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Depth Selection and In Situ Validation for Offshore Mussel Aquaculture in Northeast United States Federal Waters

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Abstract: As mariculture progresses offshore in the US Exclusive Economic Zone, technical and ecological challenges need to be overcome, such as the choice of suitable sites that favor the production of target species. The offshore culture of blue mussels, *Mytilus edulis*, is performed with submerged longlines and mussels need to withstand more motion than on coastal sites. Temperature affects the ability of the byssus to adhere to farming rope, while chlorophyll concentration provides an estimation of food availability. Together, these are important factors in predicting the suitability of offshore mussel farms. To identify suitable depth of submersion for mussel ropes in New England federal waters, historical oceanographic data of temperature and chlorophyll *a* from 2005 to 2012 were used. The results suggest that mussel ropes were submerged during summer to a minimum depth of 15 m in northern and a 20-m depth in southern areas of New England where temperature is at a species-optimum and phytoplankton biomass is abundant. For the site offshore Massachusetts, in situ biodeposition measurements validated predicted depth, confirming satisfactory mussel performance. Promising local areas have shallow thermoclines, such as offshore Long Island, Cape Ann and New Hampshire. Recommended depths can be adjusted to future temperature increases associated with climate change.

Keywords: offshore aquaculture; blue mussel; habitat suitability; submersion depth; temperature; chlorophyll; biodeposition; marine management

1. Introduction

The United States has recently become the largest national importer of seafood in the world, overtaking Japan, because of the nation's limited domestic production [1]. To satisfy the increasing demand for fisheries products, seafood production should be increased using economically and environmentally sustainable methods. With most fisheries stocks being exploited at or near maximum sustainable yield and coastal areas being overused, establishing filter-feeding shellfish farms offshore is promising. Offshore aquaculture in the US is generally defined as occurring in federally managed waters of the Exclusive Economic Zone (EEZ), extending between 3 to 200 nautical miles from the shore [2,3] and is recognized to provide a way to derive added value from US EEZ in the Northeast US Shelf [4]. It enables the optimization of marine space, as in increased sustainable use and minimization of coastal conflicts of use, while also contributing to national food security and relieving pressure on wild fish stocks [5,6].

Offshore aquaculture has many constraints related to the biology and ecology of cultivated species, which include, but are not limited to predators or biofouling [7], robustness of the farm equipment in relation to the energy of the environment [8], possible although minimal detriment to the ocean floor [9], and legal issues [10]. Discussions about the feasibility of the offshore industry recurrently become mired in social perceptions and legal aspects, such as restriction of fishing, overlaps with marine sanctuaries or military areas, habitat exclusion, and possible entanglement of protected species (see for example: Environmental Law Institute [4]; Price at al. [11]).

Nevertheless, using an exclusionary approach [12], namely selecting sites where conflicts of use are eliminated and disregarding environmental suitability that fundamentally dictates mussel performance is an imprudent approach, considering the risk and expense of offshore operations. In the busy area of New England, this approach is unrealistic and will constrain offshore seafood production (see details in Tlusty et al. [13]). Moreover, avoiding areas used for other activities is known not to lead to the best outcomes; instead, considerations by managers of tradeoffs that maximize holistic values among aquaculture, fisheries, and conservation are suggested as being more beneficial [14]. As stated by Gentry et al. [15], an essential consideration for offshore aquaculture planning is identifying sites that can be most productive and profitable. Additionally, Kite-Powell [16] concluded that mussel offshore aquaculture in New England is expected to be economically viable if good production yields are achieved. Along these lines, several studies around the world have modelled mussel growth and production outputs for heavily studied environments where aquatic farming is already developed, using local, long-term datasets and mussel farming management, farm design and previous output data (see for example: Rosland et al. [17]; Thomas et al. [18]; Sara et al. [19]). But the New England offshore area has not been comprehensively monitored, and commercial offshore aquaculture farms have not been established. Because of this state of development, a primary approach for the identification of feasible farming areas (see also Tlusty et al. [13]; Kapetsky et al. [20]) and depths should precede simulations of growth and production. Consequently, identifying farming sites with optimal oceanographic characteristics for cultivating the target species should constitute the first step in site selection considerations.

Among the most suitable species for offshore aquaculture is the commercially-important blue mussel, *Mytilus edulis*, a seafood with an established market and known culture technologies. The US production of mussels in 2012 was 335,000 kg, while imports were 75,384,000 kg and comprised the main US imported bivalve shellfish, mainly from Canada [21]. As the US consumption of mussels continues to grow, increasing national production will contribute to food security and lessen the seafood trade deficit.

Pilot projects on offshore mussel aquaculture have been performed in several countries [22], including Germany [23], New Zealand [24], England [25], the Netherlands [26], Portugal [27] and the United States, where research started more than ten years ago [4]. In the Northeast US, research was performed in small pilot farms by different institutions at different locations: the Woods Hole Oceanographic Institution's experimental farm in Rhode Island Sound near Martha's Vineyard, the University of New Hampshire's experimental farm offshore south of Isles of Shoals (NH), and Salem State University, which currently has an experimental farm north of Cape Ann (MA). New England studies included a variety of aspects related to the feasibility of mussel culture offshore, such as local spat collection, growth rates, mortality, equipment selection, and longline mooring design [28–30]. Results were generally favorable, encouraging industry development. Despite this background, offshore mussel aquaculture knowledge has not translated into commercial enterprises and still today, offshore farming consists of few permits for research purposes, possibly due to the investment risks posed by undefined regulation and supporting scientific data limited to trials of short duration and restricted to single stations within a permitted site [29,31,32]. Ultimately, additional research focused on remaining knowledge gaps, especially environmental suitability analysis considering a larger spatial coverage and detailed vertical profiles of environmental conditions, should contribute key information to assist prospective entrepreneurs seeking appropriate siting.

On the Northeast continental shelf of the United States, the complete mariculture cycle for blue mussels from seed to marketable size takes up to 1.5 years [29]; thus, mussels are exposed to repeated seasonal environmental variations. One of the main methods to ensure the success of a mariculture enterprise is selecting a site where environmental conditions are favorable for the longest period of time possible during the grow-out phase.

Temperature is one of the main environmental factors [2,5] controlling mussel physiology, including filtration rate, food absorption, growth, and heartbeat [33–35]. Blue mussel performance and metabolic activities are not efficient at temperature extremes outside the range of 5–20 °C, with optimal growth being reported between 10–20 °C [20,34,36–38]. Negative physiological effects related to temperature changes are moderated in an environment with high food availability [39–41]. In coastal and estuarine environments, temperature variation is pronounced because of the interplay of solar radiation, shallow water, and even thermal additions from industrial sources [37]. Offshore areas can offer a more stable environment with regard to amplitude and frequency of temperature oscillation [42], which can make site choices more precise. The long-term trend of increasing water temperatures on the NE US Shelf [43,44] will also be relevant to successful farm siting in the years to come.

Locating farming in high-energy offshore areas makes the ability of the mussel to support itself and remain attached to the submerged farming ropes a critical issue [45]. The tenacity of the byssus—collagenous filaments secreted by the foot and used to attach to hard substrate [46]—and its ability to support attachment of the shellfish, fluctuates according to changes in the environment, such as wave energy, biofouling, food availability, but especially temperature, which seems to prevail over other factors [47–49]. Additional trade-offs of energy allocation in a mussel's metabolism may impose further risk of byssus dislodgement.

Byssal production takes up to 44% of carbon and 22% of nitrogen produced in *M. edulis*, and trade-offs between byssus production, growth, and reproduction are expected [50,51]. Because temperature thresholds and variation rates are reportedly the most important triggers of reproduction [52], it is expected that temperature would also have an influence over byssus quantity and quality. Indeed, it is known that byssus attachment strength has a seasonal and annual cycle, being higher in winter and weaker in the summer months in New England waters [53]. Previous studies [48,53] reported an increase in individual byssal production but lower byssus strength during the summer, and lower numbers of byssus threads with higher strength in colder winter months. The strength of the byssus, instead of the number of fibers, is decisive in the ability to stay attached to any substrate, and consequently, individuals with weaker byssus are more prone to dislodgment [48]. Although early investigations were related byssus production and attachment strength to hydrodynamic conditions [46], the idea was not supported by more recent findings that established that dislodgments were expected only when high energy-events, such as storms, coincided with a weak attachment cycle, which is mainly controlled by high temperature and related biological events such as reproduction [45,47,50,54]. Likewise, Lachance et al. [47] found temperature to be the factor most strongly correlated with bysal attachment strength ($r^2 = -0.62$ $p < 0.001$); turbulence was a secondary factor, for which importance to cause dislodgments would first depend on the byssal strength condition directly forced by the first factor [54] and thirdly, followed by reproductive condition and spawning. Thus, it can be concluded that during warmer seasons, mussels may also be less able to cope with changes in the environment and sustain attachment. Consequently, especially for offshore aquaculture, a colder environment can be an important strategy to safeguard against the loss of yields and decreased profit caused by shellfish fall-offs. As low temperatures have been suggested to delay gametogenesis [55,56], trade-offs between byssus function and reproduction can also be minimized. The importance of this trade-off strategy is further supported by the fact that mussels acclimated to warmer temperatures are more resistant to air exposure than those grown in cooler waters, which might indicate that colder water mussels in temperate areas are, in general, more sensitive to temperature variations in the environment [57].

Offshore mussel farming technology consists of mooring systems supporting longlines submerged to several meters depth in the water column to avoid exposure to waves, potential rough weather conditions on the surface, and especially, to not interfere with vessel traffic (Figure 1; [8,23]). Mussels are cultured attached to ropes until harvest size, but in the early stages of culture, the mussel-seeded rope is usually housed in protection 'socks' that disintegrate within a short period as mussels grow. Although the submersion of ropes enables protection from the energy conditions at the surface, the surface buoys still transfer energy to the submerged rope backbone, which can result in production losses [8].

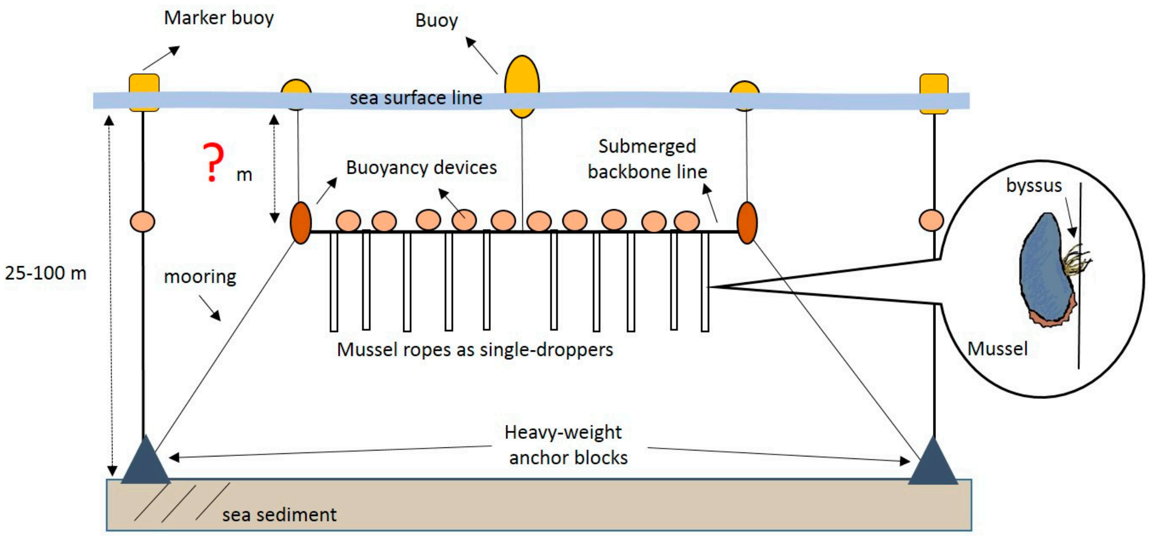

Figure 1. Scheme of offshore submerged longline system for mussels (based upon Goseberg et al. [8]; Langan & Horton [29]). The suitable area depth for offshore operation is indicated, whereas the suitable depth for submersion of mussel ropes in the water column is indicated by the symbol "?", as it is one of the objectives of this paper.

At present, in the US, no consistent regulation is in place to determine the required depth of submerged mussel farming structures, but the main concern is avoidance of vessel traffic disturbance (K. Madley 2017, *personal communication*). Thus, the guidelines provided by regulatory agencies are on a case-by-case basis during the farm permit review [4]. Notwithstanding, the depth allocation of a submerged aquaculture system should not only rely on only satisfying regulatory advice, but rather be selected to be consistent with environmental conditions at which mussels can thrive. As water temperature changes can be pronounced with depth, the importance of this variable is unquestionable for any kind of offshore aquaculture.

Moreover, as bivalve aquaculture in federal waters of Northeast is still underexplored, assessment of seasonal performance of bivalves in situ is important to support the selection of depth and the forthcoming expansion of the industry. Physiological plasticity of mussels allows for adjustments of feeding behavior in response to variations in environmental characteristics, both biotic and abiotic [58,59]. Developing indicators that can give information about the nutritional quality of a farm site is quite challenging [60], but methods such as biodeposition measurements have been well developed and can quantify the feeding performance of mussels (see details in Galimany et al. [59]).

Building upon aforementioned considerations, the objective of the present report was to estimate the optimal depth for submersion of longlines and mussel ropes to maximize the production efficiency of future commercial offshore farming operations. An environmental "habitat suitability analysis" was established based upon a relevant (not exhaustive) literature review on the ecology of blue mussels and two important environmental variables—temperature and chlorophyll *a*—as a proxy of food availability (see for example Buck [23]). Site comparisons of selected, prospective farming sites were also discussed and suggestions for vertical siting of prospective farms were made. To validate the depth suitability threshold, in situ measurements of mussel performance were performed in a current experimental farm offshore Cape Ann in Massachusetts. Mussel feeding performance was assessed together with environmental data collected at the time of the experiment. To our knowledge, this is the first work that uses historical series of environmental data and examines a large extension of the Northeast US coastal shelf ecosystem. We compared stations in different states, whereas previous trials were performed only at individual sites. Additionally, the paper reports some of the first measurements of mussel feeding performance in offshore New England, which is considered a highly suitable area for the development of the farming activity.

Multiple environmental, technical, and social aspects are of importance when holistically considering the success of an offshore farm and permit applications (see Benetti et al. [12]). It was not, however, the intention of this report to address all relevant issues combined. It would be an overly ambitious and naïve task to attempt a thorough compilation, considering that each issue (use conflicts, economics, social concerns) has been the subject of multiple ongoing research investigations around the world for the last 20 years. It was also not the objective of this paper to perform growth models, even because oceanographic and mussel samplings at the offshore sites were not extensively performed to allow for calibration, validation or general simulation robustness. Instead, this study aimed to contribute to fundamental knowledge needed by entrepreneurs for farm planning, specifically focusing on geographic location and depth deployment of longlines. Furthermore, studies such as this should be region-specific because environmental context is known to affect productivity, design, and management, and thus, the overall success of the offshore enterprise.

2. Materials & Methods

2.1. Depth Suitability for Offshore Mussel Farming in New England

2.1.1. Study Area

This study area was comprised of US EEZ offshore locations along Long Island (LI), New York (NY), and off of the states of Rhode Island (RI), Massachusetts (MA) and New Hampshire (NH; Figure 2). The study area within the United States NE shelf is very productive and widely recognized for fisheries resources [61], with fish populations contributing 25% of the value and 18% of the weight of the national, commercial, capture fisheries. The area is also under consideration for large-scale marine aquaculture. The native blue mussel is one of the main shellfish species cultured in the New England area, along with the Eastern oyster (*Crassostrea virginica*), the Northern quahog (*Mercenaria mercenaria*) and the soft-shell clam (*Mya arenaria* [62]). Currently, shellfish culture is mainly performed in coastal sites, despite the growing interest for moving aquaculture offshore in recent years [2].

Among essential considerations for an offshore mussel farm are the relative proximity to the shore to facilitate farming operations and locations between 25 m and 100 m in depth [20]. Bathymetric contour shapefile [63] was obtained from Marinecadastre.gov Data Registry and contours were used to calculate the total available horizontal area for aquaculture using calculations of polygon areas in Arc Map 10.5 (ESRI 2016). Recently, for submerged longlines in New England, the mussel ropes were set in the water column at a minimum depth of 10 m (K. Madley 2017, *personal communication*); therefore, the choice of a suitable depth was 10 m and greater. Nevertheless, surface environmental data are shown for comparison. Because the difficulty for management of operations and mooring costs increase with the longline submersion depth, our assumption was that the most suitable depth is the shallowest layer at which water temperature is within desired parameters.

Blue mussels tolerate a wide range of salinity (13–32 [64]), although they perform poorly in frequently changing salinity environments [37,65]. As prospective offshore sites are far from land-based freshwater discharges, and not susceptible to strong salinity variation from evaporation, salinity variation was narrow in the studied offshore environment [66] and within the tolerance range of mussels, posing little physiological effect on the target species (see for example Riisgård et al. [67]) and was not a focus of the present study.

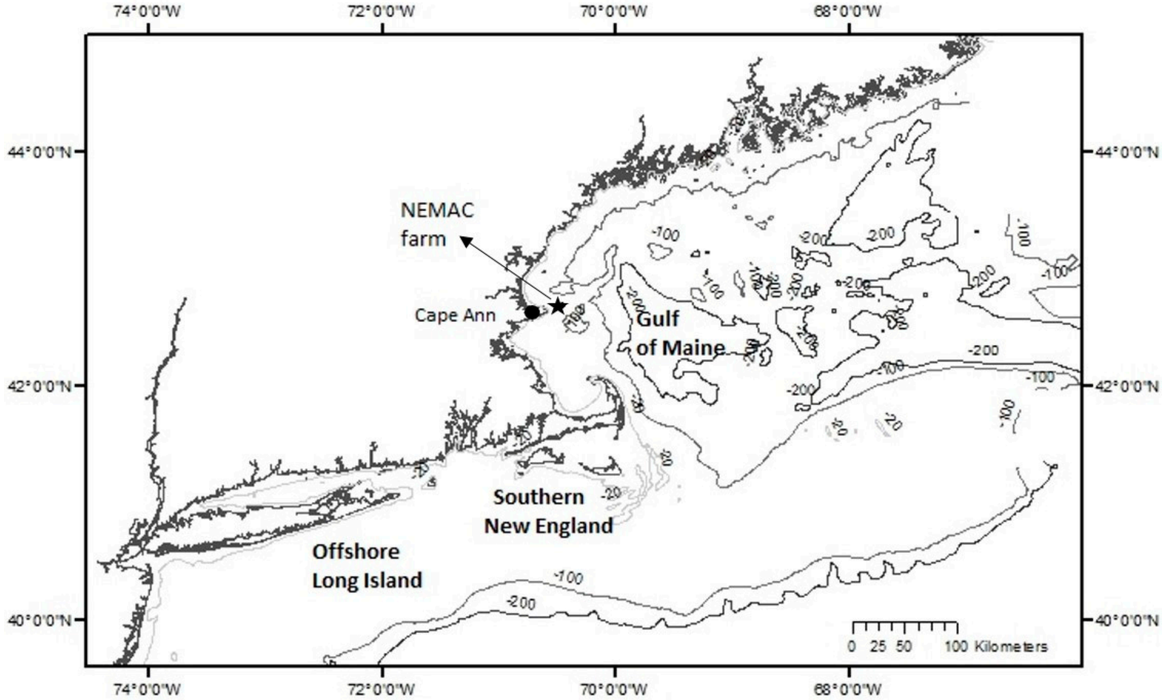

Figure 2. Inner shelf of the northeast area of the United States, including areas offshore Long Island, Rhode Island, Massachusetts and New Hampshire and detail of bathymetric contours (20 m, 100 m, 200 m depth). The star symbol locates the Northeast Massachusetts Aquaculture Center (NEMAC) experimental farming site, offshore Cape Ann.

2.1.2. Temperature Data

To confirm suspected temperature warming trends in the area, monthly average grid data from the periods of 1975–1984, 1995–2012 and 2016 were compared between three geographic regions of the Northeast Shelf: offshore Long Island, offshore Rhode Island in the Southern New England and the Gulf of Maine. By using data averaged over decades, large-scale changes and trends were visualized.

Temperature data in different layers of the water column for the entire extension of the inner shelf were analyzed as seasonal average climatology over the past 7 years during the two most extreme temperature periods: winter and summer. The main physiological characteristics of mussels of importance for offshore aquaculture, such as byssal strength and feeding, can be affected by extreme temperatures that are typical during the aforementioned periods. On the US east coast, wild mussel spawning usually occurs between spring and summer. As spawning generally occurs coincidently with increasing temperature, the actual temperature trigger may be different from that when larvae are first found [68]. Therefore, it is prudent to adopt temperature thresholds as intervals of temperature rather than at an individual temperature value. Although physiological variations can occur in areas of similar environmental characteristics, approximate thresholds can be set within which different mussel performance can be expected. These temperature thresholds were defined based on a literature review in accordance with reported spawning events and physiological considerations, such as growth and filtration performance of blue mussels (Table 1), with special attention to the reproductive seasons.

Averaged climatologies of temperature at different depth layers at $\frac{1}{4}$ degree grid resolution were obtained from the open-source database of the Global Temperature and Salinity Profile Program available at the National Centers for Environmental Information page (NCEI website: www.ncei.noaa.gov; detailed metadata information is available in Seidov et al. [69]). Winter was defined as the months of January, February, and March and summer as July, August, and September. Temperature data were used in two ways: firstly, for an overall horizontal analysis of the areas with adequate temperature at different depths (0 m, 5 m, 10 m, 15 m, 20 m and 25 m depth), and secondly, to verify and compare profiles of specific stations where blue mussel mariculture was thought to be feasible (0 m, 5 m, 10 m, 15 m, 20 m, 25 m, 30 m and 35 m depth). In order to further detail summer conditions for the whole New England area, temperature anomalies were also calculated (averaged temperature in each layer minus the annual mean). Despite the fact that distinctions between long-term and short-term diel fluctuations are often considered when using temperature as an ecological factor, offshore areas did not have as marked temperature variations as coastal and estuarine areas more affected by diurnal fluctuations [37]. As a result, temperature statistical means satisfactorily reflected the average time and temperature levels to which the mussels would be exposed. Shapefiles were extracted in Arc Map 10.5 (ESRI 2016) and plotted by depth layer at 5-m depth intervals.

Vertical profiles of temperature during winter and summer were plotted to allow comparisons of hydrological conditions of different locations at six different stations chosen to represent potential farming sites along the three states that had a history of active shellfish harvest (Table 2). Stations were located outside of Shinnecock Inlet, southwest of Block Island, southwest of Martha's Vineyard, north of Cape Cod, north of Cape Ann, and offshore New Hampshire, comprising the entire latitudinal extension of the studied area.

2.1.3. Chlorophyll *a* Data

The NE American shelf is a very productive area with an estimated primary production of 300 g·C·m^{-2}·yr^{-1} on the southern New England shelf and 260 g·C·m^{-2}·yr^{-1} in the Gulf of Maine [61]. Based on the chlorophyll threshold requirement for offshore blue mussel aquaculture reported by FAO (>0.5 µg·L^{-1} [20]), no areas would be excluded from accommodating mussel farms because of insufficient food availability; therefore, habitat suitability was based on temperature data. An overview of the estimated phytoplankton biomass in the area is shown by the remote sensing satellite data of the winter and summer in the years of 2012 (Figure 3). Historical in situ chlorophyll data were estimated with a fluorometer (Wetlabs ECO-FLRTD) attached to a high-resolution conductivity-temperature-depth profiler (CTD; SBE 911plus Sea-Bird Electronics Inc.) samplings of the World Ocean Database 2013 found at the National Oceanographic Data Center website for the period from 2005 to 2012 (www.nodc.noaa.gov/OC5/SELECT/dbsearch/dbsearch.html).

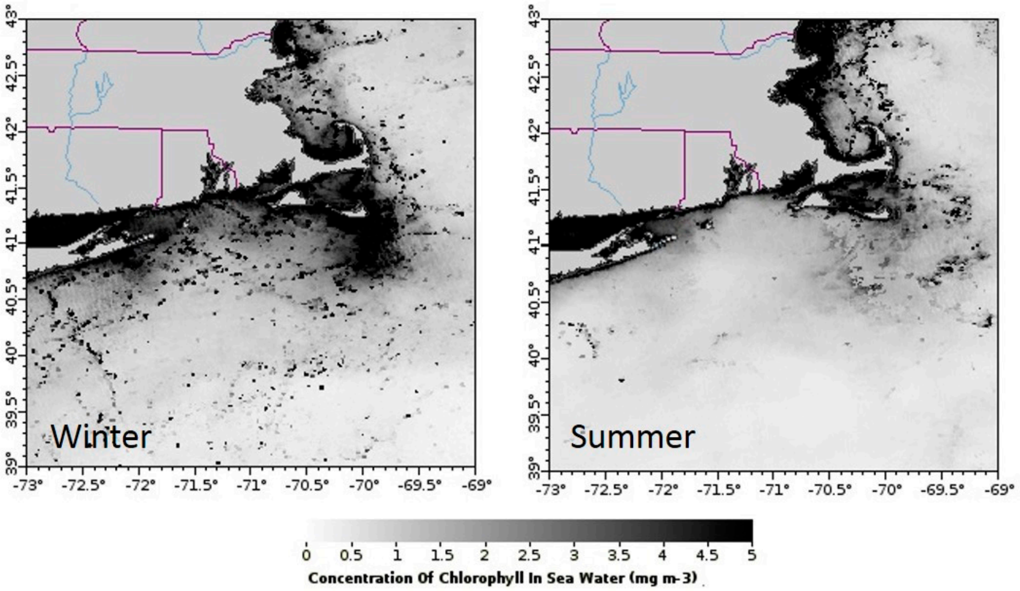

Figure 3. MODIS satellite mean winter (February 2012) and summer (June 2012) surface chlorophyll concentration image of the American Atlantic NE Shelf (Source: NOAA NFMS SWFSC ERD).

Table 1. Temperature thresholds and related effects on the physiology of blue mussel, *Mytilus edulis* New table built upon some data from Pondniesinski & McAlice [70]).

Physical Effects	Period	Study Region	Temperature (°C)	Reference
Filtration rate and growth is significantly lowered			<5	Bayne [37]; Almada-Vilelia et al. [71]; Comeau et al. [34]
Acclimating optimum			10–16	Newell et al. [72]; Helm et al. [73]
Optimum growth			10–20	Coulthard [36]; Stirling & Okumus [38]
Limit for optimum physiological performance			20	Bayne [37]
Growth lowered; mortalities			>20	Read & Cumming [74]; Almada-Vilella et al. [71]
High byssus strength	Winter	Rhode Island, New Hampshire	<6	Carrington [46]; Garner & Litivaitis [48]
Low byssus strength	Summer	Rhode Island	18	Carrington [46]
	Summer	New Hampshire	13.3	Garner & Litivaitis [48]
		USA		
Spawning	Late May to June (1969–1977)	Damariscotta Estuary, Maine	10–12	Pondniesinski & McAlice [70]
Spawning	June	Maine	10–12.5	Newell et al. 72]
Spawning	Late April to June	Stony Brook, New York	11–15	Newell et al. [52]
Spawning	August–October	Shinnecock, New York	16–22	Newell et al. [52]
Spawning	May	Milford, Connecticut	15–16	Engle & Loosanoff [75]
Spawning		**CANADA**		
Spawning	Mid June–Late July	Great Entry Lagoon, Canada	10.3–20.7	Myrand et al. [76]
Spawning	Mid June Late August	Open Sea, Canada	10–15	Myrand et al. [76]
Spawning		**EUROPE**		
Spawning	26 July–2 August 1996	Finland	14–17	Antsulevich et al. [77]
Spawning	May to July 1960	Finland	12–15	Heinonen [78]
Spawning	15-May	Sweden	8.5	Kautsky [79]
Spawning	30-May	Sweden	9.5	Kautsky [79]
Spawning	5 April to 25 April	Holland	6–8	Pieters et al. [80]
Spawning	Mid-April to end of May	England	9–12.5	Chipperfield [81]
Spawning	Middle July to August	Iceland	10–12	Thorarinsdottir [82]
Spawning	Early May	Norway	8	Bohle [65]
Spawning	May	Denmark	7–16	Jørgensen [83]
Spawning	May–June	Denmark	13–14	Rasmussen [84]

Table 2. Locations of the study stations and their importance.

Stations (Approx.)		Station	Physical Location (Related Area)	Description
Latitude (N)	**Longitude (W)**			
40.625	−72.375	1	Outside Shinnecock Inlet (LI)	Intended multi-trophic aquaculture
41.125	−71.375	2	Southwest of Block Island (RI)	Intended wind-farm co-siting
41.125	−70.875	3	Southwest Martha's Vineyard (RI)	Past trial
42.125	−70.125	4	North of Cape Cod (MA)	Area selected in the present study
42.625	−70.625	5	North of Cape Ann (MA)	Ongoing trial
43.125	−70.375	6	Offshore New Hampshire (NH)	Ongoing commercial mariculture

Unfortunately, chlorophyll data collection at different depths during surveys was sporadic and mostly concentrated in the outer shelf, thus, from 387 surveys with available chlorophyll data from 2005, 2009, 2010 and 2011, only 13.2 % (n = 51) were located in the inner shelf, namely shallower than 100 m in this study. Profiles were selected as representative samplings in order to cover the entire extension of the study area and based on location in the inner shelf, as in proximity to land and to the six previously mentioned potential farming sites.

2.1.4. Statistical Analysis

Linear regressions were used to determine how much temperature varied with increasing depth. Temperature data for winter and summer were tested for normality using the Statgraphics Plus software Version 5 (Mannugistics Inc. 2000). For selected depths, averaged standard deviations for the summer season were calculated for North and South New England areas based on stations within those areas to check for the variability of temperature data in the period of study, according to the equations:

$$\sum_{j=1}^{n} (x_j - \overline{x})^2 = \sum_{i=1}^{g} n_i s_i^2 + \sum_{i=1}^{g} n_i (\overline{x}_i - \overline{x})^2 \tag{1}$$

$$SD = \sqrt{1/N_{total}.deviance} \tag{2}$$

where $\sum_{j=1}^{n} (x_j - \overline{x})^2$ = deviance; s^2 = variance; n = number of samplings; g = stations.

Two questions were asked in relation to analyzed stations: First, were there differences in temperature, regardless of depth, between stations? For that purpose, non-parametric Kruskal–Wallis tests were performed to check for differences between medians of temperature among all stations, separately for each season. The second question was "how does the temperature vary with depth in each season?". For this question, linear regressions were performed with temperature and depth data from all stations, separately for each season.

2.2. Mussel Biodeposition Measurements at Experimental Farm in Cape Ann

2.2.1. Study Site

In situ biodeposition measurements were used to check performance of mussels, at the depth found to be optimum, at an ongoing experimental farm in the northern part of the study area. Currently, there are no offshore farms at the southern areas of New England and consequently, biodeposition was not possible for that area. Biodeposition measurements were performed at the NEMAC experimental farm, Salem State University, to which an experimental mussel farm siting permit was granted in 2015 and recently received additional funds to continue expanding the farm. The farm consists of one 6-m-header-longline with three 5-m-droppers located at a site of 45 m water column (Table 2, Station 5). It is sited southwest of the Stellwagen Bank National Marine Sanctuary to minimize interaction with protected species, such as turtles and marine mammals, which are known to seasonally use the Sanctuary. Indeed, protected species were not detected near the farm until present (Edward Maney Jr. 2018, *personal communication*). The farm is signalized by surface buoys (Figure 4) and is visited every two weeks by the responsible researchers to check for possible marine fauna interaction and collection of mussels and environmental data that will be used in separate future studies. Blue mussels (*Mytilus edulis*) spats had been collected by natural recruitment in the area and were being grown since spring of the previous year (2017).

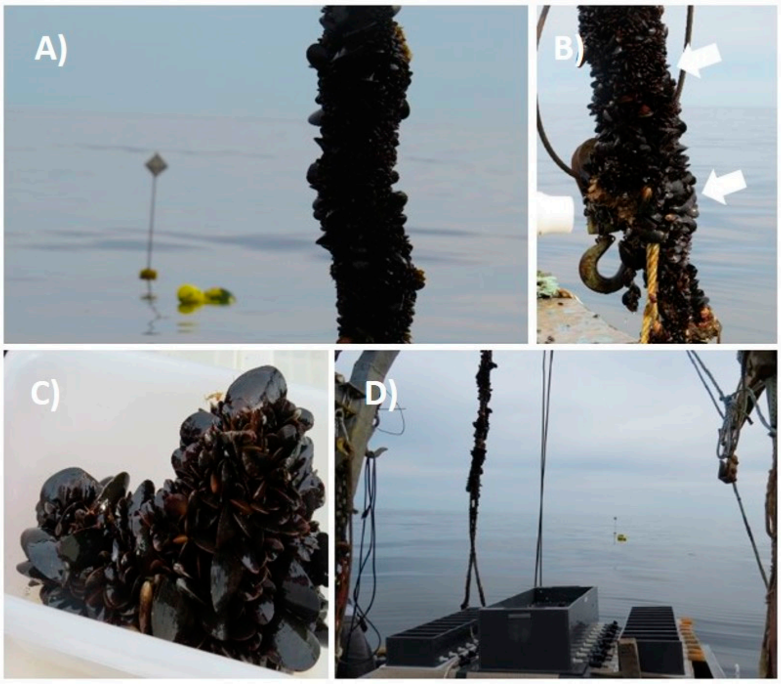

Figure 4. View of NEMAC farm: (**A**) farm demarcation; (**B**) mussel longline (arrows point to different mussel settlements—an indication of natural seeds availability); (**C**) detail of mussels with clean shells; (**D**) biodeposition onboard setup.

2.2.2. Experimental Design

Measurements were conducted during two different seasons in 2018, in early spring (May) and mid-summer (August) that were assumed as representative of the two contrasting yearly conditions, since boat samplings are not performed during winter due to security reasons related to onboard sampling in harsh sea conditions. Although sampling was limited to two cruises, at the studied depth, approximately 15 m, those samplings provide snapshots representations of the seasonal water temperature: colder not-stratified water column and stratified warmer waters, respectively.

Upon arrival at the farm, the longline and droppers were pulled from a 15-m depth to the surface and a few mussels were striped from ropes on site and left to recover from handling stress while related experimental set-up and oceanographic samplings were in course. Only larger mussels were used and new settlements with smaller shells were avoided in order to try to sample approximately the same cohort in both samplings.

Acclimation was not necessary, as mussels were previously in local ambient seawater. Experiments were conducted with different groups of mussels of similar sizes, reflecting the growth cycle in the area in each sampling period.

A portable flow-through device that allows in-situ measurements of feeding rates of mussels in natural conditions of seston and other water characteristics was used (see detailed description at Galimany et al. [59] and Galimany et al. [85]). The set-up consisted of a submersible pump (UtiliTech, 1/3 HP) deployed at a 15-m depth that continuously pumped seawater into an aerated PVC reservoir tank that feeds 20 individual chambers. From the reservoir tank, seawater flows through each chamber at a set rate of approximately 12 L·h^{-1}, which allows for homogenous distribution of particles between chambers (see details in Galimany et al. [59]).

The mussels were cleaned of all encrusting organisms prior to placement in chambers to ensure that filtration was only from the mussels and not from epibionts. The mussels were positioned in chambers with the shell hinge facing the water inflow end of the chamber to prevent influence of direct flow upon feeding activity [86,87]. One mussel was added to each experimental chamber (n = 16), in addition to four empty mussel shells (controls) in remaining chambers. Mussels were considered acclimated to the system when they opened valves and began to feed, producing visible pseudofeces deposits and/or feces.

While the experimental mussels were acclimating to the chambers, mussel gut transit time (GTT) was determined with other individuals. GTT is the minimum time for an organic particle to pass through the digestive tract of the mussel after ingestion ([59] adapted from Hawkins et al. [88]). Four mussels were placed in individual containers filled with seawater from the site and with added cultured green algae *Tetraselmis chui* (PLY429) from the NEFSC Milford Laboratory collection. Initially, mussels were closed, thus, the time of re-start of filtration was noted, and feces were examined until green colored feces were detected. The GTT was the time elapsed between the introduction the green algal culture to containers containing individual mussels actively filtering (valves open) and the production of green feces (resulting from coloration of *Tetraselmis chui*). The GTT was used to offset the collection of water samples and mussel biodeposits so that an accurate mass-balance of inorganic particulate matter could be calculated. Thus, the GTT was used to determine the start and finish of feces and pseudofeces collection in the biodeposition apparatus.

Once 100% of the mussels in the chambers were actively feeding, chambers were fully cleaned of any previously-produced biodeposits. Water samples and biodeposit collection were started. Water samples were collected to determine seston availability and composition. After the GTT passed from the beginning of water samples, feces and pseudofeces were collected to determine how the mussels had processed the seston filtered previously. Water samples (~150 mL) were collected every 30 min from three locations of the biodeposition equipment: reservoir of water input and the two exit chambers from the control chambers to quantify seston availability to mussels and any seston removed from the flow by the apparatus itself. For each individual mussel, biodeposits were separated and collected with a glass pipette until sufficient biodeposit was available for quantification.

Both water seston and mussel biodeposit samples were filtered separately on combusted (450 °C for 8 h) pre-weighed, Whatman 25-mm GF/C filters. Samples were rinsed with isotonic ammonium formate, folded in half, stored in aluminum foil, and immediately placed on ice. Filters were frozen until analysis at the laboratory. All filters were then processed for total particulate matter (TPM), particulate inorganic matter (PIM), and particulate organic matter (POM). TPM was determined by drying the filters to a constant weight at 60 °C. PIM was determined by combusting the filters at 450 °C for 4 h. POM was calculated as the difference between TPM and PIM. The organic content of the seston was calculated as a ratio of the organic and total particulate matter (f = POM/TPM). The PIM and POM from the water and biodeposits were used to calculate feeding variables of mussels [89,90]. Biodeposit filters were treated in the same way as TPM filters.

All the mussels were collected in individually labeled bags and froze until subsequent processing. The mussels were measured for shell length (mm) with a caliper and shucked. Shell was dried and weighed and soft tissue from each mussel was placed in pre-weighed aluminum weighing dish and also dried to a constant weight at 60 °C for determination of tissue dry weight to standardize all feeding variables to 1 g of dried mussel flesh, following the equation:

$$Y_s = Y_e\ (1/W_e)^b \tag{3}$$

where Y_s is the standardized physiological rate, Y_e is the experimentally-determined rate, and W_e is the measured dry body mass. The allometric exponent (b) describes how fast the feeding rate increases relative to body size [91]. We adopted a *b* value of 0.70 for the studied species, as determined by Jones and collaborators [92].

Condition index was calculated as the ratio of dry tissue weight to dry shell weight:

$$\text{CI} = (\text{dry tissue weight}/\text{dry shell weight}) \times 100 \tag{4}$$

Feeding parameters, namely clearance rate, filtration rate, rejection proportion, organic ingestion rate, absorption rate, absorption efficiency, and selection efficiency, were calculated according to Table 3.

Table 3. Explanation and calculation of physiological feeding parameters.

Term, Units	**Explanation** (Galimany et al. [85])	**Calculation** (according to biodeposition methods in Galimany et al. [59] and Iglesias et al. [93])
Clearance rate (CR), L·h^{-1}	Volume of water cleared of particles per unit of time	(mg inorganic matter from both feces and pseudofeces per unit of time (mg·h^{-1}))/(mg inorganic matter (PIM; mg·L^{-1}) in the water)
Filtration rate (FR), mg·h^{-1}	Mass of particles cleared from the water per unit of time	CR × TPM (mg·L^{-1}) in the water
Rejection Rate (RR), %	Percentage of particles filtered but rejected	[(total rejection rate mg·h^{-1})/(total filtration rate (mg·h^{-1})] × 100
Organic ingestion rate (OIR), mg·h^{-1}	Amount of particulate organic matter ingested per unit of time	(CR × POM (mg·L^{-1}) in the water)—(rejection rate of organic matter (mg·h^{-1}))
Absorption rate (AR), mg·h^{-1}	Amount of ingested particulate matter that is absorbed in the mussels' digestive system	OIR—(egestion rate of organic matter)
Absorption efficiency (AE), %	Percentage of particulate matter ingested and retained	(AR/OIR) × 100
Selection efficiency (SE), fraction	Organic food selected from the total particulates in the water	1 − [(organic fraction with pseudofeces)/(organic fraction within total particles available in the water)]

2.2.3. Vertical Profiles of Water Column

Water column profiles of temperature, chlorophyll, dissolved oxygen (DO) and salinity were obtained using an EXO multiparameter sonde (YSI Incorporated) connected to a handheld and extracted with the software EXO 2.1.0.8 (YSI Incorporated 2015).

2.2.4. Chlorophyll *a* Data

Chlorophyll concentration estimations were also obtained with the extraction method. Three replicate water samplings were also collected for chlorophyll *a* determination (200 mL in May and 500 mL in August) from the intake water for the biodeposition apparatus. Water was filtered through GF/F glass fiber filters and stored at −20 °C until analysis. Upon analysis, each filter was placed in a glass tube with 90% acetone and kept refrigerated overnight for 20 h to allow pigment extraction. Samples were subsequently centrifuged at 1000× *g* for 10 min, and the supernatant was drawn for chlorophyll *a* determination using a fluorometer (model 10-AU Turner Designs Inc., Sunnyvale, CA, USA).

2.2.5. Phytoplankton Identification

Water samples were collected for identification of main phytoplankton species. For phytoplankton identification and cell counts, water samples were preserved with 3% acid Lugol's solution (final concentration) and stored in the dark at room temperature [94]. Upon analyses, between 25 and 50 mL samples were settled in Utermöhl chambers for at least 18 h before enumeration using inverted light microscopy [95].

2.2.6. Particle Differentiation and Quantification by Flow Cytometer

For the August samples, size classes of phytoplankton were characterized. Phytoplankton and detritus were analyzed following Li et al. [96]. Upon analysis, 50 mL water samples fixed in formaldehyde were concentrated to 5 mL through centrifugation. Next, 10 to 20 µl of a known count of yellow-fluorescent, plastic microbeads (Polyscience, Inc., Warrington, PA, USA) were added to 1 mL of concentrated water sample as an internal standard for particle counts. Water samples were then analyzed by a FACScan flow-cytometer (B-D BioSciences, San Jose, CA, USA) equipped with a 488-nm laser. Phytoplankton (chlorophyll *a* containing) or "detritus" (non-chlorophyll *a* containing) particles were discriminated based on the amount of red fluorescence detected. Each type of particles was then grouped into three size categories: 2–5 µm, 5–20 µm, and >20 µm, based upon forward scattering of known size single phytoplankton species cultures.

2.2.7. Statistical Analysis

Comparisons were focused on seasonal differences, as the main objective was to assess the suitability of environmental conditions between the two samplings. TPM, POM and PIM in the two seasons were compared using a non-parametric Kolmogorov-Smirnov test (independent samples comparison). Feeding parameters were checked for normality using the distribution fitting model Shapiro–Wilk test. Individual, two-independent-sample comparisons of means with *t*-test at 95% confidence interval were performed to test for differences between seasons in each physiological feeding parameter. For non-normally distributed data, individual comparison of medians with Mann–Whitney W-tests were performed at 95% confidence interval. All analyses were performed using the software Statgraphics Centurion XVII Version 17.1.12 (Statpoint Technologies, Inc., Warrenton, VA, USA).

3. Results

3.1. Depth Suitability Analysis

3.1.1. Bathymetry

Depth requirements for submerged longlines in offshore aquaculture are between 25 m and 100 m depth [20]. The total surface area between those isobaths was calculated to be 235,927 km^2.

3.1.2. Temperature Trends

Comparisons between different averaged decades, 1975 to 1984 and 1995 to 2012, and 2016, in the regions of Offshore Long Island (OLI), Southern New England (SNE), and Gulf of Maine (GM) showed progressively warming temperatures in recent years for all regions, and although summer months in 2016 lacked data, temperatures in that year were consistently the warmest in this study area (Figure 5).

3.1.3. Temperature Thresholds

In the frequency distribution histogram, most of the blue mussel spawnings fell between 8 °C and 16 °C, with fewer events happening at temperature extremes. Within the temperature parameters, however, the number of triggered spawning events was relatively smaller between 10 °C and 14 °C (Figure 6). At temperatures below 5 °C and above 20 °C, spawning events overlapped with other unfavorable effects upon mussel physiological activity, such as slow growth, lower filtration, and mortalities (Figure 6). During winter, when water was homogeneous from surface, the relevance of depth was not as high as summer. Consequently, for spatial maps, larger temperature scales were adopted. As our assumption was that spawning in warmer months should be avoided, the grow-out should be performed in colder waters; however, extreme temperatures limiting physiological activity, as aforementioned, should be also avoided. Therefore, the threshold of 10–14 °C was subsequently used to delimit suitable deployment depths in warmer months. During summer, temperature scales for the spatial maps were divided in smaller scales of 4 °C increments, to more precisely identify the suitable threshold.

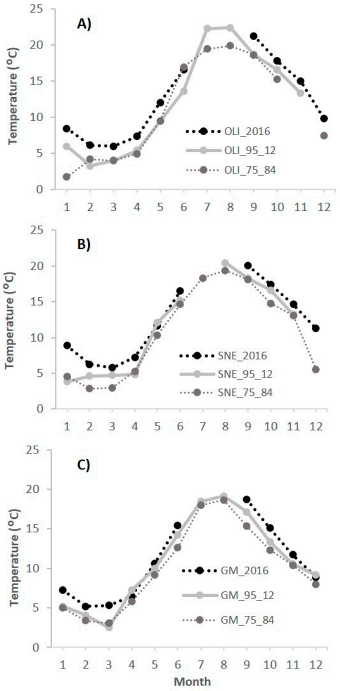

Figure 5. Monthly SST averages showing warming trends in the NE area for three different sectors: (**A**) Offshore Long Island (OLI), (**B**) Southern New England (SNE) and (**C**) Gulf of Maine (GM), in the last decades. Lines show recent 2016 year and in the past 1995–2012 and 1975–1984. The legend for each line is a combination of place and years, for example, OLI_95_12 refers to Offshore Long Island period 1995–2012. There were no summer data for the year 2016, thus, the lines for that year are not continuous.

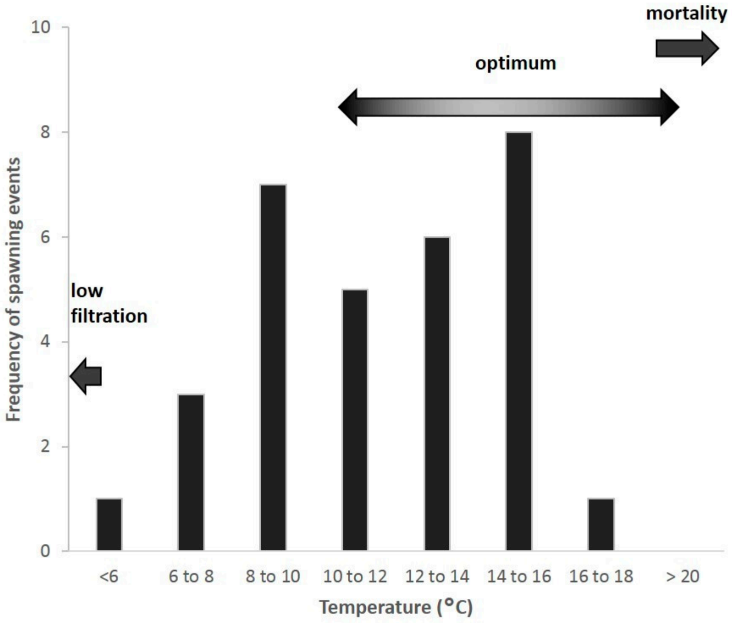

Figure 6. Frequency distribution of reported spawning events, and indication of optimal growth, lowered filtration rate, and mortalities at different temperature thresholds for the blue mussel *Mytilus edulis*, based on Table 1.

3.1.4. Thermal Stratification

In the first top 25 m of the water column, the temperature in the Northeast shelf area varied between −2.06 °C in winter and 30.8 °C in summer during the period from 2005 to 2012. The horizontal distribution of temperature showed significant spatial differences and stratification. Temperature during summer showed a strong decreasing pattern with increasing depth ($n = 659$; $y = 4.520x−89.02$; $R^2 = 0.69$). On the other hand, winter temperature did not show any correlation with depth, although there was a slight trend of increasing temperature with higher depths ($n = 899$; $y = −8.784x + 11.54$; $R^2 = 0.17$). Summer conditions were markedly different at different depths (Table 4). Water temperature was more than 5 °C higher than mean annual temperatures at surface for New England area and higher than temperature anomalies at deeper layers. Summer temperatures at different depths also varied with latitude.

Table 4. Summary of temperature summer conditions (mean ± s.d.) in New England area based on the period of 2005 to 2012.

Depth (m)	Summer Season Minus Annual Mean (T, °C)	North Area (T ± s.d. [a], °C)	South Area (T ± s.d. [a], °C)
0	5.8	16.12 ± 1.75	19.48 ± 1.98
5	5.7	15.80 ± 1.75	19.12 ± 1.99
10	5.4	14.95 ± 1.80	18.24 ± 2.24
15	4.8	13.62 ± 1.75	16.94 ± 2.51
20	4.1	12.26 ± 1.91	15.67 ± 2.70
25	3.7	11.07 ± 1.94	14.48 ± 2.70

[a] s.d. = standard deviations, calculated according to Equations (1) and (2).

3.1.5. Temperature Spatial Distribution

During winter, spatial distributions of temperature showed differences at different locations, Cape Cod being particularly cold and the presence of relatively warmer water in the south of the study area, towards the outer shelf (Figure 7). From the analysis of the spatial maps at different depth layers, the water column was well-mixed from surface to bottom throughout the Northeast Atlantic shelf. No significant changes in temperature with depth were apparent in the spatial profiles, even though the temperature intervals were set to 1 °C, which suggests that the differences were in the decimals.

The decrease in water temperature with depth during summer was visible in the horizontal spatial distributions at different layers of the Northeast Atlantic shelf, and was especially apparent off Long Island, Rhode Island, and Martha's Vineyard (Figure 8). At surface, in most of the Southern New England area, temperatures reached above 20 °C, except for the inner coastal area, where temperatures were usually between 18 °C and 20 °C. The Gulf of Maine was significantly colder, with temperatures between 15 °C and 18 °C, and patches of warmer areas were located north of Cape Cod and in the middle of Stellwagen Bank. At 5-m depth, in the Gulf of Maine, there was a larger area where temperatures were as cold as 14 °C and 18 °C; whereas, water remained largely mixed from surface to 5-m depth in the Southern New England area. The waters off Georges Bank showed relatively lower temperatures, between 10 °C and 14 °C. At 10-m depth, there was no significant change in temperature compared with the upper layers, aside from colder nodules near Shinnecock Inlet, west of Block Island and south of Martha's Vineyard, and north of Cape Cod and Cape Ann. At 15-m depth, however, there was a sharp temperature drop to between 14 °C and 18 °C in the Southern New England area, whereas relatively colder water, between 10 °C and 14 °C, was present in the Gulf of Maine (in more than 57% of the area). At 20-m depth, the temperatures largely decreased to 10 °C and 14 °C in areas in Southern New England (over 30% of the area) and were colder than 10 °C in the coastal area and to the north of Cape Cod, and temperatures further decreased at the depth of 25 m.

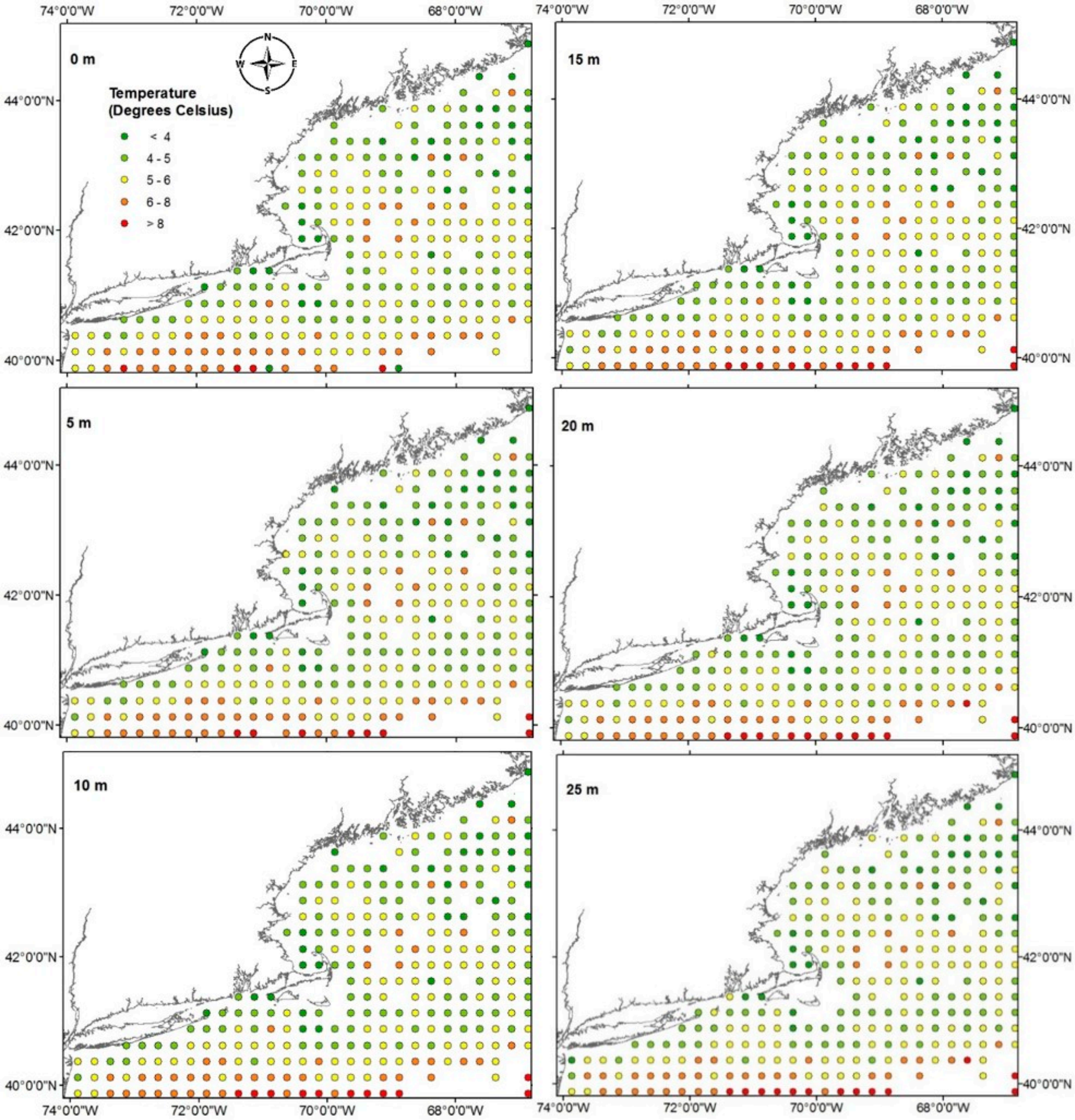

Figure 7. Depth distribution of temperatures shown as averaged means of the years 2005 to 2012 in winter.

3.1.6. Thermal Characteristics of Prospective Farming Sites

Temperature was significantly different between stations (Figure 9) both in winter and summer (df = 5, Kruskal–Wallis statistics (H) = 29.89, $p < 0.01$; df = 5, H = 14.48, $p < 0.01$, respectively); temperature variation with depth was not significant in winter but pronounced in summer ($R^2 = -0.03$, F = 0.14, $p = 0.708$; and $R^2 = 0.47$, F = 38.33, $p < 0.01$, respectively; Figure 9). Winter temperature profiles showed a typically mixed water column for the season in the study area, with homogeneous temperatures of 4.5 °C throughout the water column (Figure 9). Station 5 had the coldest sea surface temperature (3.6 °C), but temperatures increased by 2 °C within the first few meters, and at 10-m depth, temperature was 5.5 °C. In summer, sea surface temperature along the study area showed differences of up to 5 °C between Long Island, Rhode Island and south Massachusetts (stations 1, 2, 3 and 4; 40.625° N–42.125° N latitude) and the area north of Massachusetts and New Hampshire (stations 5 and 6; 42.625° N–43.125° N latitude; Figure 9). The summer thermocline was located between 5 and 15 m depth in all stations. As expected, higher latitude stations were less stratified than lower latitude ones, with station 1 near Long Island showing the most pronounced thermocline of all. Station 1, however, behaved similarly to higher-latitude stations at depths higher than 15 m, with temperatures of 14.7 °C, 11.9 °C, and 10.3 °C at 10 m, 15 m and 20 m depth, respectively. Stations 2 and 3 showed very similar temperature profiles, with comparatively warmer temperatures, as the temperature decrease rate with depth was smaller (1 °C decrease in temperature with five times the depth; a = 6.71 and a = 5.0, respectively) than the other stations (a = 1.5 to 3.9).

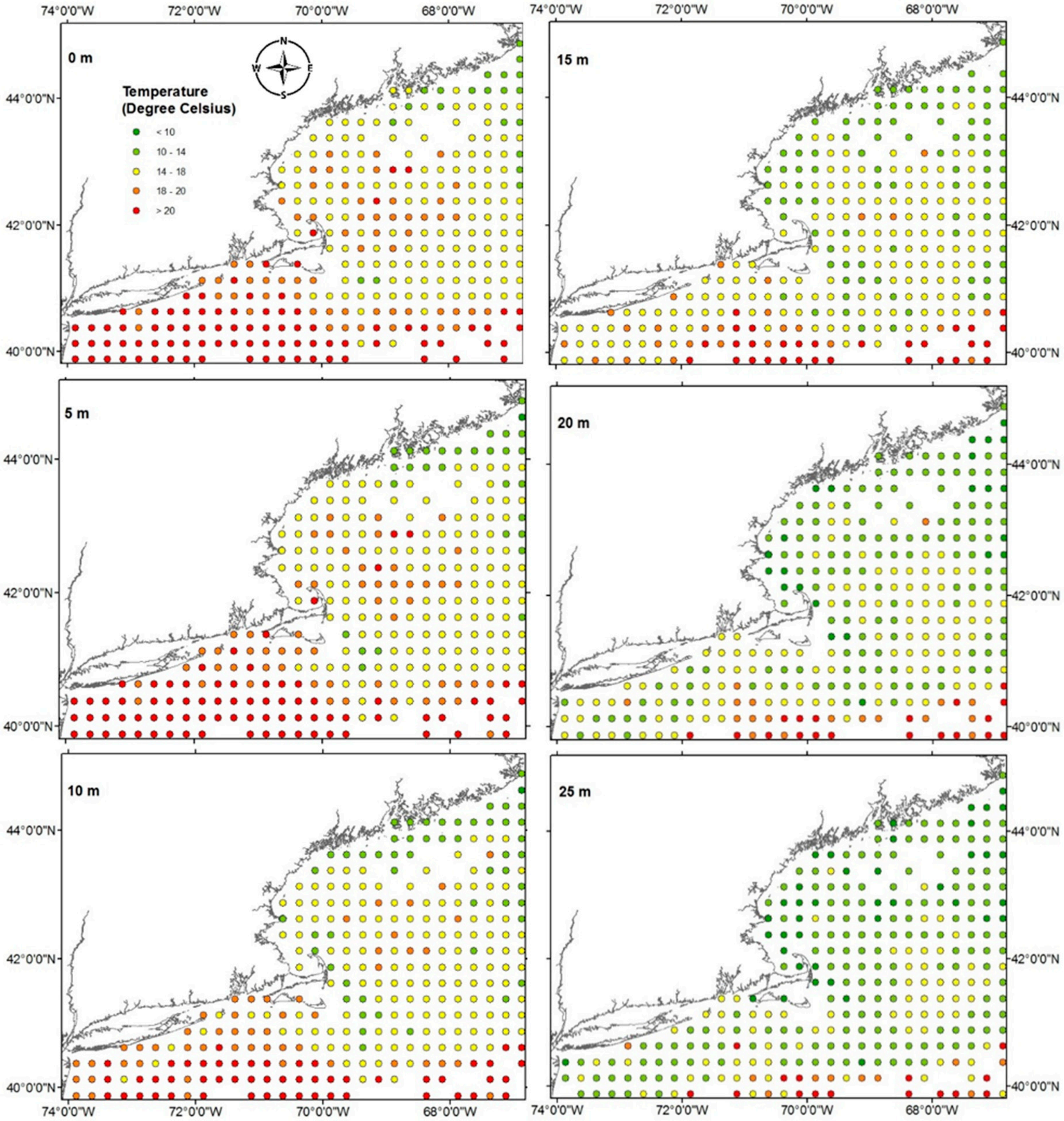

Figure 8. Depth distribution of temperatures shown as averaged means of the years 2005 to 2012 in summer.

3.1.7. Chlorophyll *a*

Chlorophyll *a* profiles in different regions of NE shelf confirmed the biomass patterns seem in the remote sensing data, as chlorophyll *a* concentrations were consistently higher than 0.5 mg/m^3 both in winter and summer cruise samplings (Figure 10). Throughout the region, as shown by the profiles of different sampling localities, the chlorophyll maximum layer was located between 13-m and 30-m depths. The chlorophyll maximum was deeper (between 18 m and 30 m depth) in the southern areas, including offshore Long Island and Southern New England, than in the northern areas (between 13-m and 23-m depth; Figure 10).

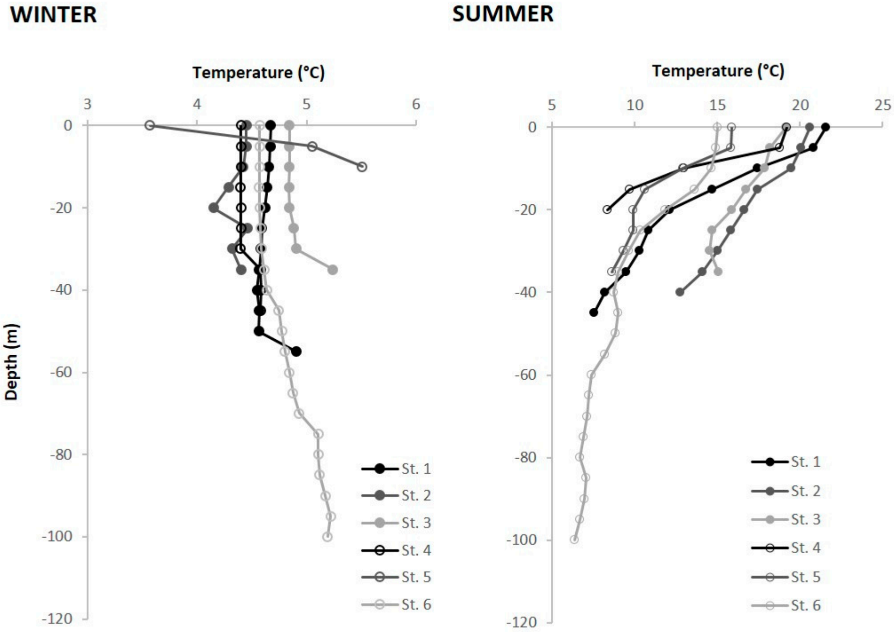

Figure 9. Temperature vertical profiles in winter and summer at stations 1 to 6.

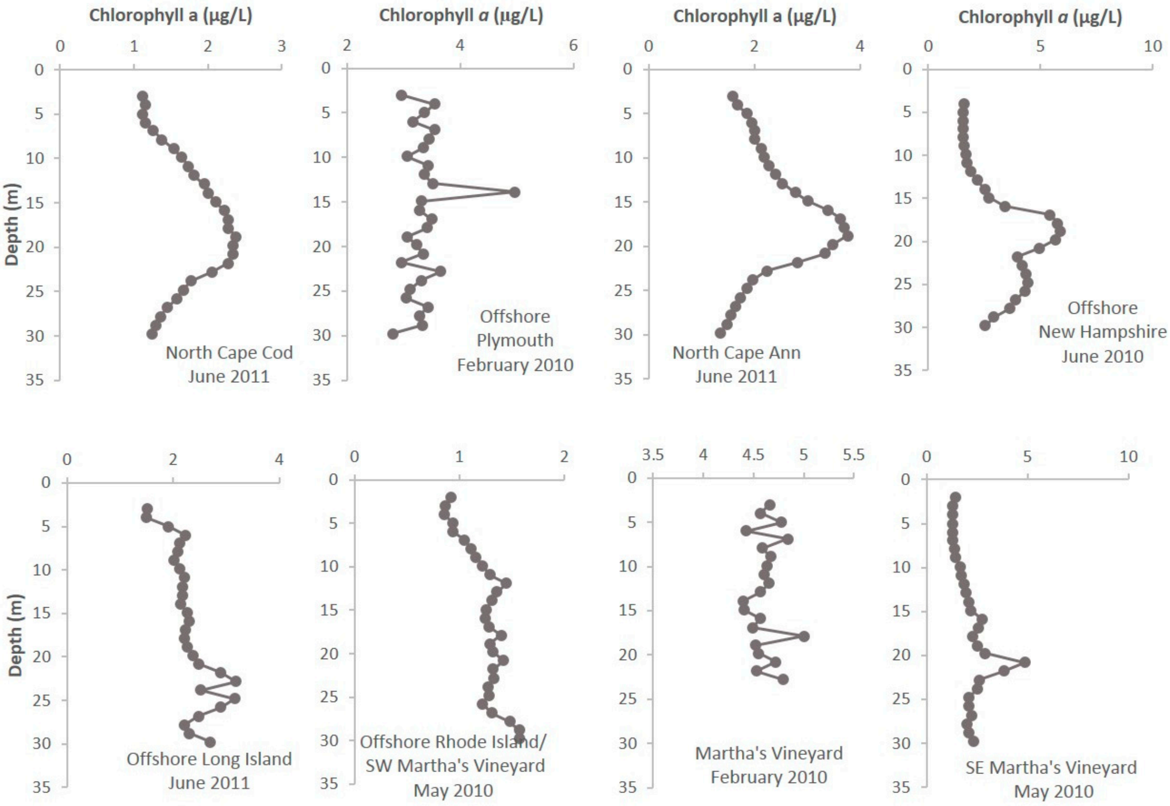

Figure 10. Vertical profiles of chlorophyll *a* at different regions along the northeast shelf during the years of 2010 and 2011, lined by region. Note the chlorophyll maximum position in the water column situated between 13-m and 30-m depth at all stations.

3.2. In Situ Biodeposition

3.2.1. Environmental Characteristics

In May, salinity varied between 26.8 and 29.9 and increased with depth (Table 5). In August, salinity and DO both increased with depth, with S = 30.08–31.13 and DO between 5.89 and 7.25 mg·L^{-1}. Conditions at approximately 15 m are shown in Table 5. Sonde profiles of temperature and chlorophyll *a* are shown in Figure 11. The water column was mixed in the first 10 m in May, and as expected, stratification was higher in summer, when thermocline was shallower starting at 6-m depth. Sonde profiles of chlorophyll *a* concentration increased to the maximum observed values at approximately 14-m depth (Figure 11). Extracted mean chlorophyll *a* values from the pumped water of 15-m depth were 2.08 ± 0.24 μg·L^{-1} in May and 2.09 ± 0.06 μg·L^{-1} in August. At some depths, the chlorophyll concentration measured with the sonde did not match the extracted values, as the latter in general showed always lower values. TPM, PIM, POM and f and were not significantly different ($p > 0.05$) between seasons (Table 5).

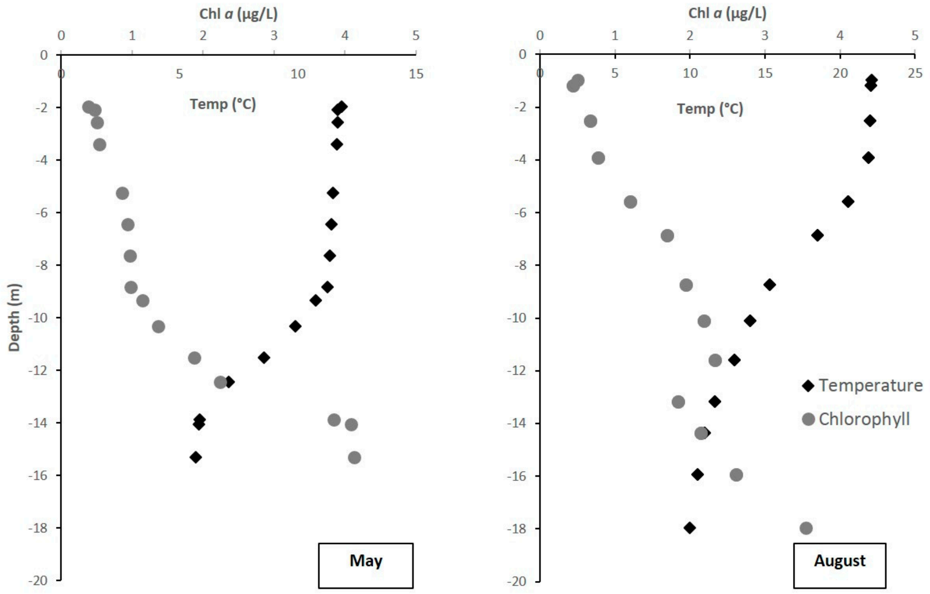

Figure 11. Vertical profiles of temperature (°C) and chlorophyll a (μg.L^{-1}) at the NEMAC farming site in the two seasons.

Table 5. Experimental conditions (mean ± s.d.), as mussel traits and seston characteristics at approximately 15-m depth.

Sampling Date									
Spring (May)	**Environmental conditions**	**T (°C)**	**DO (mg/L)**	**Sal**	**Chl *a* ^{b} (µg/L)**	**TPM (mg/L)**	**POM (mg/L)**	**PIM (mg/L)**	**f (ratio)**
		5.68 ± 0.09	11.08 ± 0.70	29.77 ± 0.08	2.08 ± 0.24	1.25 ± 0.38	0.88 ± 0.18	0.37 ± 0.22	0.70
	Mussel characteristics	**Length (mm)**	**CI (%)**	**GTT (h)**					
		54.7± 3.50	31.67 ± 3.23	1.5					
Summer (August)	**Environmental conditions**	**T (°C)**	**DO (mg/L)**	**Sal**	**Chl *a* ^{b} (µg/L)**	**TPM (mg/L)**	**POM (mg/L)**	**PIM (mg/L)**	**f (ratio)**
		10.51 ± n.a.	7.25 ± n.a.	31.04 ± n.a.	2.09 ± 0.06	1.19 ± 0.45	0.86 ± 0.19	0.37± 0.34	0.72
	Mussel characteristics	**Length (mm)**	**CI (%)**	**GTT (h)**					
		69.0 ± 3.64	26.84 ± 6.41	1.5					

^{b} = Chl *a* values of extract chlorophyll from water samples.

Phytoplankton composition was characterized by the following most abundant species: *Chysochromomulina spp.*, *Cryptomonas* spp., *Thalassionema* sp., *Thalassiosira* spp. in May and *Rhizolenia alata*, *Euratium fusus* in August and the most abundant phytoplankton size class was in the range of 5 to 20 µm, followed by the particles of 2 to 5 µm sizes (Table 6).

Table 6. Phytoplankton size classes and abundance (mean ± s.d.) during biodeposition measurements in August.

Size Class (µm)	Particle Abundance		Ratio
	Phytoplankton (cell/mL)	Non-Phytoplankton (cell/mL)	
2–5	360 ± 37	672 ± 224	0.54
5–20	805 ± 217	611 ± 285	1.32
>20	118 ± 57	327 ± 60	0.36

3.2.2. Mussel Performance

Averaged GGT was similar in both seasons and equivalent to 1.5 h (Table 5). Condition index in mussels showed average values in May (~31%) and lower values in summer time (August).

Most feeding parameters were significantly different between seasons for CR, OIR, AR, AE but not statistically different for FR, RR (%) and SE. In particular, AE was lower in summer (~36%) and higher in spring (~87%). CR and FR decreased from the spring season to the summer season (Table 7).

Table 7. Mean values (± s.d.) of physiological responses mussels standardized by 1 g weight. (*) Significant ($p < 0.05$) differences between seasons.

Season	CR (L/h) *	FR (mg/h)	RR (%)	OIR (mg/h) *	AR (mg/h) *	AE (%) *	SE
Spring (May)	1.15 ± 0.90	0.92 ± 0.72	21.67 ± 10.80	0.96 ± 0.74	0.82 ± 0.66	87.18 ± 24.13	0.91 ± 0.66
Summer (August)	0.51 ± 0.31	0.49 ± 0.30	15.37 ± 7.66	0.43 ± 0.26	0.20 ± 0.22	36.15 ± 21.63	0.94 ± 0.31

4. Discussion

4.1. General New England Area

Among the many environmental factors affecting blue mussel mariculture offshore of New England, temperature was considered as the most important in the present study, especially in the face of temperature warming trends in the area. Temperature triggers reproduction and leads to an overall low condition of individuals, also affecting byssus tenacity and production and the ability of the mussels to remain attached to the farming rope in a submerged mooring system placed in an exposed site. An important technical issue is the height of the water column in the area where a farm is to be placed, known to be necessarily over 25 m, which encompasses over 235,000 km^2 in the Northeast shelf. The actual depth to which longlines should be submerged, however, has not been evaluated thoroughly. We decided, as a premise, that farmers should strive to keep the cultivated mussels in relatively low temperature waters as much as possible throughout the grow-out season, but avoid waters below 5 °C to avoid adverse effects such as delayed growth, lowered filtration, and avoid weakened attachment strength and possible mussel dislodgments.

In the temperate climate of the study area, surface water temperature was near freezing in winter, but during the studied period, the top 25 m of the water column was completely mixed and above 5 °C, with minimum differences between southern and northern parts of the studied area (Figures 7 and 9). In summer, however, temperature varied greatly with depth; surface layer exhibited temperature patterns several degrees higher than deeper layers (Figure 8) and the thermocline extended as deeply as 15 m (Figure 9). Temperature can reach several degrees above the annual average mean in summer months, more than 5 °C in surface layers (0–10 m), 4 °C at middle layers (15–25 m) and 2 °C at greater depths. Consequently, the depth of the longlines exerts another important component for the shellfish culture. In the NE where longlines have been recently usually submerged to 10-m depth, following legal advice (K. Madley 2017, *personal communication*), the ropes have been placed in relatively warmer temperatures than if relocated to deeper layers that are more temperature-suitable for the blue mussels. Considering the ecologically-optimal temperature threshold between 10 °C and 14 °C, farming sites located in the north of New England should have the mussel ropes submerged to at least 15 m depth, a depth at which 57% of the area was within the aforementioned temperature threshold. In contrast, farm sites in the southern study region should submerge the mussel ropes to at least 20-m depth, which translated to 33% of the area being within ideal temperatures. Nevertheless, it is important to note that summer temperatures had an averaged standard deviation of ±1.75 °C at 15 m for the north area and ±2.70 °C at 20 m for the south area, leading to the conclusion that the ideal depth can vary annually towards slightly shallower or deeper zones (Table 4). Furthermore, a larger area in the southern part of our area of study may be suitable for farming using the 20-m threshold, as the yellow-coded stations indicate temperatures within 14–18 °C, corresponding to an additional 46% of the area. Moreover, as water temperature distribution was analyzed in horizontal layers within every 5-m depth, the suitable depths reported in this study where suitable environmental conditions would be found should not be interpreted as absolute values but instead considered as approximations. In addition, one should acknowledge that those might change yearly, a fact that nonetheless does not demerit the guidance provided by this study for successful long-line deployment. Depth submersion is usually based on different aspects and it is important to note that it should be considered locally. For example, in Germany, Buck [23] suggests depths of 6–7 m for mooring systems in a 12-m-deep site to avoid waves while also allowing for no contact of ropes with the bottom. In the Gulf of Maine, during preliminary trials targeting successful spat collection, Langan & Horton [29] suggested depths between 12 and 17 m, which corroborates our estimate for general mussel performance in the north part of New England. Increases in depth deployment of longlines during grow-out were used as a strategy to avoid second setting of mussels in existing production lines in Newfoundland (Canada), north of the present study area [97], which can be another positive result from deeper mussel deployment. In Norway, mussel growth was positively related with the depth of socked mussel lines, although the depths at which they were deployed were rather shallower than in this study, ranging from surface to 5 m [98]. Furthermore, the depths suggested in the present work also contribute to minimizing the common problem of cultured mussel predation by marine ducks that can dive to a maximum of 50 m but often prefer to prey upon mussels in shallower depths of around 10 m [7,99].

Biofouling may also be indirectly addressed through the suggested depths of culture. As an increase in biofouling is expected when water temperature is warmer [100], this environmental suitability analysis based upon lower temperature thresholds is also expected to help decrease fouling intensity and promote farming improvement when mussel ropes are set deeper in the water column [101].

As expected, stations off of Southern New England were warmer than those in higher latitudes of the Gulf of Maine, although sites within each area showed similar temperature profiles during winter. Since stations 2 and 3 near Block Island and Martha's Vineyard were relatively warmer compared to the others, there is indication that more appropriate locations for siting an offshore farm are situated along offshore Long Island or regions north of Massachusetts. The location of station 1 on the ocean side of Long Island poses a spatial advantage over the other Southern regions as it gets colder with depth faster, thus allowing for shallower mooring of longlines.

Areas where summer temperatures are relatively high need not necessarily be excluded from being considered as farming areas. Since in winter, the water column is homogeneous and the entire shelf extension experiences similar temperatures, differences in temperature during summer eventually dictate the choice of farming areas. Farming management techniques in relatively warm locations can include the positioning of mussel ropes lower in the water column in comparison to colder areas, or the seasonal positioning of mussel ropes deeper during warmer months. Adjustments in depth deployment should not constitute a problem as current designs of longlines allow deployment at various depths [102], and floats usually have incompressible mantles to withstand pressure without losing buoyancy [23]. This especially applies to the Southern New England area, where any specific temperature could be found in greater depths relative to the Gulf of Maine.

Apart from the natural seasonal temperature fluctuation, it is unlikely that abrupt diel changes will occur in this environment, at least in the same range as the one used to induce spawning under laboratory conditions, i.e., thermal shock procedures exposing mussels to differences of temperature of about 10 °C [73]. Although environmental cues that trigger spawning are of brief duration, those that control maturation of gametes are of a more extended time scale [103], thus, it is likely that reproduction would indeed be minimized following our temperature suggestions. Caution should be exercised in relation to the depths reported here when considering different areas other than the main studied region, because although averaged temperature values were considered for our area, in general, temperature sensitivity for mussels acclimated in different areas may vary. For instance, in some places in Europe, the temperature threshold that triggers mortalities is considerably lower than in North America (up to 37 °C in the American East Coast, 30–31 °C in Europe and 28.2 °C in Australia [35]), and the same is true for spawning thresholds, in particular in European countries (Table 1). Therefore, if the local temperature thresholds triggering diverse physical effects are particularly different from overall thresholds for the species elsewhere, considerations for the establishment of ideal depths, we reinforce, should take a local approach.

Food availability, somewhat surprisingly, does not seem to be a limiting factor for blue mussel aquaculture placement throughout the study area. Chlorophyll concentrations higher than 0.5 $\mu g \cdot L^{-1}$ are considered sufficient for the successful culture of the blue mussel [20]. According to published data, the lower temperatures in the study area will not make mussels close their valves and stop food intake because *M. edulis* is able to clear the water of food particles in near-freezing temperatures, although clearance rates can be lowered thus, and so can growth [34,104–106]. Nevertheless, food limitation can be avoided by ensuring that mussel ropes are in the mixed layer close to the subsurface chlorophyll maximum. Since some studies suggest that filter-feeders can potentially reduce phytoplankton available for wild populations (see for example: [107], although more unlikely in a highly motile offshore environment than coastal bays, hanging mussels at locations or depths of high natural productivity is a valid mitigation planning strategy [15]. Chlorophyll *a* profiles for stations geographically sparse along the study area showed the chlorophyll maximum situated between 13- and 30-m depth, coinciding with the depths found to be ideal for placement of mussel ropes based on temperature. Although the chlorophyll data were obtained with high-resolution CTD profilers, the data were not calibrated, thus, these results should be interpreted with caution. Nonetheless, they are still valid for the present work as interpretation of local general trends.

4.2. *Experimental Farm at Cape Ann*

In situ measurements corroborated the *a priori* depth suitability analysis with respect to temperature and food. At the experimental farm, particulate matter quantity and quality and chlorophyll *a* remained relatively stable (Table 5), but mussel feeding rates did vary with the seasons studied. Despite the limited number of samplings, the similar positive results of food availability and quality are noteworthy. Temperature was the only measured factor fluctuating appreciably, but variations were within the optimum expected threshold for the target bivalve species considered in the first-stage analysis of this study, as temperature thresholds in colder ($T > 5$ °C) and warm season ($T = 10$–14 °C) were confirmed.

The condition index of mussels was moderate but declined late summer, possibly following a spawning season, which can influence meat yield and decreased mussel condition [108]. At the sampled depth (approximately 15 m), the spawning season would expectedly be delayed to late summer time (August). Although mussels were grown submerged in colder and deeper layers, it is possible that before the second sampling, some of the mussels spawned, as some spent mussels were indeed observed during the shucking process. Nonetheless, the condition of mussels were above reported CI values in the well-known mussel farming area of Prince Edward Island (CI = 8–27 [109]), from where the USA imports most of its fresh mussel to satisfy current demand [110].

In the present study, temperature seems to be the most influent factor affecting the filtration and clearance rates of mussels through a negative relationship. Comeau et al. [34] described that the number *Mytilus edulis* that were actively filtrating in their experiment decreased with decreasing temperatures (from 100% to 17% when temperature was decreased from 9 °C to 0 °C). For the clam *Hiatella arctica*, in a temperate region, Petersen et al. [111] reported ceased filtration when water achieved temperatures higher than 8 °C, but increased filtration rates when temperature was increased from −1 °C to that threshold. Similarly, CR was significantly different between seasons and CR and FR lower in the summer time (Table 7). Several studies show differences in feeding behavior between bivalves acclimated to tropical and temperate regions [112], thus, it seems likely that bivalves from the offshore farm, adapted to constant low temperature waters during most of the grow-out, would be more sensitive to the effects of seasonal temperature water warming, even if temperature is relatively low, such as 10 °C.

At the farm site food availability was again confirmed and, surprisingly, chlorophyll *a* concentration did not change considerably with season and maintained levels fourfold the limiting threshold for mussel farming suitability (0.5 $\mu g \cdot L^{-1}$), satisfying even the more conservative limits (1 $\mu g \cdot L^{-1}$ [20]). Therefore, initial existing concerns [85] that offshore areas would not be able to sustain bivalve shellfish aquaculture because of possible limiting phytoplankton levels are unfounded. The studied location has abundant food and of high quality, as the seston during the two studied seasons was of high organic content (f ~ 0.70; Table 5). Local 'f' values in the studied farm corresponded to those reported in coastal waters [59], which are known to be more eutrophic. Offshore Cape Ann's 'f' value was higher than locations such as Mahone Bay in Canada or Rías Baixas of Galicia in Spain, where productive mussel farming activities are performed [113,114]. The current farm has similarities with other previously studied American offshore sites with respect to good ratios of organic to inorganic contents in particulate matter too, such as in offshore California (10 km off of Long Beach, f = 0.80), where a commercial farm is ongoing, in contrast with Martha's Vineyard location in Massachusetts (in Martha's Vineyard Island), where organic percentage is poor (f = 0.44; [85]), but was, in the past, considered to be a potential site for offshore aquaculture.

Filtration rates are known to be maximal if the concentration of chlorophyll *a* is higher than the limiting threshold of 0.5 $\mu g \cdot L^{-1}$, which could most likely make the filtering activity cease in blue mussels [87,115,116]. On the other side of the spectrum, too many particles in the water reduces filtration rates by saturation, if a threshold close to 5000 to 8000 algal cells.mL^{-1} or equivalent to chlorophyll concentrations from 6.3 to 10 $\mu g \cdot L^{-1}$ is reached [117]. Mussels in the studied offshore area were filtrating slowly (FR = 0.48–0.92 $mg \cdot L^{-1}$; Table 7), however, food was always abundant (~2 $\mu g \cdot L^{-1}$, the same concentration that resulted in maximal filtration rates in the studies of Riisgård et al. [117]) and filtration, at those conditions, could be lowered to maximize absorption efficiency.

Pseudofeces production was very limited and produced only by six mussels in the first experiment and two mussels in the second sampling. Jørgensen [83] stated that mussels do not produce mucus if undisturbed and also do not produce pseudofeces if the seston in the water is low. Pseudofeces are composed not only of material rejected by the palps based upon particle composition, but also particles in excess of the gut's processing capacity [118]. Therefore, pseudofeces production can be both a mechanism for protecting the gill from overloaded particulate material and for sorting edible particles from inorganics [58,83]. According to Jørgensen [83], above a critical concentration of 1 $mm^3 \cdot L^{-1}$, the particulate material imbedded in mucus strings would be eliminated as pseudofeces. In our sites, TPM was low (1.25 and 1.19 $mg \cdot L^{-1}$, roughly equaling 1.04 and 0.99 $mm^3 \cdot L^{-1}$ in May and August, respectively) and accordingly, particles could be processed by mussels without almost no formation of pseudofeces. TPM in May was slightly higher than in August, and mussels indeed produced relatively more pseudofeces in the first month, although the difference in concentration of TPM was minimal. The lack of pseudofeces production, as expressed by inexistent rejection rates, was already reported at another offshore sites in Long Beach, California [85], where particulate matter is also low, possibly showing a trend in offshore sites.

Absorption efficiency represents the effectiveness with which material cleared from suspension is absorbed during passage through the digestive system [119]; as it was higher in spring, it shows better adaptation of mussels to the environmental condition in the colder season, corroborating with the results of Galimany et al. [59] which found CR and AE reduced at higher water temperatures. On the other hand, selection efficiency did not differ between seasons, which is again consistent with previous work that found SE to be negatively related to the organic content of seston [58], represented here as 'f'. Considering the fact that 'f' did not change in the two sampled seasons (Table 5), SE should remain almost the same, as was indeed the case.

It is well documented in cytometric studies that mussels, in addition to optimally filtering particles between the 3–5 μm range, namely nanoplankton, are also efficient in selecting particles of 1–2 μm diameter (picoplankton), although with a reduced efficiency rate of 50% [120,121] and even bacteria with sizes from 0.3 to 1.0 μm [122–124]. It is believed that the lateral-frontal cilia play a role in bivalve feeding, creating a small sized mesh (~0.5 μm [125]). That ability is proven in embayments, where picoplankton (<2 μm) is dominant and where mussel farming thrives, such as the famous mussel production regions of Prince Edward Island [126]. The most abundant phytoplankton size in the study area measured was between 2 and 20 μm, but sizes were mostly larger than 5 μm, and therefore, food was readily available to mussels. Even the percentage of plankton with smaller sizes in the New England area [96] should not impose limitations to the ability of mussels to utilize local food efficiently. Furthermore, mussels from the current studied offshore farm grew supposedly at the same rate as mussels grown in coastal areas and were cleaner (E. Maney 2017, *personal communication*), confirming both food availability and lower biofouling incidence, which may be an indirect result of longer exposures to colder temperatures than coastal areas [127].

In general, feeding parameters generally decreased in summer, which, according to our quantitative measurements, can be attributed only to the sensitivity of mussels to seasonal water 'warming', as they are considered acclimated to cold waters. In fact, feeding parameters, such as CL, FR, OIR, and AE, were similar to previous studies in the summer season (see July sampling of Table 4 in Galimany et al. [59]), although organic content was higher offshore than in those coastal studies. This positive trait of the offshore areas did not show as an apparent advantage in feeding behavior in offshore-grown mussels.

There are many possible conceptual reasons for the apparent disconnection between feeding and environmental parameters, which in general were stable throughout the seasons. For instance, high variability in mussel clearance rates and filtration rates are not only due to individual variability in mussel performance, but also to the fact that different studies used allometric relationships based on either weight or shell length and allometric exponents for weight (b-value) that falls in a broad range [91]. Additionally, *Mytilus edulis* should be open and continuously filtering to obtain enough food and maintain the growth efficiencies found in nature [120]. It is possible that the mussels successfully performed in the area because of the stable water characteristics allowed the constant open state of the valves. Therefore, although mussels seemed to feed slowly offshore, they seemed to compensate it with high absorption rates and maintain their development. Nevertheless, farming offshore, as illustrated by this in situ experiment, is feasible in terms of productivity related to the environment.

A last important consideration in this work is that successfully minimizing the possibility of spawning through the mooring of longlines in cold waters also implies that collection of within-farm spat would be limited, although, as aforementioned, spawning could happen. In the northeast US, spat availability is a considerable constraint because relocation of spat collected in coastal areas is legally supervised to prevent the spread of shellfish diseases. This is the main reason why previous studies have considered mussel spat availability in a proposed farming area as the determinant [128,129]. Within-site collection of spat is unlikely because the duration of planktonic larval stage in mussels, before the pediveliger stage ready to settle on a hard substrate, typically ranges from one to four weeks and is related to temperature [37,130]. This is enough time to allow larval advection away from the farm site by currents, but similarly spat to be collected on offshore sites could have originated from coastal areas and estuaries, which are natural larval traps [72]) and provide a more successful source of spat. Nevertheless, spat settlement was not a concern in the particular offshore farm studied (Figure 4B). Spat for farms can also be obtained from remote setting or from hatcheries. Trials for laboratory seed production are under way with the goal of providing a reliable source of mussel seed to farmers at any time of the year [56].

Key research gaps in offshore aquaculture are the suitability and the performance of selected species under offshore conditions, in addition to site selection criteria [6]. Although in situ samples were limited to the two seasons in one offshore site, the present research addressed both gaps and opens a range of opportunities for similar research efforts in candidate sites.

5. Conclusions

Shellfish farming in US EEZ has been, until the present, based upon trial and error, with regulatory practices still being developed. Lease grants are rather heterogeneous and decided on a case-by-case basis. The depth at which to submerge the longlines and mussel ropes currently is addressed in deference to vessel traffic while disregarding environmental characteristics that eventually determine the success or failure of this aquaculture business. The present study has contributed to the development of offshore mussel aquaculture in several ways: 1. Provided an environmental suitability analysis of blue mussel offshore aquaculture covering a large area of the NE; 2. Added to the supporting literature of applied aquaculture by highlighting the importance of considering suitable depths at which to place the submerged longlines in the water column based upon the target species ecology, especially targeting mussel self-support; 3. Identified suitable depths for the submersion of longlines based upon optimal temperatures and abundant, high quality food. 4. Validated suitability of farming in federal waters by assessing performance of mussels currently being farmed at experimental status.

The rigorous winter season does not seem to be a major concern relating to ideal depth of mussel ropes because temperature is uniformly distributed vertically, but summer is a critical period that requires attention against losses of production from low performance and diversion of metabolism to reproduction and weakening of byssal attachment, possibly leading to drop-off. Based on our environmental analysis, however, we suggest mussel ropes should be submerged at a minimum of 15-m depth in the northern areas of New England, including the Gulf of Maine, and 20-m depth in southern areas. Although the depth is not absolute, approximately shallower or deeper longlines will still take advantage of the conditions discussed.

Our results at the NEMAC offshore farm, at the suggested 15-m depth, confirmed excellent local environmental characteristics and mussel performance that was at least as good as established productive farms in coastal areas. As an example, offshore Cape Ann proved not a limiting environment and is indeed a good candidate to host a productive offshore farm for commercial purposes. However, we recognize that social and legal elements should be incorporated for a more holistic approach to siting decisions, not only to the aforementioned site but in any new candidate farm.

In relation to local oceanographic environmental characteristics, the most favorable areas for commercial offshore mussel aquaculture are off Long Island, north of Cape Ann and off New Hampshire, instead of Martha's Vineyard, which had been regarded as a potential site for offshore mussel farming.

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