom in June and a large one during August and September. Potentially harmful algae were scarce at MB where only 2 short blooms were observed (Fig. 6), reaching a maximum of 40% of the total phytoplankton biomass. Although pHABs were present at all sites, SI and TI were the most affected by blooms of *Heterosigma akashiwo*, *Dictyocha speculum*, and *Protoceratium reticulatum* during June, and *Ceratium fusus* and *P. reticulatum* during August and September. *Rhizosolenia setigera* was only present at MB in low abundances during October.

Normally, tHABs reached only marginal levels of biomass, being scarce in SI while constantly present at low levels in MB. At the latter site, *Pseudo-nitzschia* spp. were common with sporadic appearances by *Alexandrium* spp. and *Dinophysis* spp. TC and TI had the highest relative abundance of toxic algae of all sites, as *Alexandrium* spp. were observed throughout July and August while *Pseudo-nitzschia* spp. were detected during the fall bloom.

Depth-manipulation experiment

At all sites and in all treatments, Oyster volume and Shell height were closely correlated in an allometric relationship described by the formula: Volume = $(0.0004 \times \text{Shell height})^{2.7234}$ ($R^2 = 0.9757$, $p > 0.0001$). Given that the initial oyster seed size was substantially different between the 2 companies participating in this study (i.e. shell height of 5.3 ± 0.04 mm at MB and SI, and 27.6 ± 4.3 mm at TC and TI), the results of the experiment are divided by sites that shared the same initial seed size (i.e. MB and SI, and TC and TI).

Correlations of instant growth and mortality with environmental variables

Instantaneous growth rate of the oysters at 3 m depth at the various sites was positively correlated only with different components of the phytoplankton community: diatoms (% of total phytoplankton biomass) at SI, dinoflagellates (% of total phytoplankton biomass) at MB, dinoflagellates (biomass) at TC, and pHABs (biomass) at TI (Table 3). Growth rate was negatively correlated with Date at TC. Instantaneous oyster growth was not significantly correlated with Temperature, Salinity, Secchi depth, or Chlorophyll concentration at any of the 4 sites (Table 3).

Instantaneous oyster mortality rate at SI was strongly positively correlated with Temperature, Diatom biomass, pHAB biomass, and Chlorophyll concentration (Table 4). The much lower mortality rate registered at MB was positively correlated with Secchi depth and negatively correlated with Temperature (Table 4). Instantaneous mortality rates at TC and TI were very low and random, not being associated with any specific environmental variable (data not shown). The cumulative mortality rates observed at TC and TI were 3 and 7%, respectively.

Final oyster volume at MB and SI

A 2-way ANOVA on the 3, 10, and 15 m controls indicated that the final volume of control oysters at the fixed depths was significantly affected by both Site and Depth, with no significant interaction between the 2 factors (Table 5). Oysters were significantly larger at MB than at SI and significantly larger when held at 3 m than when held at 10 or 15 m, with no significant difference between oyster size at 10 and 15 m (Fig. 7A).

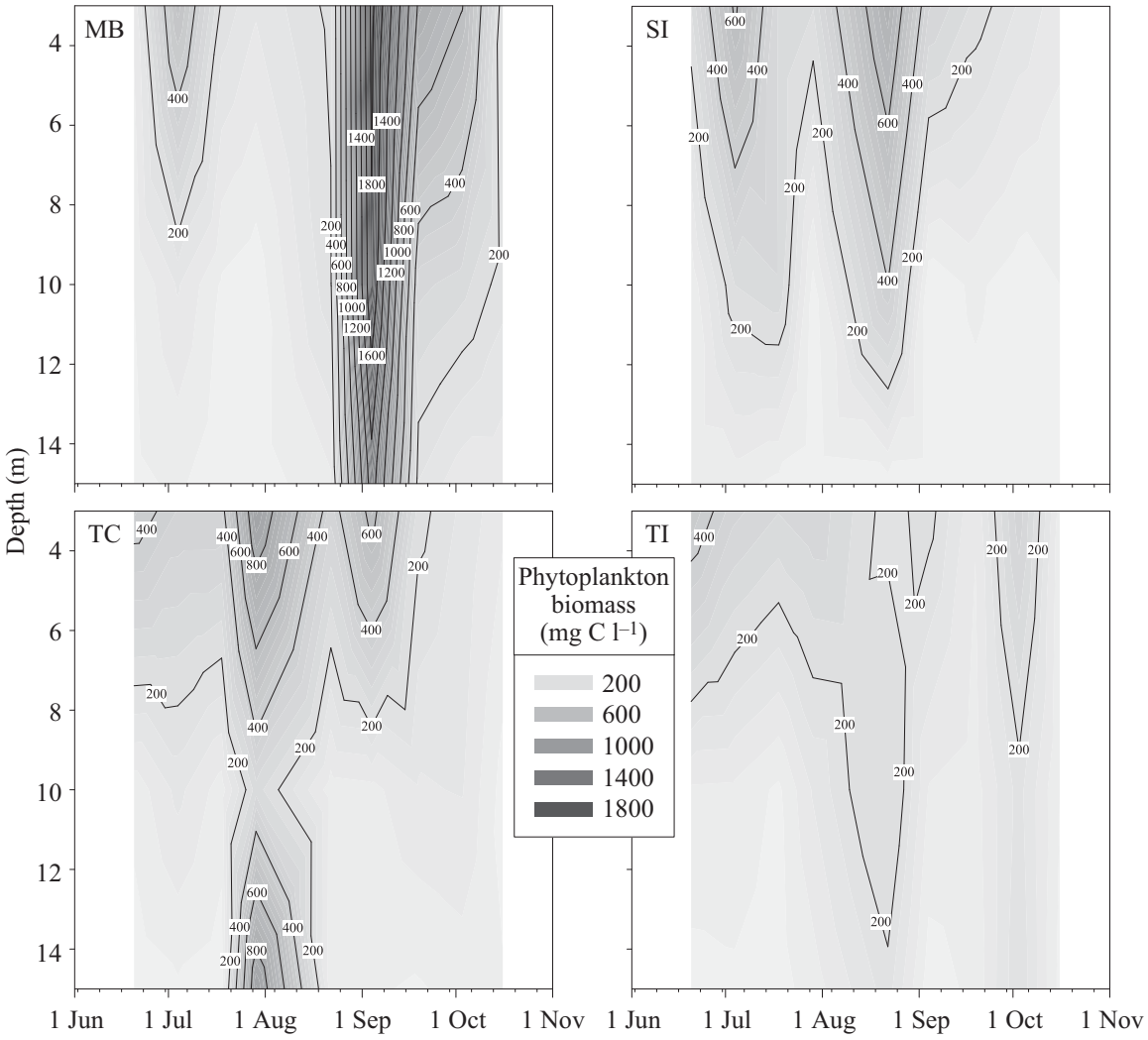

Fig. 5. Total phytoplankton biomass (mg C l^{-1}) at each study site, sampled every 2 wk (n = 1) (see Fig. 1 for abbreviations)

A 3-way ANOVA on the temperature-triggered treatments indicated that the final volume of experimental oysters at MB and SI was only affected by Site with no other significant main effects or interactions (Table 6). The depth-manipulated oysters at MB were significantly larger at the end of the experiment than those at SI (Fig. 7A). No significant differences (using Dunnett's 2-tailed tests) were observed between the 10 or 15 m temperature-triggered treatment groups and the respective 10 m control groups at either site (Fig. 7A).

Final oyster volume at TC and TI

A 2-way ANOVA on the 3, 10, and 15 m controls indicated that only Depth significantly affected the final volume of control oysters at these 2 sites, with no significant effect of Site or the Site × Depth interaction (Table 5). Oysters held at 3 m were significantly larger than those held at 10 or 15 m, but there was no significant difference in oyster volume between 10 and 15 m depth (Fig. 7B).

A 3-way ANOVA on the temperature-triggered treatments indicated that the final volume of experimental oysters at TC and TI was affected by Site and Test depth with no other significant main effects or interactions (Table 6). The depth-manipulated oysters at TC were significantly larger at the end of the experiment than those at TI, and oysters that were dropped to 10 m were significantly larger than those moved to 15 m (Fig. 7B). Comparisons between the temperature-triggered treatments and the 10 m control using Dunnett's 2-tailed test indicated no significant differences at either site (Fig. 7B). Oysters in the 15 m TC control group had the lowest final volume of all treatments.

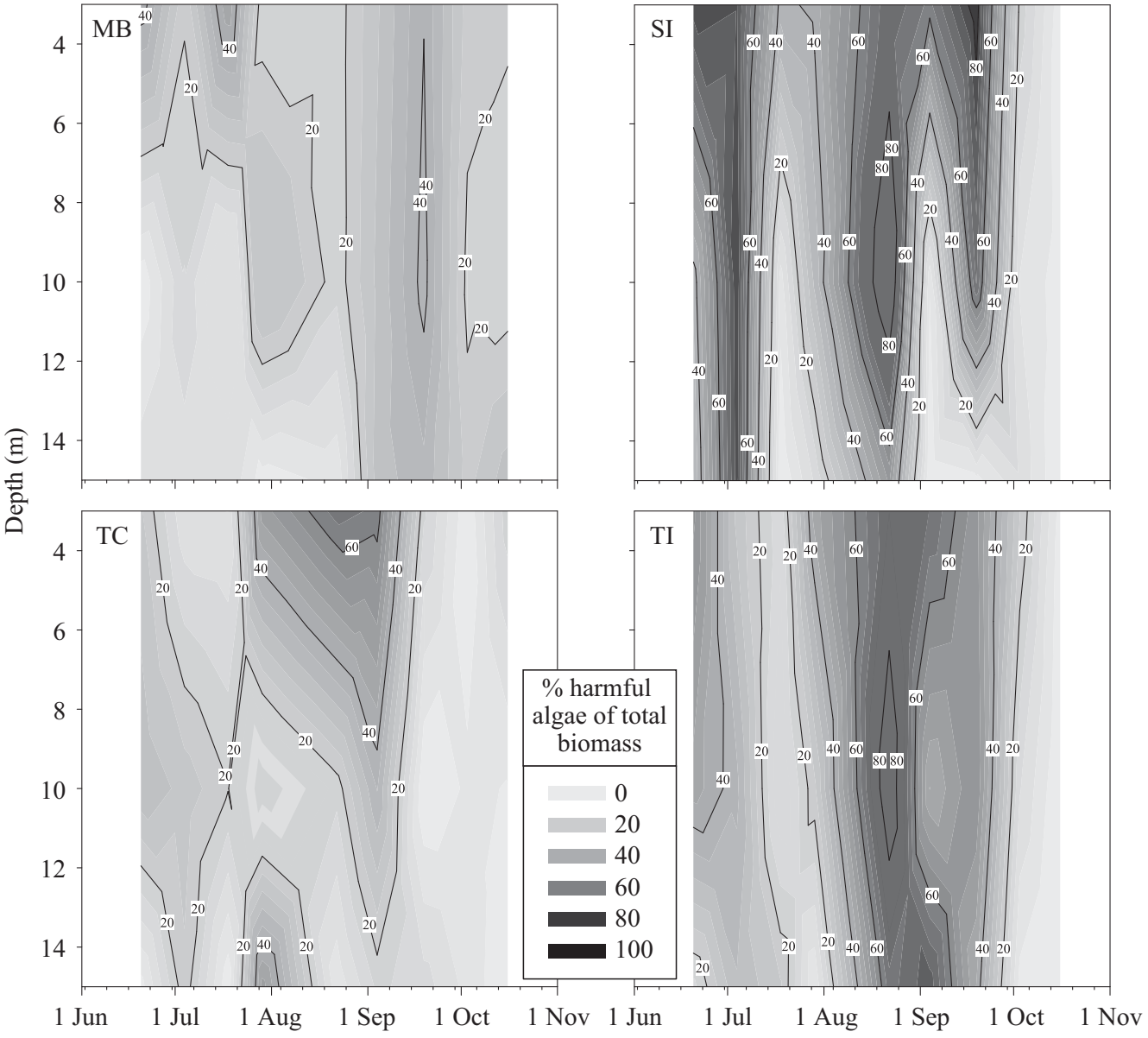

Fig. 6. Percentage of potentially harmful algae of the total phytoplankton biomass (%) at each study site, sampled every 2 wk (n = 1) (see Fig. 1 for abbreviations)

Oyster mortality at MB and SI

A 2-way ANOVA on the cumulative mortality of the fixed-depth controls at 3, 10, and 15 m at MB and SI indicated that Site and Depth significantly affected oyster mortality, whereas the interaction between the factors was not significant (Table 5). SI had significantly higher cumulative oyster mortality than MB (Fig. 8). Despite the significant Depth effect in the ANOVA, a Tukey's test on data combined across the 2 sites did not indicate any significant pair-wise comparisons among depths. The Site × Depth interaction term was non-significant ($p = 0.081$), but it may be more appropriate to examine the effect of Depth within sites instead. At SI there was significantly higher cumulative mortality at 3 m than at 10 or 15 m, while there were no significant pair-wise comparisons among depths at MB (Fig. 8).

A 3-way ANOVA on the temperature-triggered treatments indicated that cumulative oyster mortality at MB and SI was affected by Site and Depth with no other significant main effects or interactions (Table 6). The experimental oysters experienced higher mortalities at SI than at MB and had higher cumulative mortality when dropped to 10 m as opposed to 15 m (Fig. 8).

Table 3. Pearson correlations between oyster instantaneous growth (% d^{-1}) and selected variables at 3 m at each study site (see Fig. 1 for abbreviations). p-values are in brackets; **bold:** $p < 0.05$. pHAB = potentially harmful algal bloom

Variable	MB	SI	TC	TI
Date	−0.364 (0.376)	−0.110 (0.795)	**−0.709 (0.049)**	−0.667 (0.071)
Daily average temperature (°C)	0.003 (0.995)	−0.081 (0.849)	−0.297 (0.475)	−0.172 (0.683)
Diatom biomass (mg C l^{-1})	−0.241 (0.565)	0.413 (0.309)	−0.547 (0.203)	−0.147 (0.729)
Dinoflagellate biomass (mg C l^{-1})	0.196 (0.642)	−0.099 (0.817)	**0.797 (0.032)**	0.446 (0.268)
pHAB biomass (mg C l^{-1})	−0.489 (0.219)	−0.369 (0.369)	−0.275 (0.550)	**0.878 (0.004)**
% diatoms of total biomass	−0.608 (0.110)	**0.749 (0.033)**	−0.543 (0.207)	−0.335 (0.417)
% dinoflagellates of total biomass	**0.836 (0.010)**	0.097 (0.819)	0.684 (0.090)	0.119 (0.779)
% pHAB of total biomass	−0.267 (0.523)	−0.329 (0.427)	−0.359 (0.429)	0.302 (0.468)
Chlorophyll concentration (mg m^{-3})	−0.735 (0.265)	0.441 (0.274)	0.651 (0.349)	0.810 (0.071)
Secchi depth (m)	−0.267 (0.523)	−0.185 (0.661)	−0.773 (0.125)	−0.677 (0.210)
Salinity	−0.520 (0.187)	−0.251 (0.548)	−0.345 (0.569)	−0.606 (0.279)

Table 4. Pearson correlations between oyster instantaneous mortality (% d^{-1}) and selected variables at 3 m at Metcalf Bay (MB) and Sykes Island (SI). p-values are in brackets; **bold:** $p < 0.05$. pHAB = potentially harmful algal bloom

Variable	MB	SI
Date	0.632 (0.093)	−0.451 (0.262)
Daily average temperature (°C)	**−0.709 (0.049)**	**0.735 (0.038)**
Diatom biomass (mg C l^{-1})	0.054 (0.898)	**0.924 (0.001)**
Dinoflagellate biomass (mg C l^{-1})	−0.165 (0.696)	−0.242 (0.564)
pHAB biomass (mg C l^{-1})	0.076 (0.857)	**0.707 (0.050)**
% diatoms of total biomass	0.399 (0.327)	0.645 (0.084)
% dinoflagellates of total biomass	−0.358 (0.385)	−0.598 (0.117)
% pHAB of total biomass	−0.148 (0.727)	−0.284 (0.495)
Chlorophyll concentration (mg m^{-3})	−0.020 (0.980)	**0.771 (0.025)**
Secchi depth (m)	**0.906 (0.002)**	−0.396 (0.331)
Salinity	0.628 (0.096)	−0.316 (0.446)

Table 5. Two-way ANOVAs on final oyster volume (ml) and cumulative oyster mortality (%) in the 3, 10, and 15 m fixed depth controls at study sites (see Fig. 1 for abbreviations) that share the same initial oyster size; **bold:** $p < 0.05$; n = 3

	df	MS	*F*	p
Oyster volume				
MB and SI				
Site	1	420.494	57.304	**<0.0001**
Depth	2	466.551	63.580	**<0.0001**
Site × Depth	2	5.692	0.776	0.482
Error	12	7.338		
TC and TI				
Site	1	18.801	0.336	0.573
Depth	2	1216.208	21.737	**0.0001**
Site × Depth	2	114.540	2.047	0.172
Error	12	55.950		
Oyster mortality				
MB and SI				
Site	1	22865.793	503.918	**<0.0001**
Depth	2	286.292	6.309	**0.013**
Site × Depth	2	141.397	3.116	0.081
Error	12	45.376		

DISCUSSION

Temperature, salinity, and chlorophyll

Seawater temperature and salinity at the 4 sites had typical profiles for estuaries around the Strait of Georgia during the summer and fall (Thomson 1981). The temperature at most of the sites reached a maximum close to 19°C, which is the metabolic optimum for Pacific oysters (Bougrier et al. 1995). The exception was SI, which presented slightly higher temperatures during the summer. The sites presented a gradient of salinity regimes with MB on one end, with relatively high values throughout the water column due to strong tidal currents, TI and TC in an intermediate position, and SI with the lowest values and the largest difference between surface and deeper waters. The salinities measured during the present study were always at levels that are not likely to jeopardize oyster physiology (Bernard 1983), and salinity did not have significant correlations with instantaneous oyster growth or mortality at any of the study sites. Chlorophyll levels were within the values expected for inlets around the Strait of Georgia during the summer (Haigh et al. 1992, Masson & Peña 2009).

Phytoplankton and harmful algae

General phytoplankton

The sites monitored during this study cover many of the marine environments present around the Strait of Georgia (Thomson 1981), being similar in oceanographic conditions, phytoplankton composition, and species succession to those studied by Haigh et al.

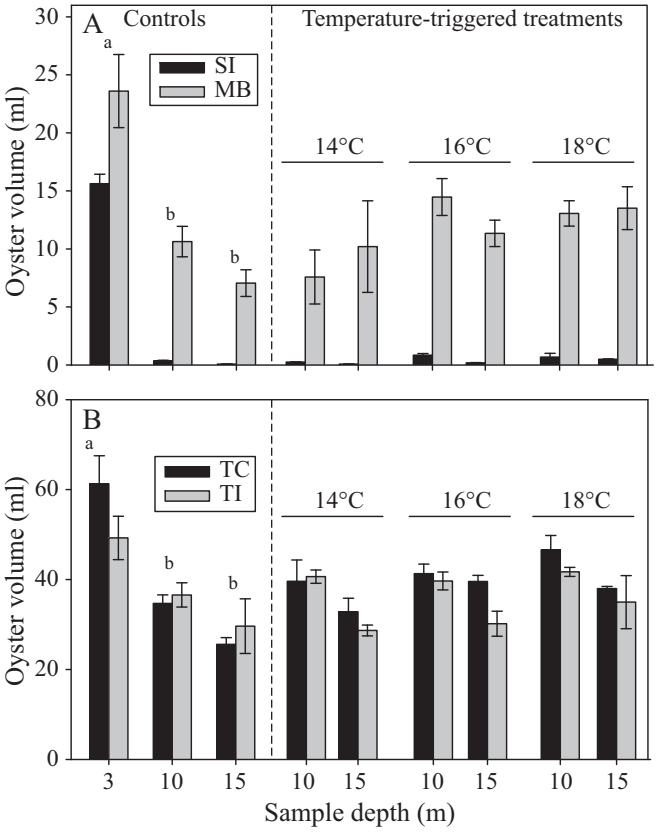

Fig. 7. Final oyster volume (ml, mean ± SE, n = 3) at (A) Sykes Island (SI) and Metcalf Bay (MB), and (B) Thor's Cove (TC) and Trevenen Inlet (TI) for controls and for each treatment combination (14, 16, or 18°C temperature trigger and 10 or 15 m depth). Note scale difference between graphs. Different letters above bars indicate significantly different (Tukey's, $p < 0.05$) depths among sites

Table 6. Three-way ANOVAs on final oyster volume (ml) and cumulative oyster mortality (%) at sites (see Fig. 1 for abbreviations) that share same initial oyster size. TT: temperature trigger; **bold:** $p < 0.05$; n = 3

	df	MS	*F*	p
Oyster volume				
MB and SI				
Site	1	1314.616	191.947	**<0.0001**
TT	2	23.046	3.365	0.052
Depth	1	1.786	0.261	0.614
Site × TT	2	16.632	2.428	0.110
Site × Depth	1	0.041	0.006	0.939
TT × Depth	2	5.862	0.856	0.438
Site × TT × Depth	2	4.593	0.671	0.521
Error	23	6.849		
TC and TI				
Site	1	121.474	4.882	**0.037**
TT	2	71.236	2.863	0.077
Depth	1	513.571	20.638	**<0.0001**
Site × TT	2	11.768	0.473	0.629
Site × Depth	1	30.836	1.239	0.277
TT × Depth	2	10.567	0.425	0.659
Site × TT × Depth	2	18.657	0.750	0.483
Error	24	24.884		
Oyster mortality				
MB and SI				
Site	1	33619.454	484.972	**<0.0001**
TT	2	73.647	1.062	0.362
Depth	1	722.333	10.420	**0.004**
Site × TT	2	146.323	2.111	0.144
Site × Depth	1	52.688	0.760	0.392
TT × Depth	2	74.246	1.071	0.359
Site × TT × Depth	2	6.208	0.090	0.915
Error	23	69.323		

(1992): a diatom-dominated narrow channel with strong currents mediating seawater mixing (MB), a flagellate-dominated and strongly stratified bay with important freshwater input (SI), and 2 intermediate (mid-channel) sites with an equal representation of the major taxonomic phytoplankton groups (TC and TI). The phytoplankton species succession also followed the normal general pattern for fjords located around the Strait of Georgia—a bloom of flagellates at the end of spring, followed by the onset of summer species and the fall diatom bloom (Harrison & Yin 1998). Temperature and salinity determined the composition of the phytoplankton community.

Potentially harmful and toxic algae

Two bloom periods of pHABs were identified at the 4 study sites during the summer: *Heterosigma akashiwo* and *Dictyocha speculum* during June and July, and

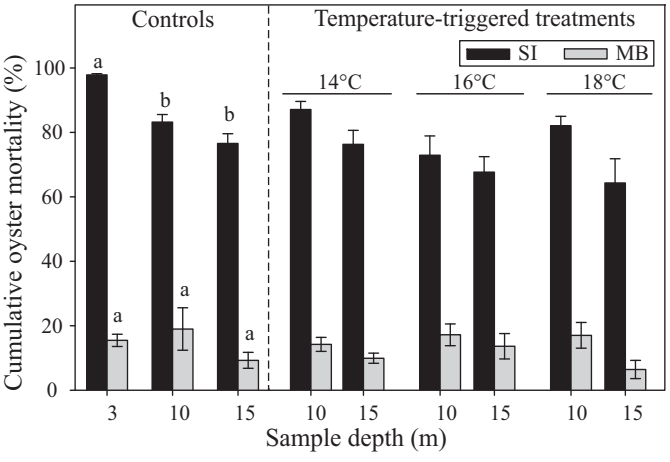

Fig. 8. Final cumulative oyster mortality (%) at Sykes Island (SI) and Metcalf Bay (MB) in each temperature trigger and depth treatment combination and in controls (mean ± SE, n = 3). Different letters above bars indicate significantly different (Tukey's, $p < 0.05$) depths within sites

Ceratium fusus and other dinoflagellates mainly during August, although with large differences in the intensity, persistence, and species composition among the sites. Strong and enduring summer stratification was associated with blooms at SI (Taylor et al. 1994, Taylor & Harrison 2002). TC and TI had a small *H. akashiwo* bloom at the end of spring and a larger, mixed dinoflagellate bloom during late summer. Potentially harmful algae at MB were limited to transient periods of low abundance. A high abundance of pHABs can lead to lower oyster growth rates and survival (Gainey & Shumway 1988, Alexander et al. 2006, King et al. 2006). During the present study, pHABs and oysters interacted differently at the 4 sites: pHABs were positively correlated with instant oyster mortalities at SI and with instantaneous growth rate at TI, suggesting that larger oysters (used at TC and TI) were not as susceptible to the blooms' harmful effects.

Heterosigma akashiwo was the most common and abundant potentially harmful algal species noted during this study, with the duration and intensity of its blooms being the most evident differences among sites in the phytoplankton community composition. This raphidophyte damages the digestive system in shellfish (Keppler et al. 2005), and pHAB biomass was indeed positively correlated with SI oyster mortality. Diatoms were also highly correlated with instant oyster mortality at SI, although they only represented <6% of the total biomass at this site. The highest abundance of diatoms (22% of total biomass) occurred during the peak and decline of a bloom of *H. akashiwo*, thus, this correlation could be a coincidence. An increase in oyster mortalities was registered during the fall at MB after a bloom of the potentially harmful diatom *Chaetoceros socialis* (Lauder). This and other bloom-forming diatoms may cause clogging of the gills in shellfish (Landsberg 2002).

Toxic dinoflagellates and diatoms were more common when the water column was well mixed, such as at MB throughout the sample period, and towards the end of summer at TC and TI. These algae normally cause shellfish harvest closures, due to paralytic shellfish poison, in areas of the Strait of Georgia in August, as previously observed at TC and TI (Taylor & Harrison 2002).

Depth-manipulation experiment

Fixed oyster-culture depth significantly affected the final volume and cumulative mortalities of oysters: individuals held at 3 m depth had larger final volumes than those in the 10 and 15 m depth control groups at all 4 sites, and oysters experienced significantly higher cumulative mortalities at 3 m than at 10 and 15 m at SI. In addition, the test depth to which the temperature-triggered treatments were dropped had a significant effect on final oyster volume at TC and TI and on cumulative mortalities at MB and SI. Those oysters that were dropped deeper had lower volumes and cumulative mortalities, but did not differ significantly from the fixed 10 and 15 m controls. These results agree with other studies in which higher growth and mortality rates were registered closer to the surface (Dégremont et al. 2005, Gagnaire et al. 2006, Ngo et al. 2006). For instance, Pacific oysters grown in Gosung Bay (Korea) at 0 to 2 m had a higher growth rate, gonadosomatic index, and fecundity than those held at a depth of 3 to 5 m, most likely due to higher temperatures and/or an increased food supply (Ngo et al. 2006).

Growth

Several studies have investigated the growth and mortality of Pacific oysters across geographically and oceanographically distinct areas (e.g. Brown & Hartwick 1988a,b, García-Esquivel et al. 2000, King et al. 2006). These studies and our results indicate that oysters grow better and have lower mortality rates at sites with higher diatom relative abundances, weaker haline and thermal stratification, and smaller temperature variations. The final oyster volumes in the current study were strongly site specific, confirming results from previous studies (e.g. Brown & Hartwick 1988a). Despite identical initial oyster seed size, large final differences were found between MB and SI; oysters at MB grew to a final size ~20 times larger than at SI in most treatments (the exception was the 3 m control treatment where SI oysters attained 65% of the volume achieved by MB oysters). However, major differences in final oyster volume were not evident between TC and TI.

Phytoplankton is the main driving force for oyster growth (Ren & Schiel 2008), and phytoplankton quality and quantity are strongly correlated with both oyster growth rates (Toro et al. 1999) and survival (Hyun et al. 2001, King et al. 2006). Similarly, the main variables significantly correlated with instantaneous oyster growth rate in the present study were components of the phytoplankton community. Diatoms are the preferred food for oysters (Dupuy et al. 2000, Marshall et al. 2010) and were positively correlated with oyster instantaneous growth at SI despite being scarce at this site. In contrast, dinoflagellates were correlated with instantaneous oyster growth at MB and TC, although the phytoplankton at MB was dominated by diatoms. Dinoflagellates have a higher content of carbon and protein per unit volume than diatoms, which could make them trophically preferable for oysters in a

diatom-rich environment (Menden-Deuer & Lessard 2000). The lack of significant correlations of chlorophyll concentration and Secchi depth with instantaneous oyster growth rates indicates that the phytoplankton composition, rather than the total amount of phytoplankton biomass in the water, is the main factor in fuelling oyster growth.

Current speed is an important factor for oyster performance, mainly due to its effects on food acquisition (Lenihan 1999). All sites were subjected to tidal and wind-driven currents and, although no direct measurements of flow speed were made at the sites, no large differences in flow were observed during sampling. Our data did not differ significantly between protected (TI) and exposed (TC) sites, corroborating the results of a previous study which used nearby locations in Desolation Sound (Wiley & Zahradnik 1981).

The initial size of the oysters in the present study was also an important factor for their growth rate, as oysters grow rapidly during their first year and more slowly thereafter (Sumner 1981). Our results reflect this growth pattern, as the larger seed oysters (at TC and TI) reached ~8 times their initial size while the smaller seed (at MB and SI) grew up to 200 times their starting volume, similar to results obtained by Gangnery et al. (2003).

Mortality

Large differences in cumulative oyster mortality were found between MB and SI as oysters at the latter site had 3 to 4 times lower survival than those at the former site. Cumulative oyster mortality observed at MB during the present study was similar or lower than the 25 to 30% reported as being normal for Pacific oysters during their first year in culture (García-Esquivel et al. 2000, Burge et al. 2007). Instant oyster mortality rates varied at MB throughout the summer, similar to results reported by Soletchnik et al. (2006), but increased towards the fall, as was also observed by King et al. (2006). The increase we recorded in the fall was possibly linked to a bloom of *Chaetoceros socialis*. Conversely, SI had high oyster mortality rates at the start of the study, as was also seen in 7 mm long oysters by Dégremont et al. (2005), levelling off later in the summer. Soletchnik et al. (2006) also described a peak in summer mortalities during June, which was associated with physiological stress due to accelerated growth. At SI, instantaneous oyster mortality was positively correlated with temperature, pHAB biomass, diatom biomass, and chlorophyll concentration, while at MB it was negatively correlated with temperature and positively correlated with water transparency. Although seawater temperatures at these sites rarely reached levels that could cause stress in the oysters, high temperature periods have been identified as one of the main factors in summer mortality events (Cardwell et al. 1979, Brown & Hartwick 1988a,b, Burge et al. 2007). In the present study, the oyster mortality rate at SI was higher during the warmer, more stratified periods and near the water surface. At MB, the correlation with temperature was negative, as the highest mortality rates occurred during the fall.

Pacific oysters acquire adult capabilities for particle processing and selectivity (being able to reject large, spiny and some toxic algal species; Cassis & Taylor 2006) at a shell length of ~2.4 cm (Cannuel & Beninger 2007). The oysters at TC and TI were at or above this critical size at the start of our study, whereas the seed at MB and SI only reached it during late July. The reduced particle selectivity of smaller oysters and the high abundance of harmful algae at SI could be major causes of the large oyster mortality rate at this site. In contrast, oyster growth was fast and mortality rates were negligible during the early summer at TC and TI despite abundant pHABs. Chlorophyll concentration was also positively correlated with instantaneous oyster mortality at SI, probably because abundant pHABs produced a similar increase in the total chlorophyll concentration. Transparency (Secchi depth) was correlated with instant mortality at MB throughout the study period. Nonetheless, the elevated mortalities observed during the fall might have been partially caused by a bloom of *Chaetoceros socialis*, which could clog the gills of shellfish due to the large size of their colonies.

High temperature and low salinity were the factors that best separated high (MB) and low (Si, TC, TI) mortality sites (Fig. 9). Salinity was not significantly correlated with instantaneous mortality at either MB or SI; nevertheless, it may have acted as the initiator in a cascade of events that led to increased oyster mortalities at SI. High freshwater input during the spring reduced the surface salinity, inducing stratification in the water column. This surface water was then heated by the sun, and the strong stratification probably prevented heat transfer to deeper waters. These high-temperature, low-salinity, and strongly stratified waters have been described as ideal environments for halotolerant motile algae but inadequate for diatoms (Bearon et al. 2006). SI was characterized by large blooms dominated by *Heterosigma akashiwo* during June and *Ceratium fusus* during August, while diatoms accounted for only 6% of the total phytoplankton biomass. The oysters at this site were then faced with periods of high temperatures (up to 26.7°C), HABs, and lack of nutritive particles overlapping in quick succession. Stress, starvation, and malnutrition caused by pHABs during the summer could result in oysters with a reduced immune response (Galimany et al. 2008). This could then lead

to a higher susceptibility to infection by parasites and opportunistic diseases (Friedman et al. 1991, Chu et al. 2002, Burge et al. 2007) and thus increased mortalities in the stressed oysters. The particularly extended period of low salinity and strong stratification that was conducive to large blooms of *H. akashiwo* and *C. fusus* seen at SI was not observed at any other site, except for a short period at TC and TI. The low stratification and strong tidal mixing prevalent at MB were favorable to diatoms. TC and TI presented intermediate values of salinity and temperature, although closer to MB than SI (Fig. 9); in addition, their phytoplankton was an average of the SI and MB extremes.

CONCLUSIONS

MB had the best oyster-growing conditions, having a well-mixed water column, high salinity, low temperature, and dominance by preferred diatoms. Undesirable conditions at the SI site—strong and enduring stratification, a long period of low salinity, high temperature, and pHABs which resulted in large mortality rates and reduced growth—should be avoided for the culture of small oyster juveniles. Site selection is critical for culture of seed oysters throughout the Strait of Georgia.

Significantly higher growth and mortality rates were seen in oysters held closer to the surface (3 m) than in those cultured deeper (10 or 15 m). The 3 m fixed culture depth was seen as the optimum, due to the larger final oyster volumes obtained, despite the higher mortality rates registered at this depth. Depth manipulation, based on temperature as the trigger for oyster movement, failed to produce significantly better growth or survival than the fixed controls at similar depths. Depth manipulation of oysters remains as a potential management option to reduce summer mortalities, but needs to be researched further as the present study showed that temperature was inadequate as a sole trigger for significantly reducing oyster mortality rate. Potential trigger variables for further study would include various phytoplankton taxonomic groups. Oyster culture sites should be studied in terms of temperature and salinity regimes as well as phytoplankton composition and species succession, to optimize the balance between oyster growth and mortality.

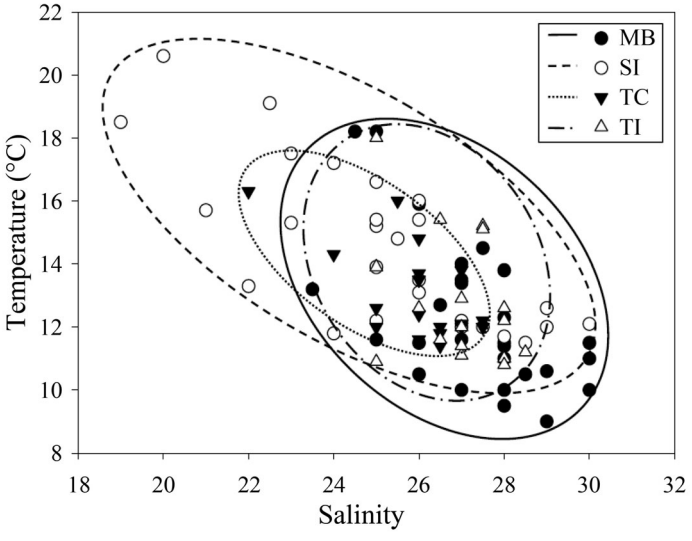

Fig. 9. Seawater temperature (°C) and salinity at each study site, measured every 2 wk (see Fig. 1 for abbreviations)

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