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**THE INFLUENCE OF ABIOTIC AND BIOTIC FACTORS ON TWO  
NUDIBRANCHS FEEDING UPON *Membranipora membranacea* IN THE  
SOUTHERN GULF OF MAINE**

**BY**

**MEGAN I. McCULLER**

**B.S., Marine Biology, Texas A&M University at Galveston, 2008**

**THESIS**

**Submitted to the University of New Hampshire**

**in Partial Fulfillment of**

**the Requirements for the Degree of**

**Master of Science**

**in**

**Zoology**

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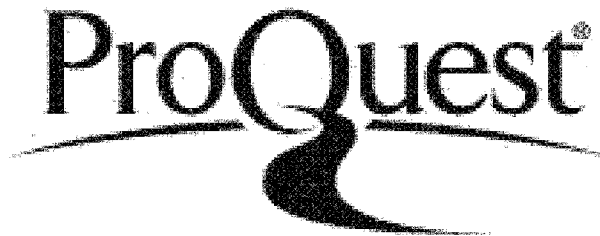


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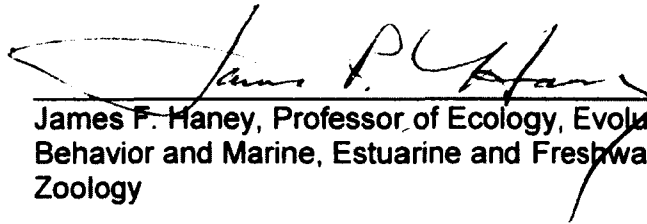


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\_\_\_\_\_  
Thesis Director, Larry G. Harris, Professor of Biology and  
Marine, Estuarine and Freshwater Biology and Marine  
Sciences and Zoology



\_\_\_\_\_  
James F. Haney, Professor of Ecology, Evolution and  
Behavior and Marine, Estuarine and Freshwater Biology and  
Zoology



\_\_\_\_\_  
Walter J. Lambert, Professor of Biology, Framingham State  
University

8/13/2012

\_\_\_\_\_  
Date

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## ABSTRACT

### INFLUENCE OF ABIOTIC AND BIOTIC FACTORS ON TWO NUDIBRANCHS FEEDING UPON *Membranipora membranacea* IN THE SOUTHERN GULF OF MAINE

by

Megan I. McCuller

University of New Hampshire, September 2012

The abiotic (temperature and flow rate) and biotic factors within fouling communities at three marinas located along the southern Gulf of Maine from June to December in 2010 and 2011 were surveyed. The goal of this study was to determine what is driving the recent population increase of the nudibranch, *Corambe obscura*, and whether the native nudibranch, *Onchidoris muricata*, is transitioning prey species. In addition, the affects of temperature on aspects of *C. obscura*'s life history were determined by laboratory experiments.

Results suggest that abiotic factors influence basic community members such as the kelp host, *Saccharina latissima*, and the invasive bryozoan, *Membranipora membranacea*, biotic factors such as settlement substrate and prey species are more important to the predatory nudibranchs. Consequently, while *C. obscura*'s presence would not be possible without the presence of *M. membranacea*, temperature has allowed them to have high turnover rates and reproduction which increases their population size.

## INTRODUCTION

Interactions among species combined with the influence of abiotic factors on the biotic environment results in diverse communities. Intrinsic qualities of individuals such as growth and reproduction rates in the community may further muddle extrinsic interactions with other species or the environment (Weis 2010). Introduced species increase community complexity and may make communities more susceptible than the native state to environmental changes, as interactions and balance between organisms in the marine environment are complex and fragile (Ruiz *et al.* 1997, Ruiz *et al.* 1999, Zacharias and Roff 2000). Marine communities are capable of changes within short periods of time relative to terrestrial systems (Steele 1985, Carr *et al.* 2003), therefore, they are ideal to study how communities change over time due to non-native species.

Human transport of aquatic species by boat removes dispersal barriers at exponential rates and facilitates invasions (Perron 1981, Carlton 1985, 1987, Grosholz and Ruiz 1996). Invading species often fail to survive in new environments, however, those that do survive may alter native community structure (Ruiz *et al.* 1999). In addition to anthropogenic introductions, range expansions of natural or introduced species may also occur. Both types of introductions rely on favorable abiotic and biotic conditions to thrive in the new habitat. Addition of introduced species leads to increasing complexity of interactions in marine environments and evolution of the recipient community and its inhabitants (Vermeij 1996).

Temperature plays a substantial role in the range expansion of species (Harris and Tyrrell 2001, Hellberg *et al.* 2001, Roy *et al.* 2001, Hellmann *et al.* 2008, Ling 2008, Gamelin 2010, Pitt *et al.* 2010, Saunders *et al.* 2010, Keith *et al.* 2011). Temperature increases caused by changes in the East Australian Current have allowed for the southward range expansion of the sea urchin, *Centrostephanus rodgersii* (Ling 2008). The European shore crab, *Carcinus maenus*, has been introduced to multiple locations world-wide and is spreading from each respective point of origin based on favorable climate ranges and has the potential to spread even further (Cohen *et al.* 1995, Carlton and Cohen 2003). Temperature is also mediating the expansion of the Asian shore crab, *Hemigrapsus sanguineus*, on the northwestern Atlantic shoreline and may be limiting reproduction of *H. sanguineus* in the extreme north and south latitudes (Gamelin 2010). Persistently cooler water after El Niño periods in the northeast Pacific has allowed Humboldt squid, *Dosidiscus gigas*, to expand their range both north and southward (Ruiz *et al.* 1999).

Ocean currents appear to have an indirect role in the climate-driven range expansion of species (Southward *et al.* 1995). For marine benthic organisms with passive larval dispersal, flow is an important factor in their distribution and settlement (Mullineaux and Butman 1991, Carlon and Olson 1993, Abelson 1997, Hart and Finelli 1999, Gaylord and Gaines 2000, Fingerut *et al.* 2011). An organism's dispersal ability often depends on the amount of time larvae spend in the water column; larvae with extended pelagic periods typically have greater dispersal ability than those with short pelagic periods (Shanks *et al.* 2003,

Shanks 2009). Behavioral aspects of planktonic larvae with high dispersal capabilities can affect the distance they travel (Shanks *et al.* 2003, Shanks 2009), which ultimately increases their chance of finding a suitable settlement substrate (Olson 1985, Hadfield and Koehl 2004, Koehl and Hadfield 2010).

As larval behavior can reduce long dispersal, biological interactions may be just as, or more important than, abiotic factors with regards to range expansion (Jones and Gomulkiewicz 2012). The importance of the species interactions on range expansions is greatly overlooked in comparison to climate change (Davis *et al.* 1998). The aforementioned range expansion of the Humboldt squid, *D. gigas*, allowed them to fill the niche of overfished large pelagic predators such as tuna in order to take advantage of increases in prey fish populations. This biological impact seemed to be an afterthought to this study on climate change (Ruiz *et al.* 1999).

Range expansions specifically in response to new food resources are rare and studied primarily in terrestrial systems. For example, Grey-headed Flying-foxes, *Pteropus poliocephalus*, underwent a southern expansion of their range by establishing small camps in Melbourne, Australia. The increase in food resources due to urbanization allowed extremely large camps to form after 17 years (Williams *et al.* 2006). Availability of food resources contributed to their increased abundance in Melbourne, though climate change may have contributed to their initial expansion into Melbourne (Williams *et al.* 2006).

As the previous example shows, population increases of non-native species may not be instantaneous. The population expansion phase often lags

behind the initial introduction and the length of the lag period depends on abiotic factors and intrinsic properties of organisms (Carlton 1985, Rilov *et al.* 2004, Unmack and Fagan 2004). The natural range expansion of a species may lag if it is only able to maintain a small population in the new range due to the absence of preferable abiotic conditions, habitat, or prey. For example, the invasive Red Sea mussel, *Brachidontes pharaonis*, only began to form massive beds on the Israeli coast after a lag period of 120 years, after environmental changes created preferable habitat that allowed large beds to form when previously small, single beds were prevalent (Rilov *et al.* 2004). In contrast, zebra mussels, *Dreissena polymorpha*, had a very short lag period and quickly became a problem in the US Great Lakes region. The zebra mussels' high fecundity, larval dispersal, and ability to attach to hard substrates allowed them to rapidly expand their distribution (Padilla 2005).

The influence of range expansion depends on abiotic, biotic, and intrinsic factors, which are clearly inter-related and complex. Influence of one specific abiotic or biotic factor is often the focus of studies concerning range expansions of invasive species. Unfortunately, contributing factors other than those set as the focus of studies are often only briefly mentioned.

The southern Gulf of Maine was used to examine abiotic and biotic factors influencing a fouling community which is undergoing complex changes due to a series of invasions. This community is composed of a native kelp species (*Saccharina latissima*), an invasive bryozoan (*Membranipora membranacea*) which negatively affects the native kelp host, and two predatory nudibranchs, one



which has expanded its range from south of Cape Cod, MA to the Gulf of Maine (*Corambe obscura*) and one that is native (*Onchidoris muricata*). This study was designed to answer the following questions: (i) Which factors (temperature, current, host size, prey percent cover) are most important to each community member and how do the interactions of these factors contribute to the population increase of *C. obscura*? (ii) What role does temperature play on feeding, growth, and reproduction of *C. obscura* feeding on a new prey source? (iii) Is *O. muricata* making a transition from native to invasive prey? These questions should give an idea of how each of these factors interact, which may be applicable to similar systems and species.

### **Survey System**

The Gulf of Maine is an ideal area to survey the interactions between the abiotic environment and interactions between native and invasive species because there are a number of epifaunal species that are invaders in this area. The variety of invasive species include the ascidians *Ciona intestinalis*, *Asciidiella aspersa*, *Botryllus schlosseri*, *Botrylloides violaceus*, *Diplosoma listerianum*, and *Didemnum vexillum*, the green alga *Codium fragile fragile*, and the bryozoan *Membranipora membranacea* (Pederson *et al.* 2005).

The invasive species in the Gulf of Maine have been recently introduced leaving possibilities for surveying interactions and temporal changes in community structure. For instance, lush kelp beds are removed by urchin fronts, resulting space is filled by *Codium fragile ssp. fragile*, which is now fed upon by

the generalist algae-feeding sacoglossan, *Placida dendritica* (Harris and Mathieson 2000, Trowbridge 2004, Harris and Jones 2005). Another example in the Gulf of Maine is the interaction between *C. maenus* and *H. sanguineus*. Both of these crab species are invasive, but *H. sanguineus* was introduced years after *C. maenus* (Tyrrell and Harris 1999). *H. sanguineus* populations have recently increased, and they now appear to be outcompeting *C. maenus* in rocky intertidal habitats (Griffen and Delaney 2007).

Kelp blades represent small ecosystems on which this bryozoan and its nudibranch predators live, making it simple to observe over time. Furthermore, this fouling community is an opportunity to study interactions between invasive, native, and recently range expanded species (Berman *et al.* 1992, Harris and Mathieson 2000).

#### The ecosystem of *Saccharina latissima*

*Saccharina latissima* is a temperate marine kelp that occurs in intertidal and shallow subtidal habitats world-wide (Bolton and Luning 1982, Davison *et al.* 1991). The range for *S. latissima* is from Rhode Island up into Canada in the north-west Atlantic, with Maine being the center of its distribution (Brady-Campbell *et al.* 1984, Gerard and Dubois 1988). Blades may reach 3 meters long and growth occurs from an intercalary meristem between the stipe and blade; the blade erodes at the distal end (Mann 1973). Blades are typically covered in a variety of epifauna such as solitary and colonial tunicates, mussels, hydroids, and the invasive bryozoan, *Membranipora membranacea* (Seed and O'Connor 1981, Pederson *et al.* 2005).

The first record of *M. membranacea* in the Gulf of Maine was in 1987 at the Isles of Shoals off the coast of New Hampshire and Southern Maine (Berman *et al.* 1992). It has since become the most abundant kelp epibiont in the Gulf of Maine, tripling its abundance between 1989 and 1990 (Berman *et al.* 1992, Lambert *et al.* 1992). *M. membranacea* is an encrusting colonial bryozoan that settles and grows on a variety of sub-tidal algae in the Gulf of Maine, including *Saccharina latissima*, *Laminaria digitata*, and *Agarum clathrata*; it has also been found on *Ulva lactuca*, *Palmaria palmate*, *Fucus vesiculosus*, and filamentous algae such as *Desmarestia aculata* (Harris, unpubl. obs.). *M. membranacea* has an annual life cycle. In the Gulf of Maine, *M. membranacea* settles during the summer and covers blades once established until colonies senesce in the fall. Remaining colonies overwinter and then grow and reproduce in the spring (Ellison and Harvell 1989, Berman *et al.* 1992).

In the Gulf of Maine, *M. membranacea* previously had no record of specialist predators with the exception of Harris and Mathieson's (2000) observation that newly settled *Onchidoris muricata* were found on *M. membranacea* in 1997. More recently, it is fed upon not only by *O. muricata*, but also *Corambe obscura*. Both nudibranch species use suctorial feeding and feed only upon the polypide of the bryozoan.

*O. muricata* is native to the Gulf of Maine. This nudibranch has an annual life cycle. Reproduction typically occurs in the spring and summer and larvae settle in late summer and adults feed over winter (Todd 1978b, 1987, Bleakney 1996). In this region, *O. muricata* feeds upon a native bryozoan, *Electra pilosa*,

but now has been found on *M. membranacea* despite the concurrent presence of *E. pilosa* (Harris and Mathieson 2000) even though *O. muricata* prefers *E. pilosa* (Pratt and Grason 2007). Now that *C. obscura* is feeding upon *M. membranacea*, there is a seasonal overlap with *O. muricata*.

The native range of *C. obscura* is from south of Cape Cod, Massachusetts to Texas (Gulf of Mexico) (Franz 1968). It has since become common in the southwestern portion of the Gulf of Maine (Harris, unpublished observations). Introductions of *C. obscura* have occurred in the Netherlands (Swennen and Dekker 1995), France, and the Black Sea (Roginskaya and Grinzov 1990) where it has been hypothesized that they were transported from the Northwest Atlantic. Very little is known of *C. obscura*'s ecology and life history outside of the study by Perron and Turner (1977).

*C. obscura* is an extremely cryptic nudibranch of the Family Corambidae found primarily in brackish, subtidal habitats with salinities ranging from 6.7 to 32.1ppt (Franz 1968, Swennen and Dekker 1995). They have a rounded, dorsally flattened body shape and reach a size of up to 7.5mm (Perron and Turner 1977).

*C. obscura* has a biphasic life cycle: a veliger larva metamorphoses into an adult sea slug. Veligers are planktotrophic and spend at least 9 days in the plankton before competency. Once competency is reached, larvae have 14 additional days to settle (Perron and Turner 1977). Once a suitable bryozoan substrate is encountered, metamorphosis is induced (Perron and Turner 1977). The veliger casts its larval shell and then feeds upon detritus on the bryozoan's surface until it is capable of transitioning to the adult prey (Perron and Turner

1977). However, nudibranchs in the study by Perron and Turner (1977) were found to settle only on *Electra crustulenta* in laboratory experiments.

*C. obscura* is a specialist feeder on encrusting bryozoans; slugs feed by piercing the bryozoan's protective membrane and then sucking out the contents of the zooid. *C. obscura* has been found on colonies of *Electra crustulenta* in the central Northwest Atlantic and in the European Black Sea (Perron and Turner 1977, Swennen and Dekker 1995), but it has also been found feeding on *Alcyonidium verrilli* and *Membranipora tenuis* in Barnegat Bay, NJ (Franz 1968). In the southern Gulf of Maine, *C. obscura* feeds on *Membranipora membranacea*; the interaction of *C. obscura* with this invasive bryozoan in this region has not yet been studied.

### Objectives

It appears that *C. obscura* has undergone a range expansion into the Gulf of Maine from their native range south of Cape Cod, MA. It is unclear why *C. obscura* is only now increasing in abundance despite *M. membranacea*'s two-decade long presence in the Gulf of Maine (Harris and Mathieson 2000). Lag times associated with dispersal or climate change may be contributing factors, as the Gulf of Maine has been experiencing temperature increases since the introduction of *M. membranacea* (Dijkstra *et al.* 2011). *O. muricata* also seems to be taking advantage of the more abundant food resource that *M. membranacea* offers relative to the native *E. pilosa*, but whether *O. muricata* is beginning to choose *M. membranacea* for settlement more often than *E. pilosa* is unclear.

Teasing apart the influence both abiotic and biotic factors play in invaded marine habitats is crucial in understanding how predators may be responding to these interactions. The objectives of this study are as follows:

1. To characterize and quantify abiotic and biotic factors at three sites along the coast in the southern Gulf of Maine coast through summer and fall.
2. To determine how these abiotic factors affect prevalence of community members and how these members interact with each other, resulting in the abundance increase of *C. obscura*.
3. To determine the settlement and adult feeding choices of *O. muricata* and how they change over seasons.
4. To determine how temperature affects *C. obscura*'s life history.

By answering above questions, correlations between abiotic and biotic factors should become more apparent and allow for a better understanding of how invasive, native, and range expanded species interact and how facilitation of range expansions may occur in the marine environment. Testing how temperature affects life history through laboratory experiments should give further insight as to how *C. obscura* responds to climate change and seasonality, affecting their reproductive output and feeding rates. In addition, results should allow for speculation on how this habitat overlap of predators may impact their invasive prey and the native kelp host. Thus, results from this study may be a useful predictor for future changes in this and similar communities.

## MATERIALS AND METHODS

### Study Sites

Surveys were conducted at three evenly distributed coastal sites, ranging from northern Massachusetts to southern Maine (Figure 1A). Sites were chosen based on kelp availability, location, and ease of access. All sites are boating marinas located in brackish water (~29ppt) at the entrance to harbors or bays. Marinas were of similar sizes, with primarily plastic floats that are in the water year-round. Although all sites were dominated by the brown kelp *Saccharina latissima*, biodiversity of kelp epifauna and fouling organisms differed. Characterization of individual sites below illustrates those differences.

#### Spring Point Marina (SPM), South Portland, ME

This is the northernmost marina, located within Casco Bay (43°38'55.35"N, 70°13'53.80"W). It consists of nine docks, which run parallel to shore (Figure 1B). Floating docks B-H were sampled, as docks A and I lacked kelp. Floats are primarily covered by filamentous diatoms, *S. latissima*, and *Ulva lactuca*. *S. latissima* is primarily covered by filamentous diatoms at docks proximal to shore, while *M. membranacea*, *Electra pilosa*, and tunicates cover kelp blades distal to shore. Before tunicates become present, blades are often covered by *Mytilus edulis* spat. In November to February, kelps are perforated due to grazing by the snail *Lacuna vincta*. Longer kelps are often slashed or cut due to boat traffic.

### Wentworth Marina (WWM), New Castle, NH

Located at the mouth of New Hampshire's Great Bay (43° 3'29.85"N, 70°43'29.70"W), this site is characterized by five docks which run perpendicular to shore (Figure 1C). Dock E lacks boat slips. Floats are often covered by *M. edulis* and associated epifauna such as anemones, colonial and solitary tunicates, and barnacles. Algae at this site primarily consist of *U. lactuca* and *S. latissima*. *M. membranacea*, hydroids, and colonial diatoms dominate growth on *S. latissima*.

### Beverly Port Marina (BPM), Beverly, MA

This marina is located at the mouth of Beverly Harbor (42°32'27.91"N, 70°52'56.88"W). Docks are perpendicular to shore (Figure 1D). Float cover is dominated by *M. edulis* and a variety of colonial and solitary tunicates. Other algae attached to floats include *U. lactuca* and *Codium fragile fragile* (rarely). Kelps are primarily covered by *M. membranacea*, but may also have aggregations of mussel spat and tunicates in July and early August.

### Field Surveys

Surveys were completed from August to December, 2010 and June to December, 2011, though the starting date for Beverly Port Marina was September, 2010. Sites were sampled monthly in 2010 and bi-weekly in 2011, though in the fall of 2011 sampling dates were sometimes missed. Missed dates included early June for WWM and BPM, mid-August for WWM, and late September for WWM and BPM (Table 1).



## Temperature and Flow Data Collection

To determine the effects of abiotic factors on the distributions of animals, temperature, salinity, and flow were measured. Historical sea surface temperature was accessed through the Northeastern Regional Association of Coastal and Ocean Observing Systems (NERACOOS). Data were taken from Casco Bay (buoy #44007), Boston Harbor (buoy #44013) and the UNH Coastal Marine Lab Field Station (CML) buoys. Temperature was originally recorded with a YSI meter, but this information was similar to NERACOOS data, therefore, NERACOOS buoy data were used to get a more accurate representation of temperature fluctuations.

Flow ( $\text{cm s}^{-1}$ ) was measured with a General Oceanics low-velocity flow meter (Model 2030R6) at the beginning and end of all docks at each site (Figure 1). The flow meter was placed at 1 meter depth and measurements were recorded at 30 second intervals for a total of 2.5 minutes (5 replicates) at mid-Spring tides.

## Plankton Surveys

To determine the probability that a specific plankter will encounter a suitable substrate based on the amount of flow at a site, a 5 meter horizontal plankton tow (50cm diameter, 50  $\mu\text{m}$  mesh) was repeated five times per site at one point farthest from and nearest to shore. A single plankton survey was collected in mid-December, 2011 (Table 1).

Live plankton were transported to the lab in plastic containers with seawater then sieved through a similar sized mesh ( $\sim 50 \mu\text{m}$ ) and preserved in

95% Ethanol. Plankton samples were counted in a square plastic dish with a 1x1in grid. Only zooplankton larvae were counted.

### Community Survey

At each site, ten *S. latissima* kelps from slips at each dock for a total of 50-70 kelps per marina (Docks B-H at SPM, A-E at WWM, and A-G at BPM) were haphazardly chosen for non-destructive sampling. Late in the year fewer kelps were present at WWM and BPM, therefore, only 5 kelps were sampled (at BPM, almost no kelps remained so those that did were sampled). The length (end of stipe to end of blade) and width (widest part of blade) were recorded with a rigid tape measure to the nearest centimeter. Sizes of kelps were not measured during the preliminary survey in 2010, but were measured every other week from June to December, 2011.

Total *M. membranacea* cover on both sides of blades was estimated by a ranking from 0-5 (Table 2). Presence of other kelp epifauna was recorded when ranking *M. membranacea* cover. In this case, the ranking corresponded to the amount of *M. membranacea* that could be seen if overgrowth of *M. membranacea* by other epifaunal species had occurred.

The number of *Corambe obscura* and their egg masses were recorded and all individuals were measured with dial calipers to the nearest 0.01mm. All *Onchidoris muricata* were also recorded and the species of bryozoan each individual was associated with was documented. The number of *Electra pilosa* colonies was also recorded.

## Analysis

Calculations. Flow rate ( $\text{cm s}^{-1}$ ) was calculated by using the following series of formulas:

$$1. \text{ Distance (m)} = \frac{\text{Difference in counts} \times \text{Rotor constant}}{999999}$$

$$2. \text{ Speed (cm s}^{-1}\text{)} = \frac{\text{Distance (m)} \times 100}{\text{Time (s)}}$$

Replicates were averaged to estimate an overall current at each dock.

Kelp length and width were used to compute the total surface area that takes into account both sides of the blade:  $2(L \times W)^2 = SA$ . The number of kelps encrusted with *M. membranacea* (any ranking over 0) was divided by total number of sampled kelps (hereafter called Percent of Kelps Encrusted, PKE). The number of kelps with *C. obscura* present was then divided by the number of *M. membranacea* encrusted kelps (hereafter called Percent Encrusted Kelps Occupied, PEKO).

Percent cover of *M. membranacea* was calculated by averaging mean rank percents for encrusted kelp samples at each dock (Table 2). Proportion of *O. muricata* on their respective bryozoans was calculated by dividing number of slugs on each bryozoan by the total amount of slugs found.

Statistics. Differences between sites for PEKO by *C. obscura*, mean nudibranch abundance among all kelps and per occupied kelp, PKE by *M. membranacea*, mean percent cover of *M. membranacea* encrusted kelps, *O. muricata* proportions and abundances per bryozoan; and kelp surface area were analyzed using a General Linear Model Univariate Analysis of Variance (GLM UniANOVA) with "Date Group" (no site was sampled on the same date so a

grouping of similar sample dates were made for analysis purposes) as a random factor with Tukey's HSD Test. Between year analyses by site for each variable (with the exception of kelp size that was measured only in 2011) were also done using a GLM UniANOVA with year as the fixed factor and Date Group as the random factor.

Correlation matrices and linear regression was used to quantify interactions among variables, with regressions between abiotic (temperature and current) and biotic factors (larval availability, kelp surface area, *M. membranacea* cover, abundance from PEKO by *C. obscura*, and *O. muricata* on *M. membranacea*/*Electra pilosa*) and species correlated with each other. Split site correlations were also done to test if factor importance differed within sites. Correlations were also used to test the relationships between temperature and size of nudibranchs and between the amount of nudibranchs and amount of egg masses and between flow rate and plankton counts.

All statistical analyses were performed using IBM SPSS 19.

### **Temperature and the Biology of *Corambe obscura***

#### **Nudibranch Collection and Care**

Individuals of *Corambe obscura* were collected from BPM, Beverly, Massachusetts due to their abundance in summer and fall, 2011. Nudibranchs were only collected at this site to prevent error from the possibility of different nudibranch populations at sites (Lambert *et al.* 2000).

All lab experiments were conducted at four temperatures (4°C, 10°C, 15°C, and 20°C). Nudibranchs were brought to the lab and assigned a treatment temperature. Those assigned to extreme temperatures (4°C and 20°C) were acclimated at 10°C or 15°C, respectively, for 2 days before transfer. Each individual was placed on a small square of kelp approximately 35x35 mm that was covered by *M. membranacea* and then placed within a Toby Teaboy®. Kelps were either collected from the UNH Coastal Marine Lab in New Castle, NH or field sites. Squares were replaced weekly.

Each treatment was comprised of multiple sterilite containers (6qt. for 4°, 10° and 15° treatments; 10qt. for 20° treatment to decrease effects from increased oxygen consumption) and each container held 3-4 Toby Teaboys®. All containers held water at ambient cold room temperature, with the exception of 20° containers, which were held in the 15° cold room and heated with a 25 watt Stealth Pro aquarium heater. Each container was aerated and covered to reduce evaporation. Filtered seawater was collected from Great Bay Aquaculture in Portsmouth, NH and salinity was maintained at 29ppt. Water was changed weekly.

In an attempt to standardize nudibranch sizes for lab experiments, egg masses were collected from nudibranchs held in the lab in 2010 and an effort was made to raise veligers. No veligers settled or metamorphosed during this attempt. Therefore, nudibranch size was not standardized for any lab experiments due to the wide variation in nudibranch sizes in the field during collection days.

### Feeding Rates

Because nudibranchs were more prone to crawling off of the kelp piece provided in the Toby Teaboy® floats, small rectangular Sterilite containers (1.5 L) were used for this experiment. Squares of kelp contained *M. membranacea* colonies with no empty zooids. Squares used were covered by large, continuous colonies of *M. membranacea* on both sides and clipped on one corner to keep track of front and back. The kelp squares were placed into the Sterilite containers at each temperature treatment and photographs were taken to visualize each *M. membranacea* polypide. Each container was a replicate (N=10 for 4°C and 10°C, N=9 for 15°C and 20°C). In the 20° treatment, the 25W Stealth Pro Heaters were too large for the Sterilite boxes, so boxes were kept within 10qt. containers holding seawater maintained at 20°.

Nudibranchs were taken from holding containers after being starved for 24 hours and placed on their respective kelp square. After 24 hours, photographs were taken before and after removal of the nudibranch (a photograph before nudibranch removal gave a good starting point for where to look for empty zooids). Photographs were compared to measure the number of zooids consumed.

### Growth rates and Longevity

Nudibranchs were kept in containers as previously described (5 containers for 4 °C and 20 °C, 7 containers for 10 °C and 15 °C treatments). New nudibranchs were collected at intervals (on BPM survey dates) and measurements began one week after an acclimation period as described above.

Every other day, nudibranchs were measured using digital calipers and wet weights were recorded using a digital scale (Mettler AC 100) until the death of the animal (laboratory survival). Percent daily growth (in length and weight) was calculated and length of time until slugs died during the experiment. Amount of spawn and whether the nudibranch had moved off of the kelp between measuring dates was noted.

### Fecundity

Egg masses were collected from containers during the growth and feeding rate studies and photographed under a dissecting microscope to estimate the amount of eggs per mass. If the eggs were uncleaved, they were carefully separated from the kelp and *M. membranacea* and placed on a microscope slide. These masses were then placed under a compound microscope fixed with a digital camera; twenty ova and capsules from each mass were photographed and subsequently measured diameter using cellSens® digital imaging software to the nearest  $\mu\text{m}$ .

### Analysis

Feeding Rates. One-Way ANOVA was used to test the significance of temperature on feeding rate over a period of 24 hours with Tukey's HSD to test for differences among treatments.

Growth rates. Mean percent daily growth (length and weight) for each nudibranch was calculated using the formula:  $\left[ \left( \frac{\frac{L/W_n - L/W_i}{L/W_i}}{\text{Lab survival}} \right) * 100 \right]$ . Both factors were then analyzed using ANOVA to determine whether temperature influenced growth of *C. obscura*, with Tukey's HSD Test.

**Fecundity.** Photographs of egg masses taken with a dissecting microscope were opened in Adobe Photoshop CS4 and overlaid with a pie chart divided into eight equal pieces. The piece located over the outward end of the mass was designated as piece one and all eggs in that and the piece opposite were counted and multiplied by four to get an estimate of eggs in each egg mass. One-Way ANOVAs were used to evaluate the effect of temperature on ovum/capsule sizes and the amount of eggs per mass, with Tukey's HSD Test. Correlations tested whether ovum and capsule size were related and whether egg size and the amount of eggs per mass were related.



**Table 1: Table of survey dates and their respective sampling "group." Dates for plankton tows noted.**

<b>Year</b>	<b>Sample #</b>	<b>SPM</b>	<b>WWM</b>	<b>BPM</b>
<b>2010</b>	1	20-Aug	1-Aug	
	2	21-Sep	1-Sep	1-Sep
	3	29-Oct	19-Oct	8-Oct
	4	14-Nov	30-Nov	11-Nov
	5		30-Dec	16-Dec
<b>2011</b>	1	10-Jun	missed	missed
	2	29-Jun	28-Jun	30-Jun
	3	15-Jul	13-Jul	14-Jul
	4	4-Aug	2-Aug	3-Aug
	5	17-Aug	missed	18-Aug
	6	30-Aug	29-Aug	1-Sep
	7	13-Sep	16-Sep	15-Sep
	8	27-Sep	missed	missed
	9	10-Oct	7-Oct	6-Oct
	10	27-Oct	17-Oct	21-Oct
	11	15-Nov	18-Nov	11-Nov
	12	29-Nov	2-Dec	25-Nov
		<b>Plankton sample</b>		
		10-Dec	11-Dec	9-Dec
	13	15-Dec	19-Dec	13-Dec

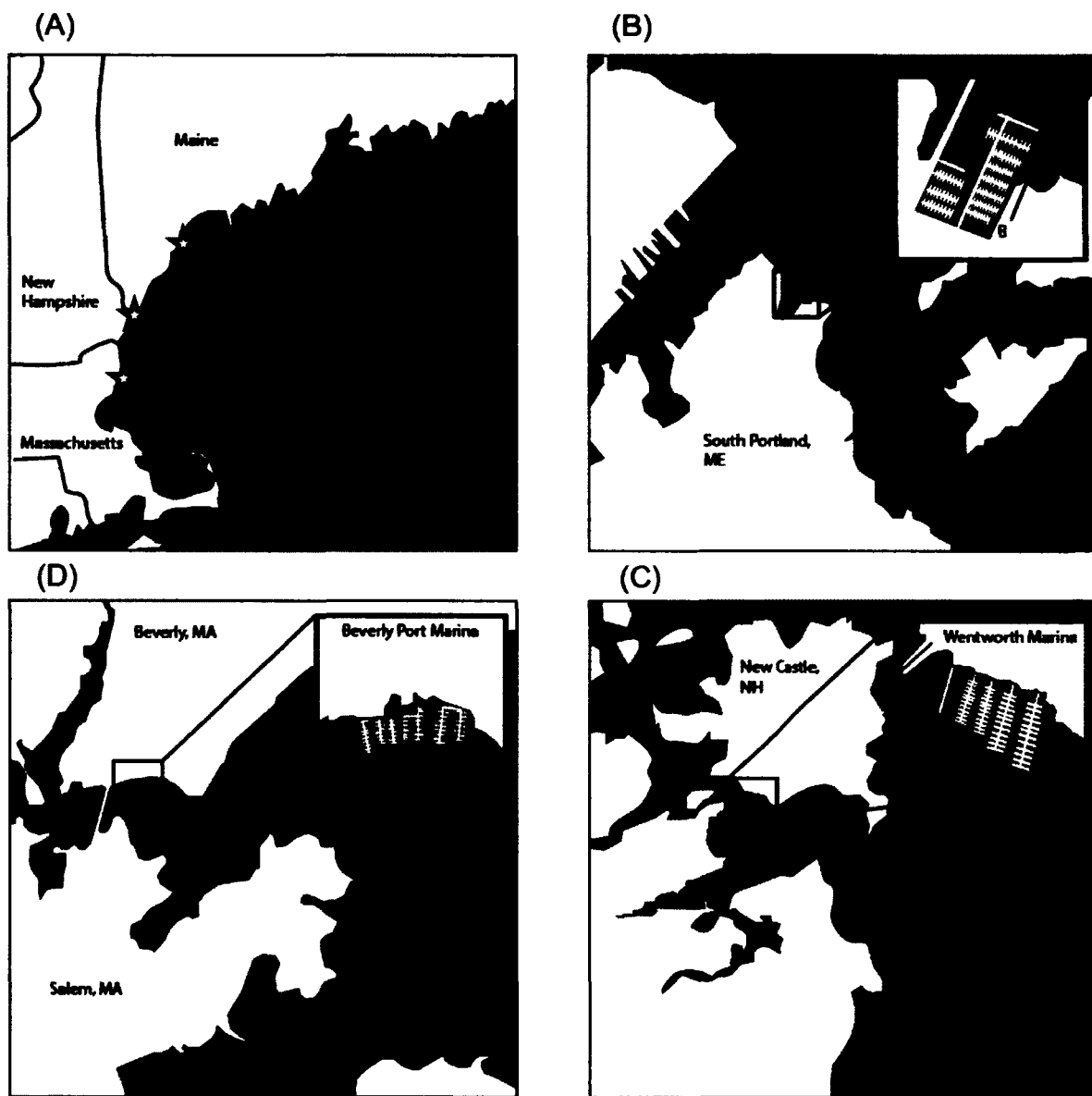


Figure 1: Sites surveyed. (A) Location of sites in the southern Gulf of Maine. (B) Spring Point Marina, South Portland, ME. (C) Wentworth Marina, New Castle, NH. (D) Beverly Port Marina, Beverly, MA. Inlays illustrate dock layout.

**Table 2: The conversion of *M. membranacea* ranking to percentages.**

<b>Rank</b>	<b>Percent Range</b>	<b>Average Percent</b>
<b>0</b>	<b>0%</b>	<b>0%</b>
<b>1</b>	<b>1-20%</b>	<b>10.50%</b>
<b>2</b>	<b>21-40%</b>	<b>30.50%</b>
<b>3</b>	<b>41-60%</b>	<b>50.50%</b>
<b>4</b>	<b>61-80%</b>	<b>70.50%</b>
<b>5</b>	<b>81-100%</b>	<b>90.50%</b>

## RESULTS

### Field Surveys

In general, the most southern site, BPM, had the highest abundance of *M. membranacea*, while the most northern site, SPM, had the lowest abundance of *M. membranacea*. This same trend was found for abundance of *C. obscura*, but for *O. muricata*, slugs were found primarily at SPM.

### Observations

The abundance of kelps at each site varied. SPM had the highest abundance of kelps and WWM had the lowest abundance. During the fall, kelps began to disintegrate and fall off of floating docks. The highest amount of defoliation was at BPM; while SPM had some defoliation, the abundance of kelps in the fall stayed higher than both other sites.

Each site had its own unique set of epifaunal organisms which covered kelps in addition to *M. membranacea* (Table 3). SPM had a high prevalence of solitary ascidians, some colonial ascidians, *Lacuna vincta*, *Mytilus edulis* spat, and diatoms. WWM had the fewest species of epifauna. Kelps at BPM were covered by colonial ascidians and encrusting bryozoans (Table 3).

Once *M. membranacea* began to grow, it overgrew the native bryozoan *Electra pilosa*. In addition, with high prevalence of nudibranchs, the skeleton of *M. membranacea* would slough off the kelp in patches. From October through December, *M. membranacea* would often be covered in other epifaunal species,

most typically found were invasive ascidians such as *Ciona intestinalis*, *Botrylloides violaceus*, and *Botryllus schlosseri*.

Nudibranchs of both species were found on all parts of *M. membranacea* colonies, but seemed to be most abundant in the centers. When overgrowth of *M. membranacea* occurred, nudibranchs appeared to get stuck in patches of bryozoan surrounded by ascidians.

#### Abiotic factors

Both temperature and flow rate varied by site. Temperature fluctuated throughout the year, and though all sites trended with the same general pattern of temperatures peaking from mid-June to August, actual peak time depended on site. BPM's peak temperatures occurred earlier than WWM and SPM. Sea surface temperature at all sites during 2010 tended to be higher than temperatures in 2011 up until July, where in 2011 temperatures overtook temperatures in 2010 until December (Figure 2). Both 2008 and 2009 were generally cooler than 2011, but appeared to follow similar trends as 2010 (Figure 2). Mean survey seasonal temperature was lowest at WWM in 2010 (11.20 °C), but in 2011 SPM was lowest (11.35 °C). The highest survey season temperatures were at BPM (2010=12.55 °C; 2011=15.20 °C). Mean sampling date temperatures were higher in 2011 than 2010 at all sites, with BPM showing the highest change of about 2.5 degrees (Figure 3). The differences between maximum and minimum water temperature was also larger in 2010 than 2011,

trending towards lower maximum summer temperatures and higher minimum fall temperatures (Figure 3).

Flow rates were different between and within sites. Current at SPM ( $0.525 \text{ cm s}^{-1}$ ) was lower than both WWM ( $3.67 \text{ cm s}^{-1}$ ) and BPM ( $4.21 \text{ cm s}^{-1}$ , Figure 4). Flow rate at BPM was slightly higher than WWM. Flow rate was lower at the docks close to shore of all marinas (Figure 4). Flow at docks within sites varied greatly at both WWM and BPM because they run perpendicular to shore, whereas SPM has docks parallel to shore and a gradation of flow from 0 (no flow could be detected by the flow meter at innermost dock) to  $1.35 \text{ cm s}^{-1}$  (outer dock).

#### Biotic factors

The density of larvae in December, 2011 was highest at BPM and lowest at WWM. Planktonic larvae that were found consisted primarily of nauplii, cyprids, and veligers. There was a higher larval availability in the protected areas (closest to shore) of all marinas compared to the exposed area (furthest from shore), despite higher flow rates measured at the exposed areas (Figure 5A). However, as plankton tows were only conducted once during the survey, this is merely a snapshot of larval densities at each site in December, and not indicative of occurrences at other times of the year. Using the estimates of larval density and flow rates, it can be calculated that over time (60 s), more larvae typically flow by a fixed point in areas with high, despite lower initial larval densities (Figure 5B).

Kelps sampled at SPM were largest ( $1222.30 \pm 30.00 \text{ cm}^2$ ) and significantly larger than kelps at BPM ( $833.69 \pm 37.62 \text{ cm}^2$ ) in 2011. SPM also had kelps with the widest, shortest blades ( $12.91 \times 44.01 \pm 0.16 \times 0.54 \text{ cm}$ ) whereas BPM had narrower, longer blades ( $10.37 \times 48.89 \pm 0.14 \times 1.11 \text{ cm}$ ; Figure 6).

Across all sites, kelp size decreased over time regardless if bryozoans were present (Figure 7). Kelps with a high prevalence of *M. membranacea* were generally larger than those with little to no *M. membranacea* cover. However, kelps highly encrusted with bryozoan colonies decreased in size over a short period of time (Jun-Sept) while those with little to no bryozoans decreased in size over a longer period (June-Oct) (Figure 7).

Kelp blades that were sampled also had a high prevalence of *M. membranacea*, with nearly 100% of kelps encrusted by some (>0 rank) of *M. membranacea* cover at both WWM and BPM (Figure 8A). The percentage of encrusted kelps was significantly higher in 2010 than in 2011 at SPM ( $F=4.05$ ,  $P<0.05$ ) and WWM ( $F=6.00$ ,  $P<0.001$ ); at SPM the difference in percent coverage between 2010 and 2011 was highest and at BPM the difference was lowest between years. The mean percent cover of *M. membranacea* on kelps was highest at BPM and lowest at SPM. Again, encrusted kelps in 2010 had a higher coverage of *M. membranacea* than those from 2011 at all sites (Figure 8B).

The percent of bryozoan encrusted kelps that had nudibranchs present (regardless of abundance) was similar at all sites in 2010. In contrast, SPM had

the lowest percent of bryozoan-encrusted kelps with nudibranchs and WWM and BPM had higher percentages of nudibranch kelps in 2011 (Figure 9A). The mean abundance of *C. obscura* per kelp for all kelps sampled ranged from 0.39 – 2.38 nudibranchs (Figure 9B), but ranged from 1.41 – 3.85 slugs when taking into account only those kelps with nudibranchs present (Figure 9C). Nudibranch abundance was significantly different between years at BPM only.

The percent of kelps encrusted with bryozoans was often maintained at or near 100% at WWM and BPM from August to December, 2010 and from July to December, 2011 (Figure 10). At SPM, there was a gradual increase in percent of kelps encrusted with bryozoans, with the peak occurring in December, 2011. In contrast, the percent of bryozoan-encrusted kelps was maintained at approximately 100% from September to November, 2010 (Figure 10). The percent cover by *M. membranacea* on kelps was highest at BPM and decreased at WWM and SPM. Also the percent cover of *M. membranacea* on kelps was less in 2011 than 2010. *M. membranacea* cover peaked latest at SPM (mid-Oct), a few days earlier at WWM (early-Oct), and earliest at BPM (late Aug) and coverage began to drop at all sites around October with the exception of BPM, which started to decrease in September (Figure 11).

Both the percentage of bryozoan-encrusted kelps infested by *C. obscura* and the abundance of *C. obscura* typically peaked in October (Figure 10 & 11).

#### Settlement and feeding preference of *Onchidoris muricata*

In order to determine whether *O. muricata* were more abundant on *M. membranacea* or *Electra pilosa*, the proportion of small (about 1mm) and



juvenile/adult *O. muricata* found on each bryozoan was quantified in 2010 and 2011 at all sites. While *O. muricata* abundance was counted at all sites, WWM and BPM had little to no *O. muricata*.

The proportion of *O. muricata* on *E. pilosa* and *M. membranacea* changed during the sampling season. Newly settled (~1 mm) *O. muricata* found in August were more abundant on *E. pilosa* than *M. membranacea* (Figure 12). In September and October, 2010, *O. muricata* juveniles and adults were still primarily found on *E. pilosa*, but there was a higher abundance of *O. muricata* on *M. membranacea* than in August. In 2011, newly settled *O. muricata* were found more on *M. membranacea* from early to mid-August than in 2010 and juveniles/adults were more abundant on *M. membranacea* during subsequent months. There was a higher proportion of *O. muricata* associated with *M. membranacea* in 2011 than 2010, though there were also fewer *O. muricata* sampled in 2011 than in 2010, with a ten-fold decrease in late August (Figure 12).

### Ecological Interactions

Abiotic Factors. There did not appear to be a correlation between temperature and kelp size, but kelps were seen to decrease in size as temperatures became warmer (Figure 7). Temperature had the strongest correlation with percent cover of *M. membranacea* ( $R^2=0.28$ ,  $P=0.000$ , Figure 14). The correlation between temperature and *C. obscura* was significant, but weak. There was no correlation between *O. muricata* and temperature (Table 4).

Current had a significant weak correlation with *M. membranacea* cover in 2010 and 2011. The percent cover of *M. membranacea* increased with flow rate at SPM (Figure 13). Highest percent cover of *M. membranacea* was at flow rates around 2.91-2.94 cm s<sup>-1</sup> at WWM, but was highest from 6.07-6.16 cm s<sup>-1</sup> at BPM (Figure 13).

Current and abundance of *C. obscura* and *O. muricata* was significant and weak as well, but only in 2010. *Electra pilosa* was more abundant at lower flow and was most abundant at SPM (Figure 13). Abundance of *C. obscura* was highest in a lower flow area of SPM – 0.73 cm s<sup>-1</sup>, but at both other sites seemed to prefer the flow rate to be from 1.87-2.94 cm s<sup>-1</sup> (Figure 13). Abundance of *O. muricata* followed a similar trend as *C. obscura* at SPM, as they appeared to be most abundant on docks with intermediate flow rates (Figure 13). Both WWM and BPM had little to no *O. muricata* present.

Biotic Factors: There was a significant weak correlation between the size of kelp blades and the amount of *M. membranacea* coverage (Table 4). However, kelps decreased in size over time both with and without the presence of *M. membranacea* (Figure 7). There was a high correlation between number of *Electra pilosa* colonies and abundance of *O. muricata* ( $R^2=0.60$ , Figure 14), but no correlation between *M. membranacea* cover and *O. muricata* abundance. There were significant correlations between *C. obscura* and *M. membranacea* cover in 2010 and 2011 (Table 4, Figure 14).

Abundance of *C. obscura* appeared to correspond to the percent cover of *M. membranacea*, but there appeared to be a lag period between peaks of

predator and prey abundance. The length of the lag period depended upon site, with SPM's lag around 1 month and BPM's lag a little over 1 month (Figure 11). WWM did not appear to have a lag time.

### Field Morphology of *Corambe obscura*

Size of *C. obscura* found in the field may be biased towards larger individuals, as no individuals less than 1 mm were found. Length of *C. obscura* were similar in size at all sites within years, but when comparing years, mean *C. obscura* size was smaller in 2011 than 2010 (Figure 15). Nudibranchs measured in 2010 were over 1 mm larger than those in 2011 despite the warmer temperatures during the 2011 surveys.

The sizes of *C. obscura* varied across survey sample dates. Some dates had size frequencies with a unimodal distribution and others had bimodal distributions (Figure 16 & 17).

### Temperature and the Biology of *Corambe obscura*

#### Feeding Rates

The number of bryozoan zooids consumed per hour by *C. obscura* was highest at 10°C ( $2.86 \pm 0.37$ ) and significantly higher than feeding rates at 4°C ( $0.92 \pm 0.087$ ,  $P < 0.05$ ), but was not significantly higher than feeding rates at 15°C ( $1.61 \pm 0.36$ ) or 20°C (Figure 18). More zooids were consumed per hour at 15° than 20° (Figure 18). While all treatments had nudibranchs that did not feed, the number of non-nudibranchs in the 4°C was highest (Table 5). Non-feeding nudibranchs were not included in the analysis.

### Growth Rates and Longevity

Nudibranch length and weight were positively correlated ( $r=0.640$ ,  $P<0.0001$ ). Nudibranch growth per day at 4°C ( $0.92\pm0.20\text{mm/d}$ ) was significantly lower than growth of nudibranchs in both warmer treatment temperatures (15°C,  $2.07\pm0.40\text{mm/d}$ ; 20°C,  $3.50\pm0.59\text{mm/d}$ ; ANOVA,  $P<0.05$ , Figure 19A).

Nudibranchs grew fastest at 15°C and 20°C treatments. Nudibranchs gained weight the slowest at 4° ( $16.31\pm3.38\text{mg/d}$ ) and 10°C ( $19.14\pm3.95\text{mg/d}$ ). Highest growth was at 15° ( $32.07\pm2.40\text{mg/d}$ ) and 20° ( $29.04\pm9.20\text{mg/d}$ ). Despite these different trends, no treatments were significantly different from each other.

Largest daily weight gain was at 15°C and lowest at 4°C (Figure 19B).

Longest laboratory survival times were seen at 4°C ( $31.8\text{d}\pm7.33\text{d}$ ) and survival decreased with increasing temperature (10°C,  $24.43\text{d}\pm4.70\text{d}$ ; 15°C,  $23.86\text{d}\pm5.79\text{d}$ ; 20°C,  $21.6\text{d}\pm2.70\text{d}$ ), though none were significantly different (Figure 20A). Maximum survival times observed out of all nudibranchs were 36 days at 20°C and 49 days at 10°C.

### Fecundity

The maximum number of egg masses laid over a nudibranchs time in the growth experiments was fewest at 4°C ( $1.17\pm0.17$ ) and increased at each higher treatment temperature (10°C,  $3.53\pm1.17$ ; 15°C,  $6.87\pm1.79$ ), with the highest number of eggs laid at 20°C ( $8.60\pm2.18$ , Table 6).

Diameter of egg capsule was correlated to the diameter of egg ova ( $r=0.581$ ,  $P<0.0001$ ). Capsule sizes were significantly different at all temperatures ( $F= 31.51$ ,  $P<0.01$ ); nudibranchs at 10°C produced the largest

capsules and nudibranchs at 20° produced the smallest capsules (Table 7). Only ova laid at 20°C were significantly smaller than those laid at lower temperatures ( $P>0.0001$ , Table 7). The lowest ovum/capsule ratio was at 10°C and the highest was at 4°C.

The average number of eggs in each spawn mass was highest at 15°C (1618.73±222.44 eggs) and lowest at 10°C (1008.80±214.09 eggs). The mean number of eggs in a spawn mass by nudibranchs at 4°C was not determined due to the low number of spawn laid at this temperature (Figure 21).

Table 3: Epifaunal species associated with *S. latissima*. *M. membranacea* not shown. Asterisks indicate level of prevalence based on observations: High prevalence (\*\*), low prevalence (\*), not present (0).

Group	Species	SPM	WWM	BPM
Solitary	<i>Ciona intestinalis</i>	**	0	*
Ascidians	<i>Ascidiella aspersa</i>	**	0	0
	<i>Botryllus schlosseri</i>	*	0	**
Colonial	<i>Botrylloides violaceus</i>	*	0	**
Ascidians	<i>Diplosoma listerianum</i>	0	0	**
	<i>Ectopleura spp.</i>	0	*	0
Hydroids	<i>Obelia geniculata</i>	0	*	0
	<i>Electra pilosa</i>	**	*	*
	<i>Hippothoa hyalina</i>	0	0	*
Bryozoans	<i>Bugula simplex</i>	*	*	0
Bivalves	<i>Mytilus edulis spat</i>	**	*	*
Phytoplankton	Diatoms	**	*	0

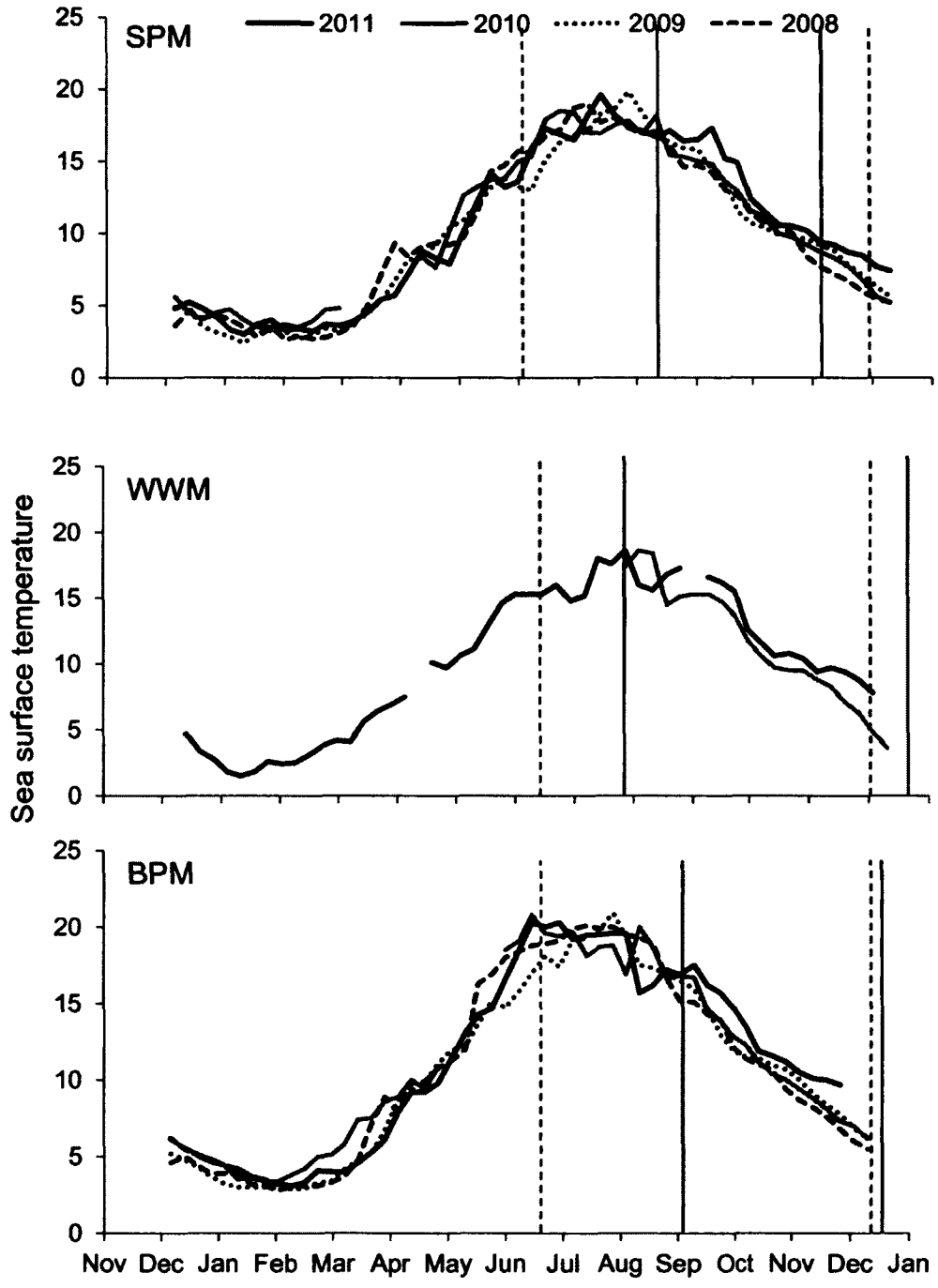


Figure 2: Mean weekly sea surface temperature (°C) in the southern Gulf of Maine and the differences in temperature from 2008-2011. NERACOOS lacked data for 2008 and 2009 at the Coastal Marine Lab buoy. Vertical bars represent survey periods: 2010 (solid), 2011 (dashed). 2008 and 2009 are representative of the years that *C. obscura* was not yet abundant (2008) and when increased *C. obscura* abundances were first noticed (2009).

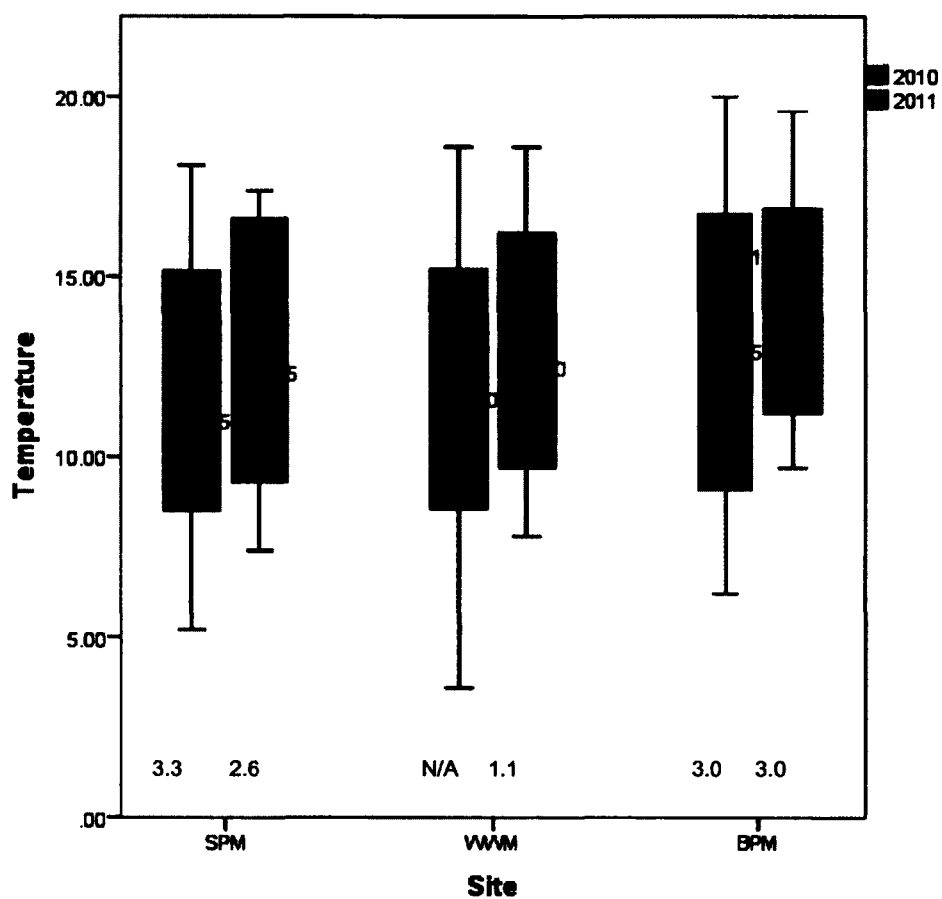


Figure 3: Mean survey season temperatures by site across 2010 and 2011 sampling dates. Temperature was derived by averaging weekly temperature averages from NERACOOS during sample seasons from August-December. Numbers below plots indicate minimum temperature of preceding winter season.



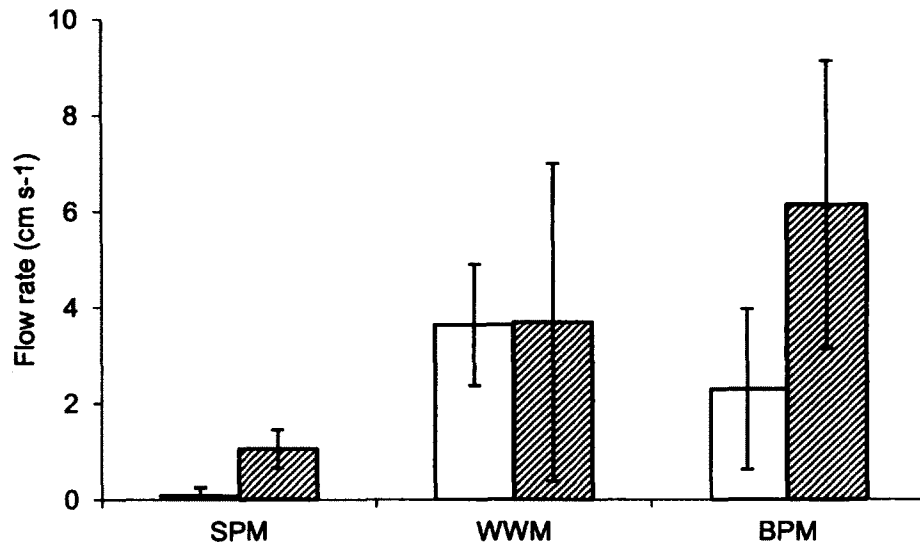


Figure 4: Flow rate ( $\pm$ SE) at docks closest to shore (open) and docks furthest from shore (striped) areas by site.

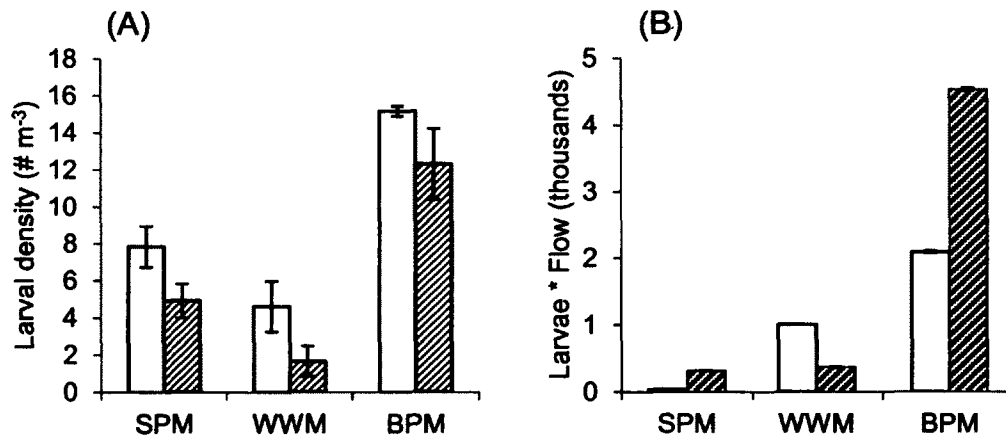


Figure 5: (A) Mean larval density ( $\pm$  SE) at docks closest to shore (open) and furthest from shore (striped) locations within each site. (B) The amount of larvae ( $\pm$  SE) that is estimated to flow past a fixed point in 60 seconds.

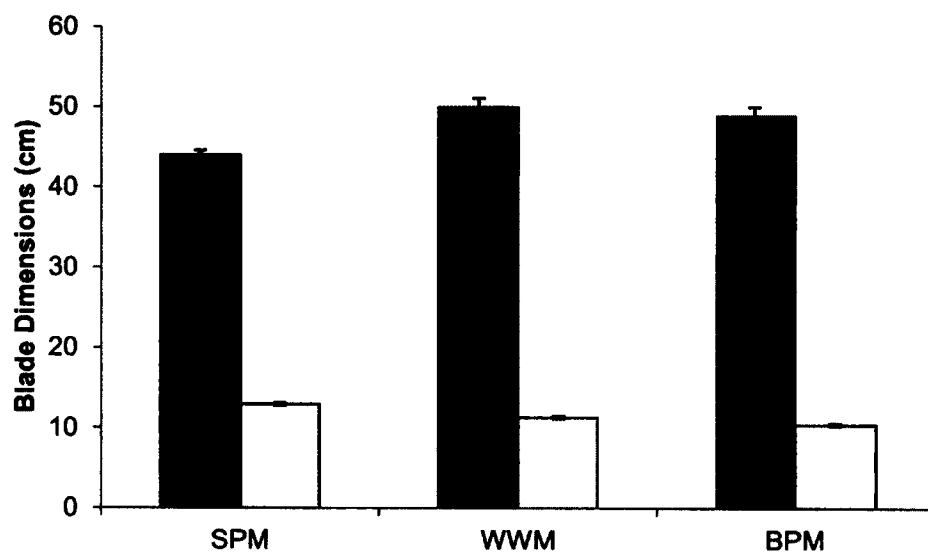


Figure 6: Kelp blade dimensions ( $\pm$ SE) at each site. Dark columns=length, light columns=width.

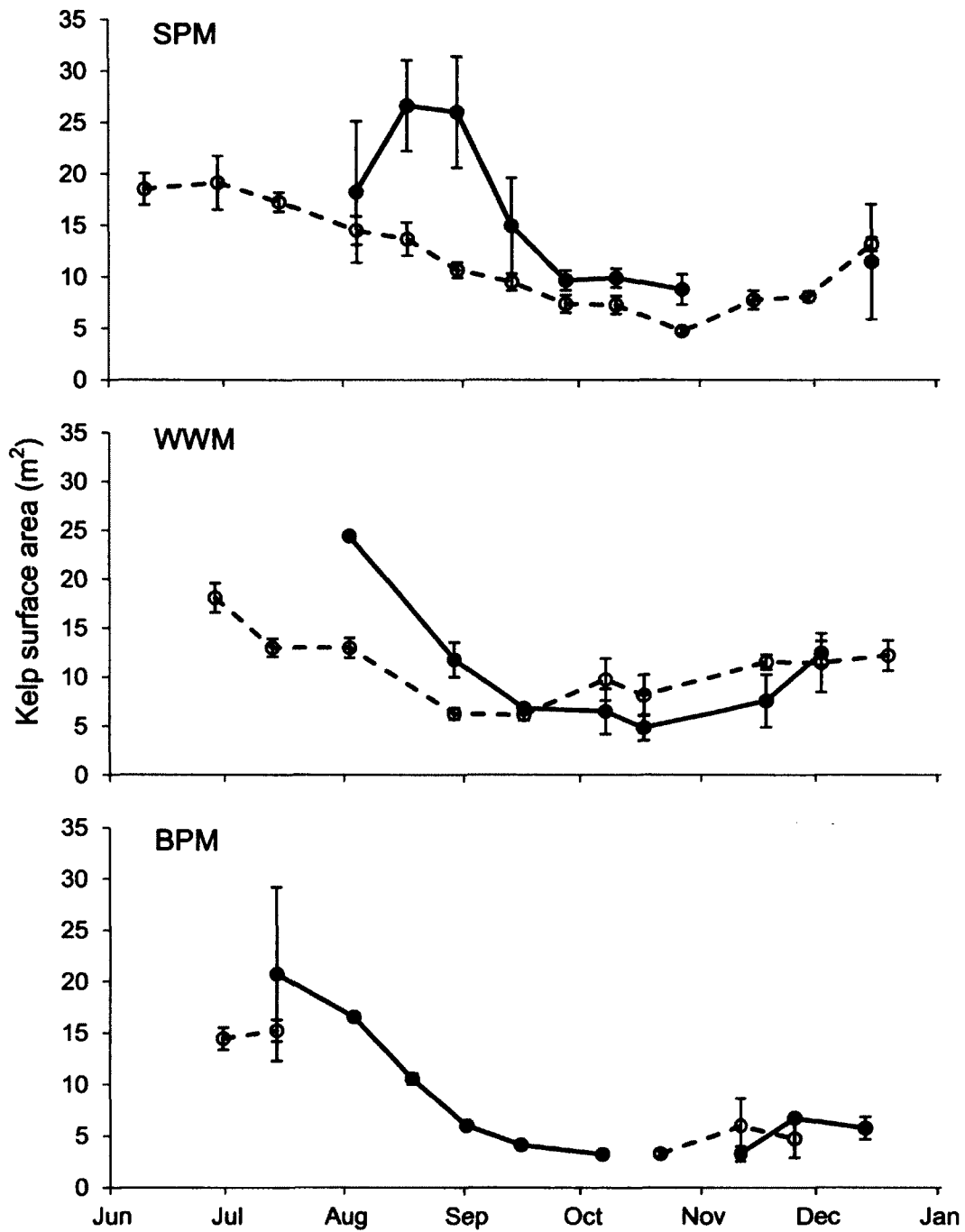


Figure 7: Mean surface area of kelps ( $\pm$ SE) at each site over survey dates with high (41-100%) cover (solid) and little to no (0-20%) cover (open dashed) of *M. membranacea*. Missing data points due to no kelps with little to no cover (BPM) or high cover (SPM).

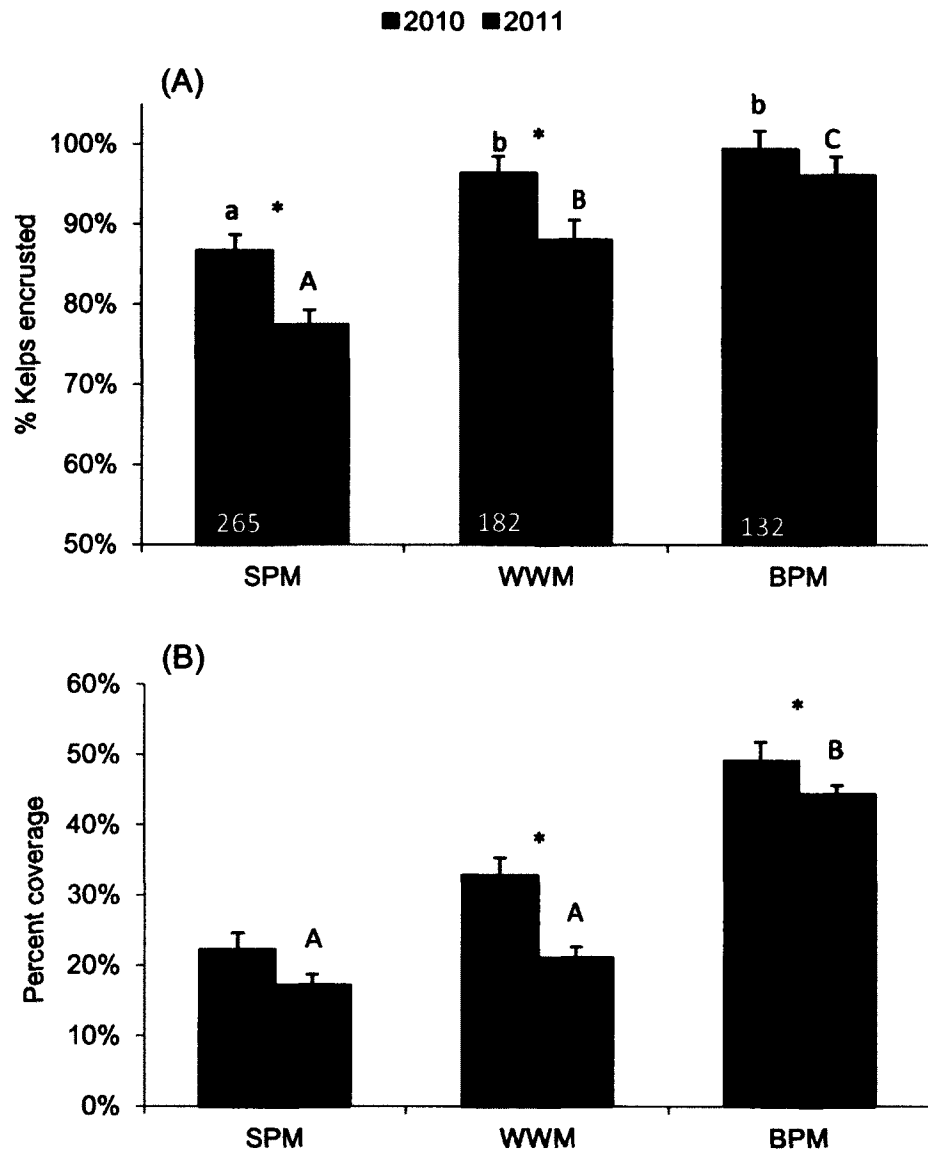


Figure 8: (A) Mean percent of kelp blades encrusted with *M. membranacea* ( $\pm$  SE) by site and year. Numbers indicate amount of kelps sampled. (B) Mean percent coverage ( $\pm$  SE) of kelps by *M. membranacea* by site and year. Asterisk (\*) represents significant difference between years ( $P < 0.05$ ). All sites were significantly different from each other between years. Letters represent homogeneous subsets.

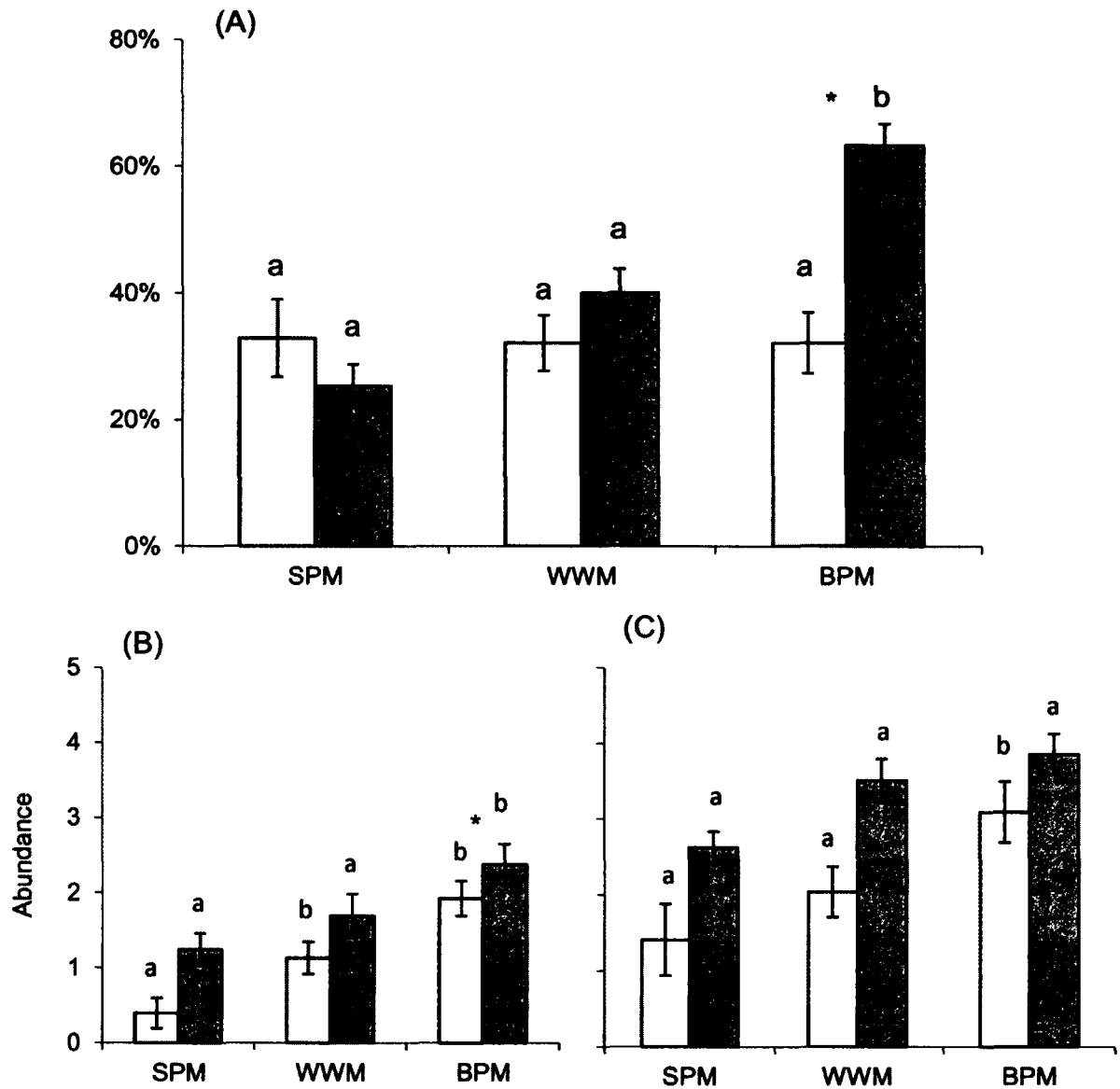


Figure 9: (A) Mean percent of *C. obscura* infested kelp blades encrusted with *M. membranacea* ( $\pm$  SE) at each site by year. Numbers indicate the number of kelps encrusted with *M. membranacea*. (B) Mean abundance of *C. obscura* ( $\pm$ SE) from all kelp blades sampled. (C) Mean abundance of *C. obscura* ( $\pm$ SE) when a kelp blade had *C. obscura* present. Asterisk (\*) represents significance between years. Letters represent homogeneous subsets among sites: lower case=2010, upper case=2011.

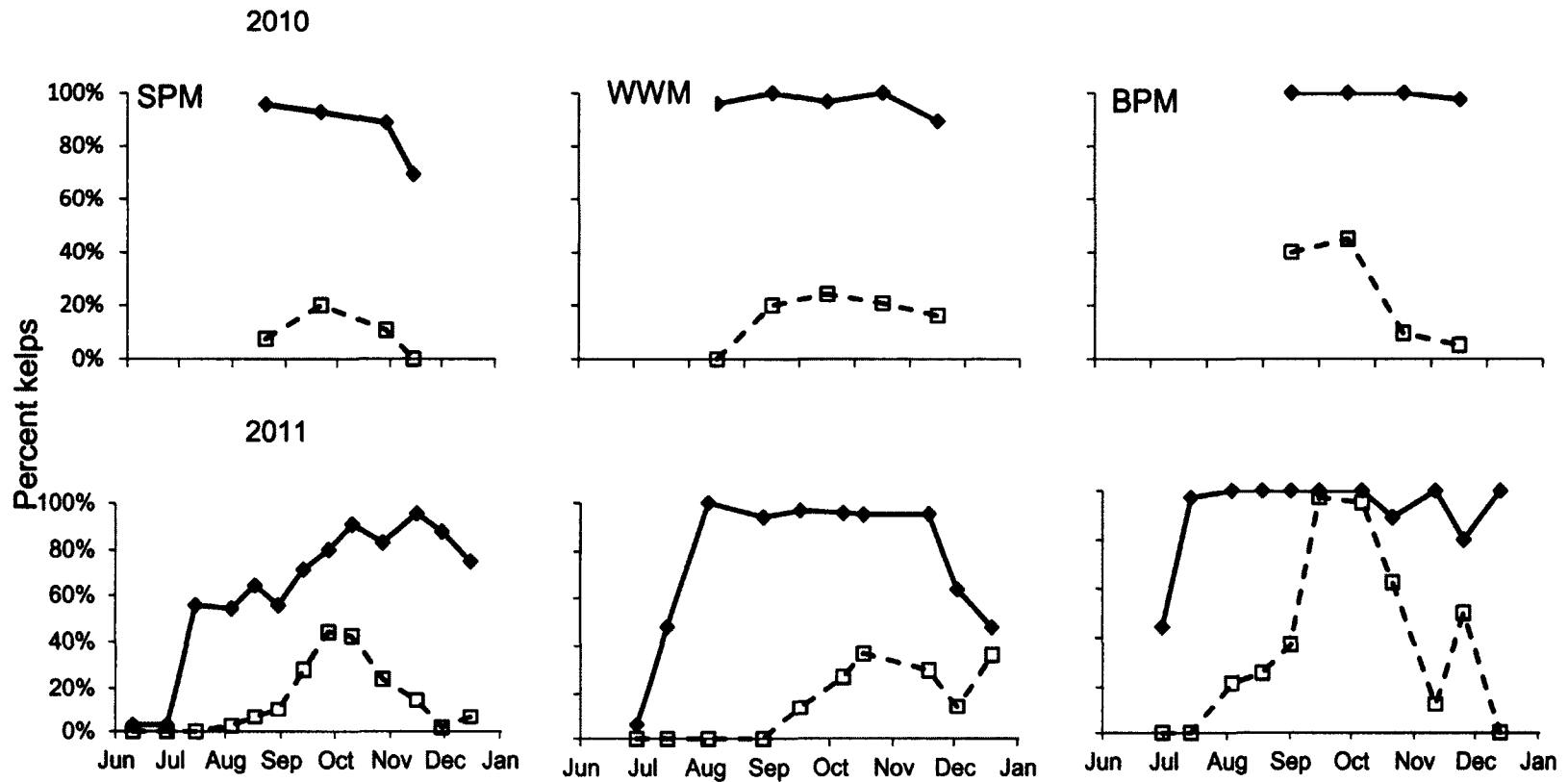


Figure 10: Temporal changes in mean percent of kelps encrusted with *M. membranacea* (solid diamonds) and percent of encrusted kelps infested with *C. obscura* (dashed squares) at each site for both survey years.

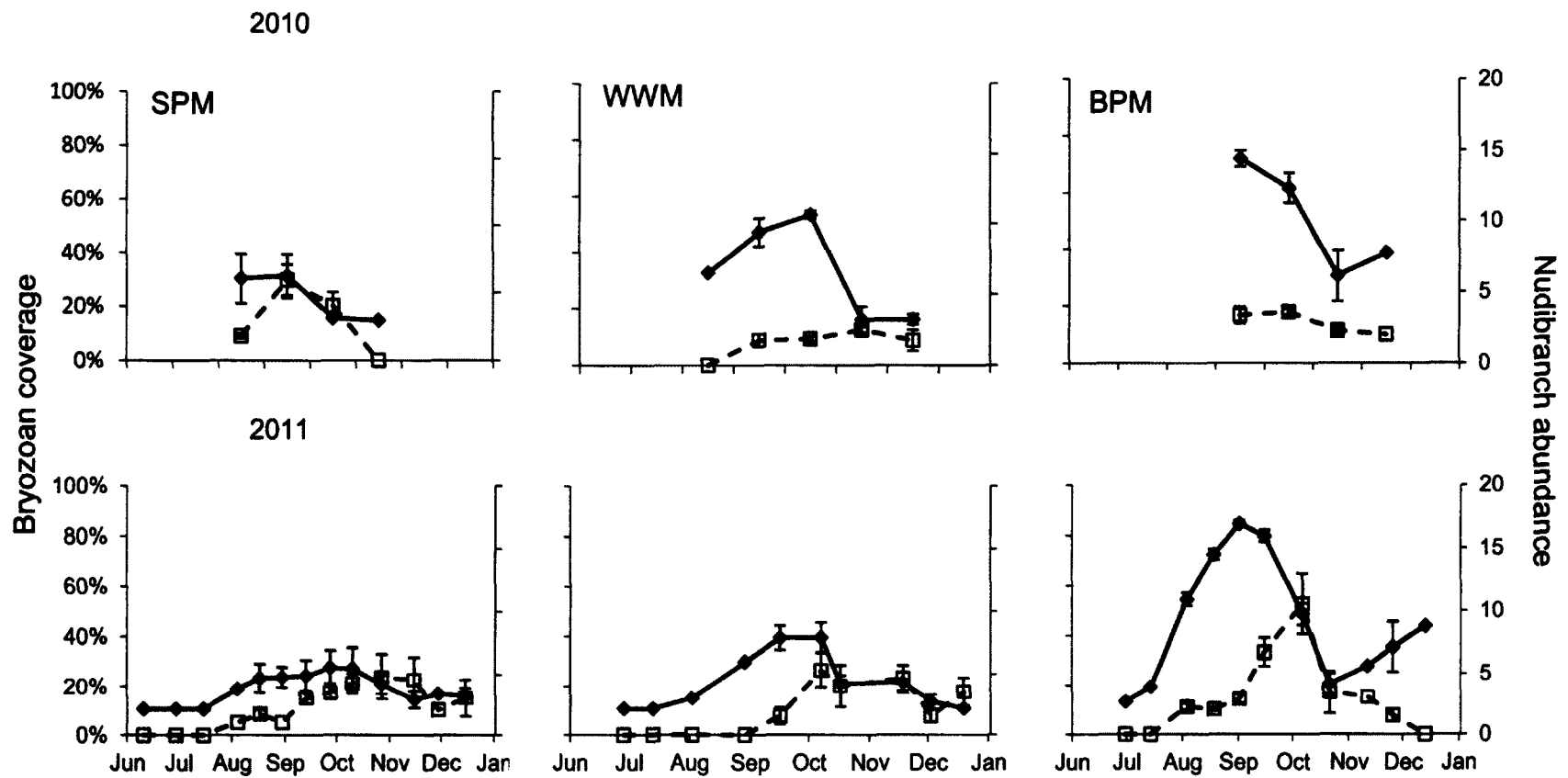


Figure 11: Temporal changes in mean percent coverage ( $\pm$ SE) of *M. membranacea* on kelps (solid diamonds) and mean abundance of *C. obscura* per blade (dashed squares) on kelps encrusted at each site in 2010 (top) and 2011 (bottom).

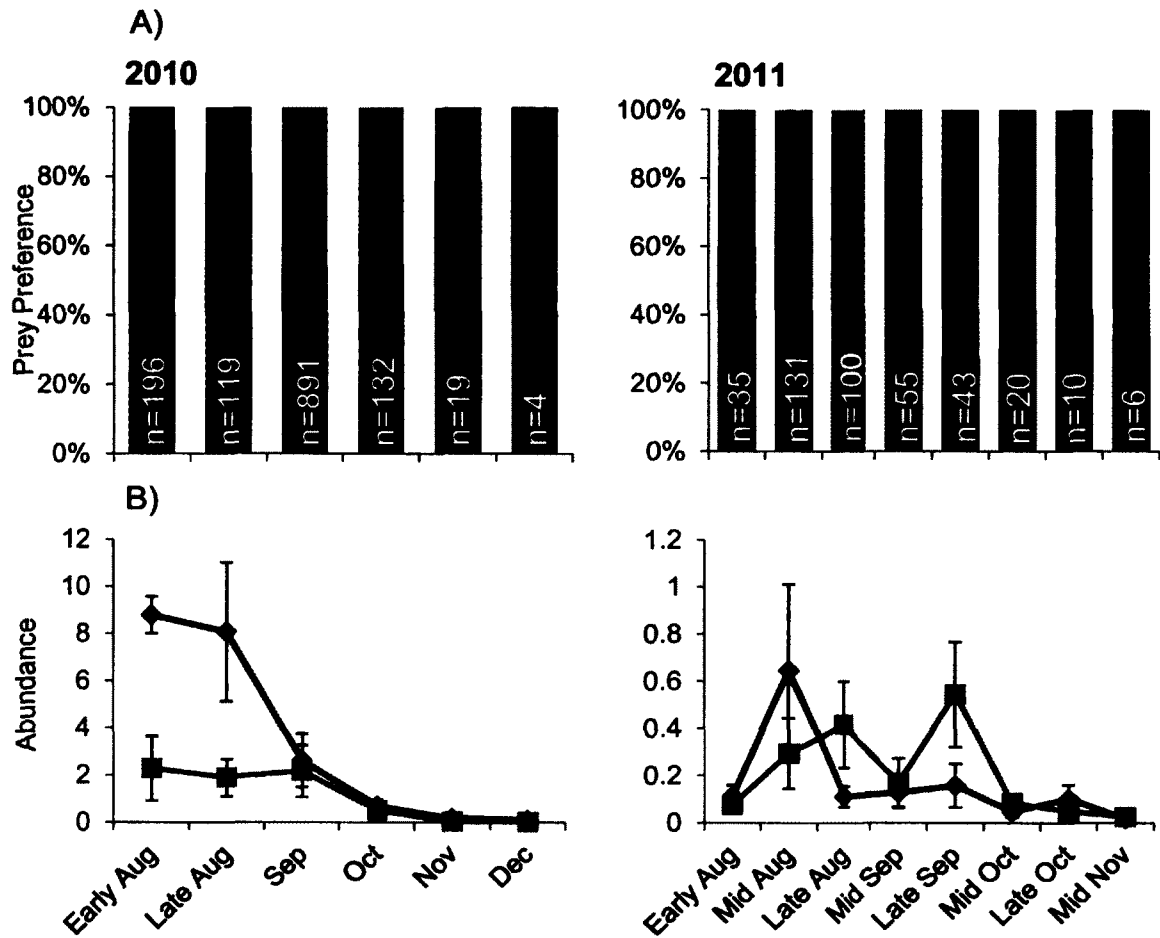


Figure 12: *O. muricata* abundance on bryozoans at Spring Point Marina. (A) The proportion of slugs found of *Electra pilosa* (dark) and *Membranipora membranacea* (light). (B) The mean abundance ( $\pm$  SE) of *O. muricata* on their respective bryozoans.



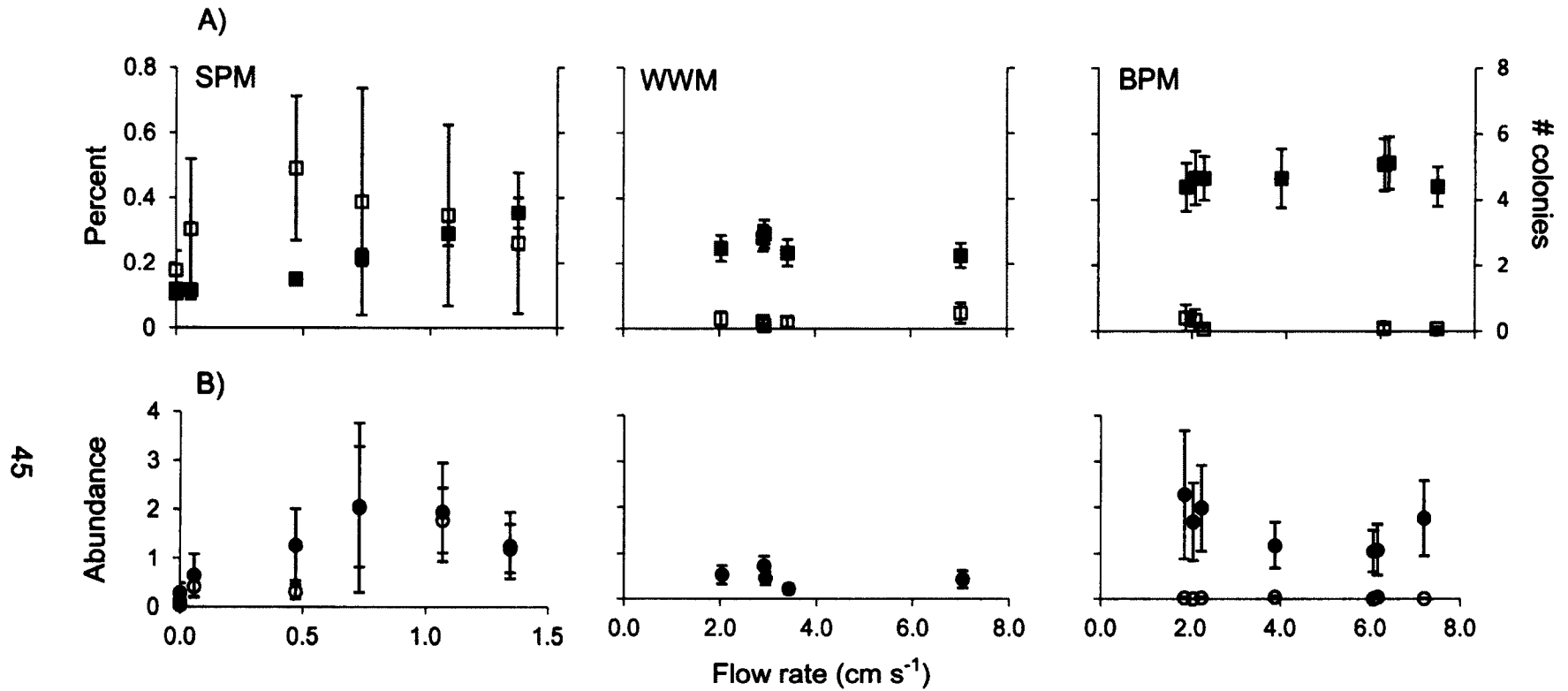


Figure 13: (A) The mean *M. membranacea* percent coverage (filled squares) and # *Electra pilosa* colonies (open squares,  $\pm$  SE) and (B) Mean nudibranch (filled circles, *C. obscura*; open circles, *O. muricata*) abundance ( $\pm$  SE) by flow rate measured within sites.

Table 4: Linear regression of abiotic and biotic factor interactions. Values are R<sup>2</sup> coefficients with P values in parenthesis.

	Year	Temperature	Current	Kelp Size	# <i>E. pilosa</i> colonies	<i>M.</i> <i>membranacea</i> % cover
	2011	0.05 (0.001)				
	2011	0.09 (0.000)	0.13 (0.000)	0.17 (0.000)		
	2011	0 (1.000)	.015 (NS)			0.19 (0.000)
	2011	0.02 (NS)	0.01 (NS)			0.00 (NS)

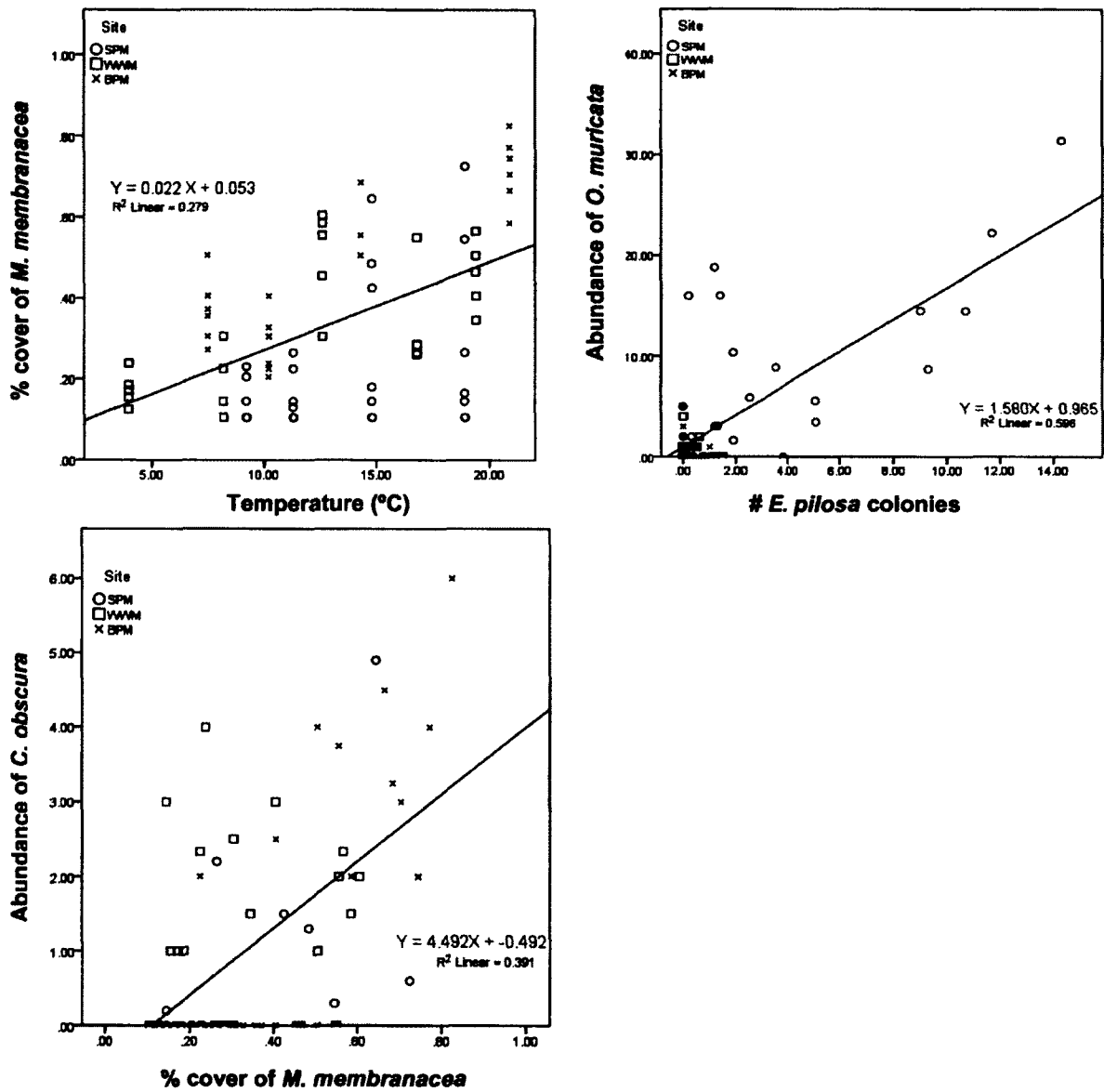


Figure 14: Scatter plots showing the most influential factors to percent cover of *M. membranacea* (temperature), abundance of *C. obscura* (percent cover of *M. membranacea*), and abundance of *O. muricata* (number of *E. pilosa* colonies).

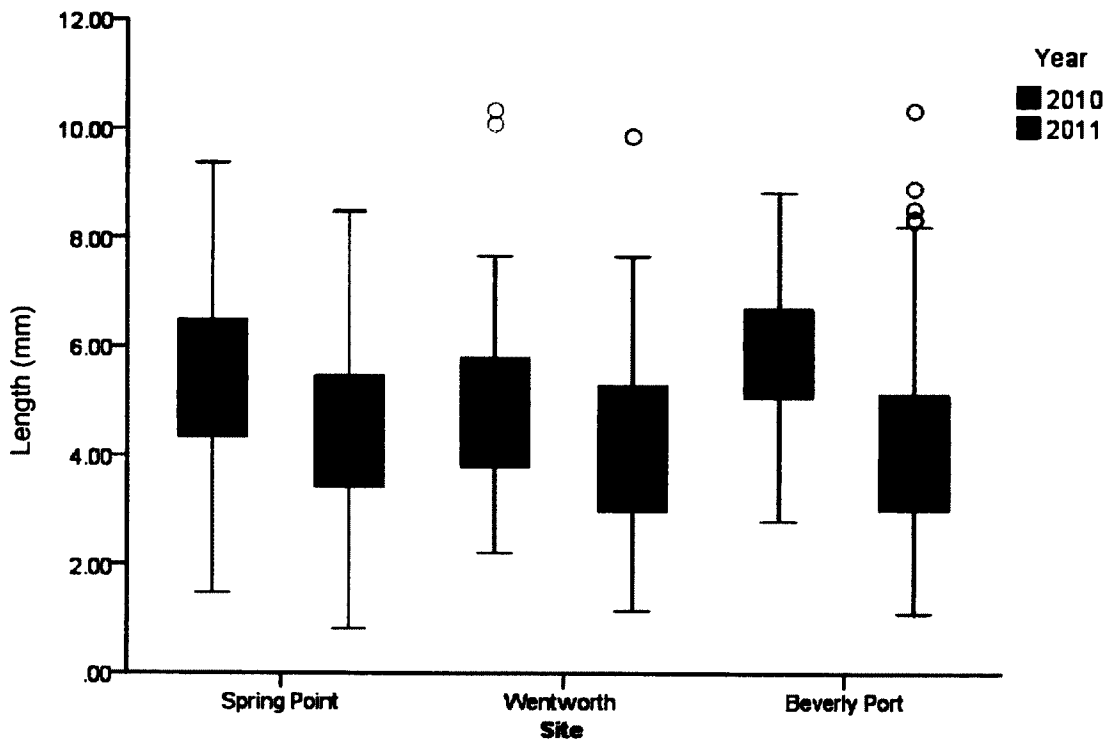


Figure 15: Minimum, mean, and maximum lengths of *C. obscura* surveyed at all field sites both years.

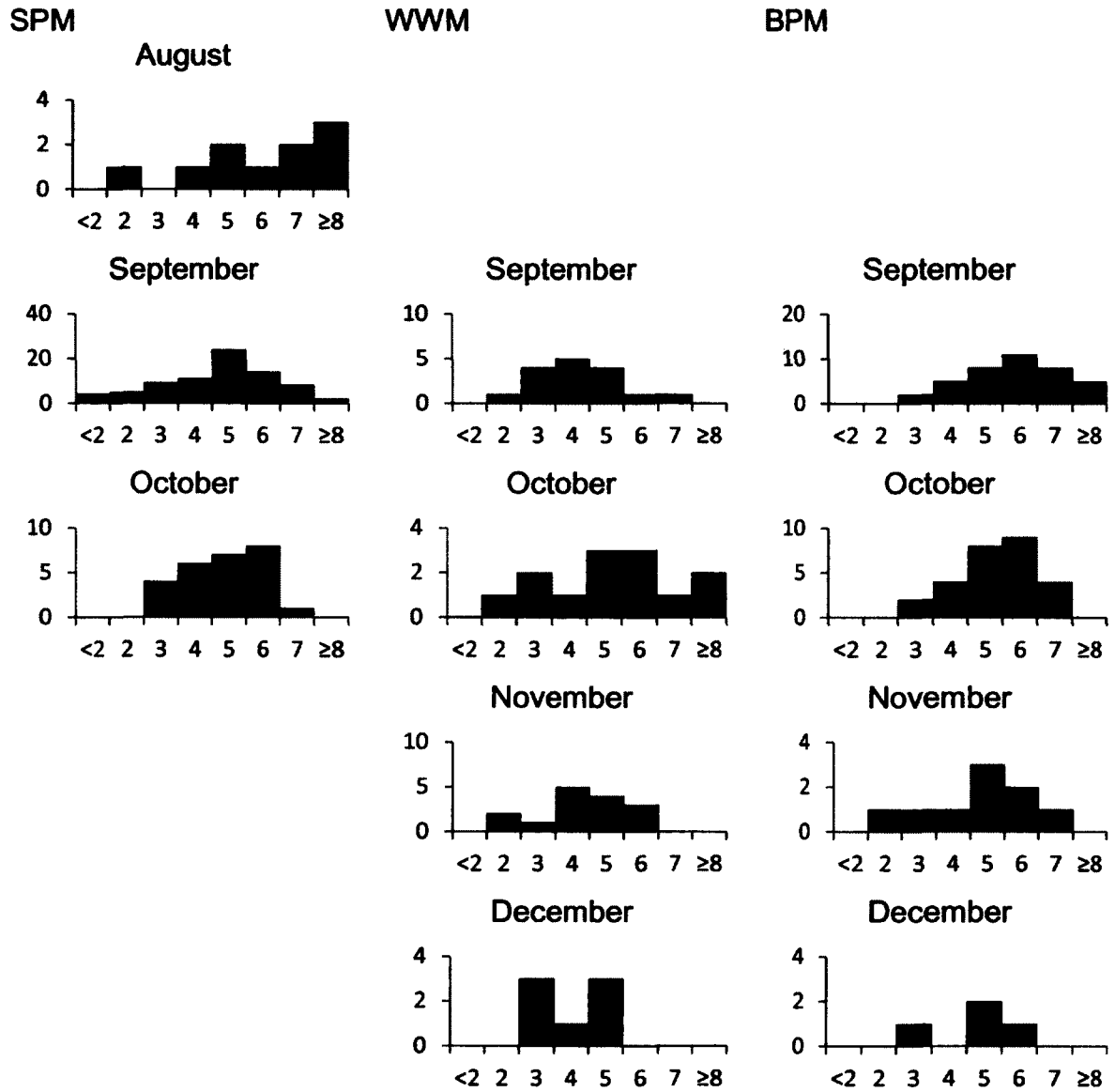


Figure 16: Monthly size-frequency distributions of *C. obscura* for 2010.

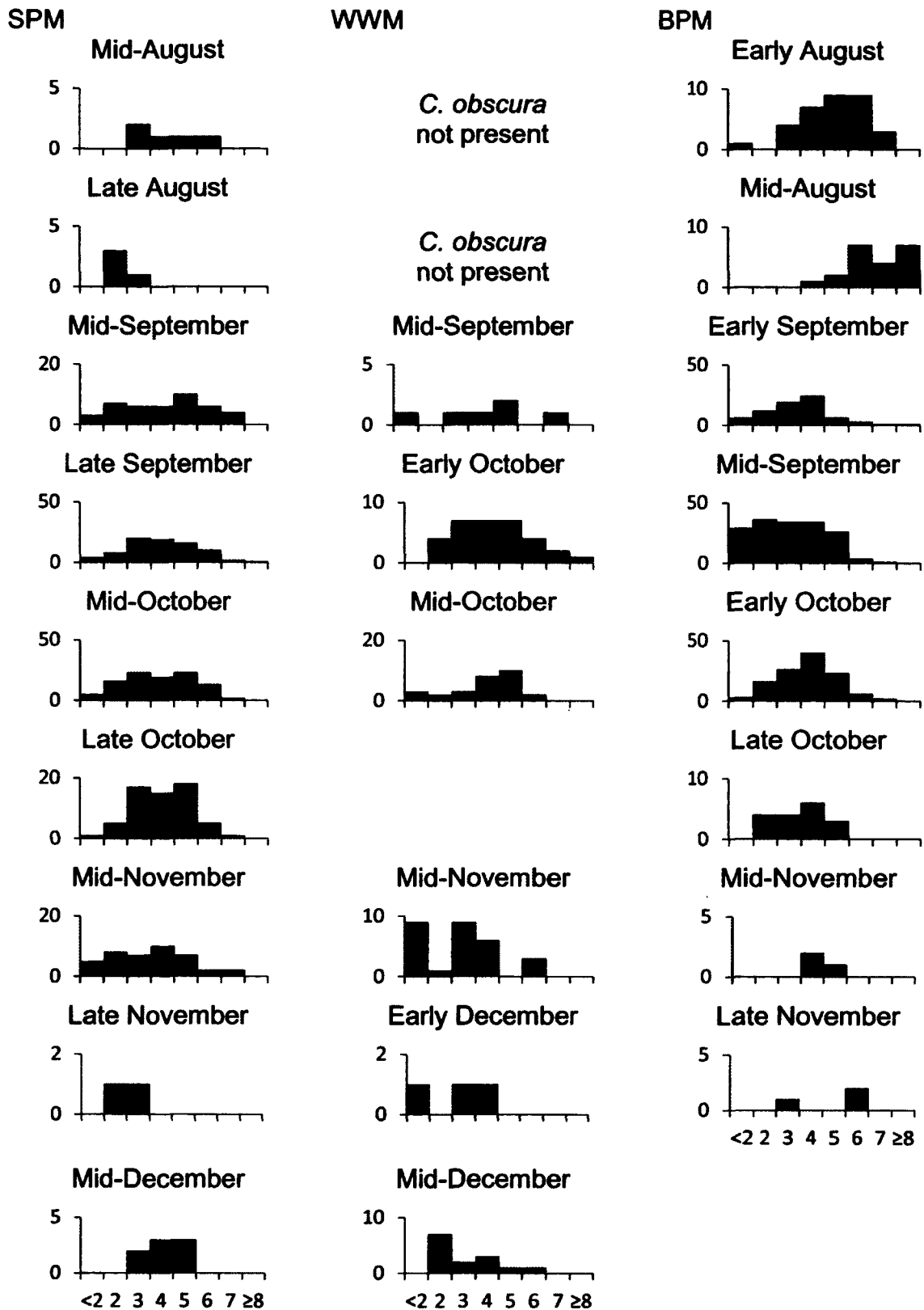


Figure 17: Seasonal size-frequency distributions of *C. obscura* for 2011.

Table 5: The number of *C. obscura* feeding and not feeding in the feeding trials at each temperature treatment.

	Treatment			
	4°	10°	15°	20°
<b>Did not feed</b>	7	3	3	3

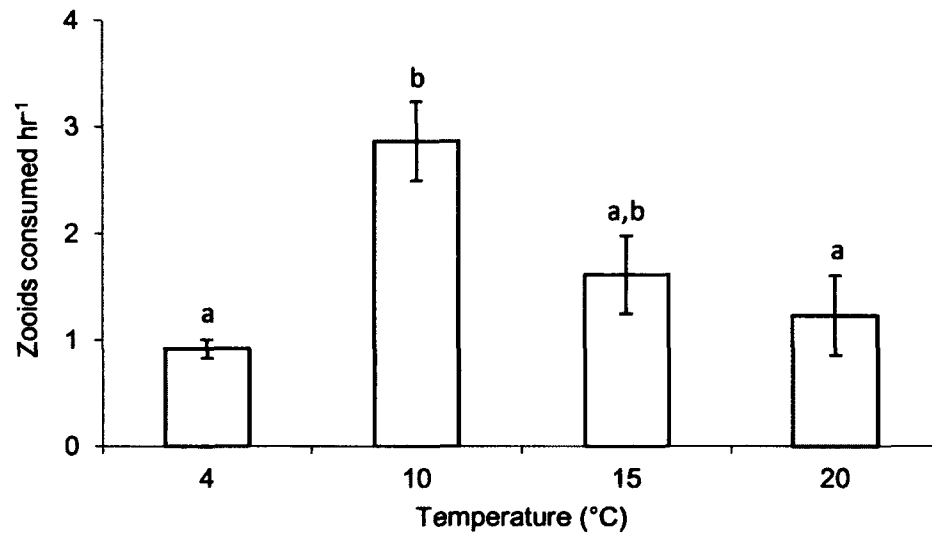


Figure 18: Mean number of zooids consumed per hour ( $\pm$  SE). Letters indicate homogeneous subsets.

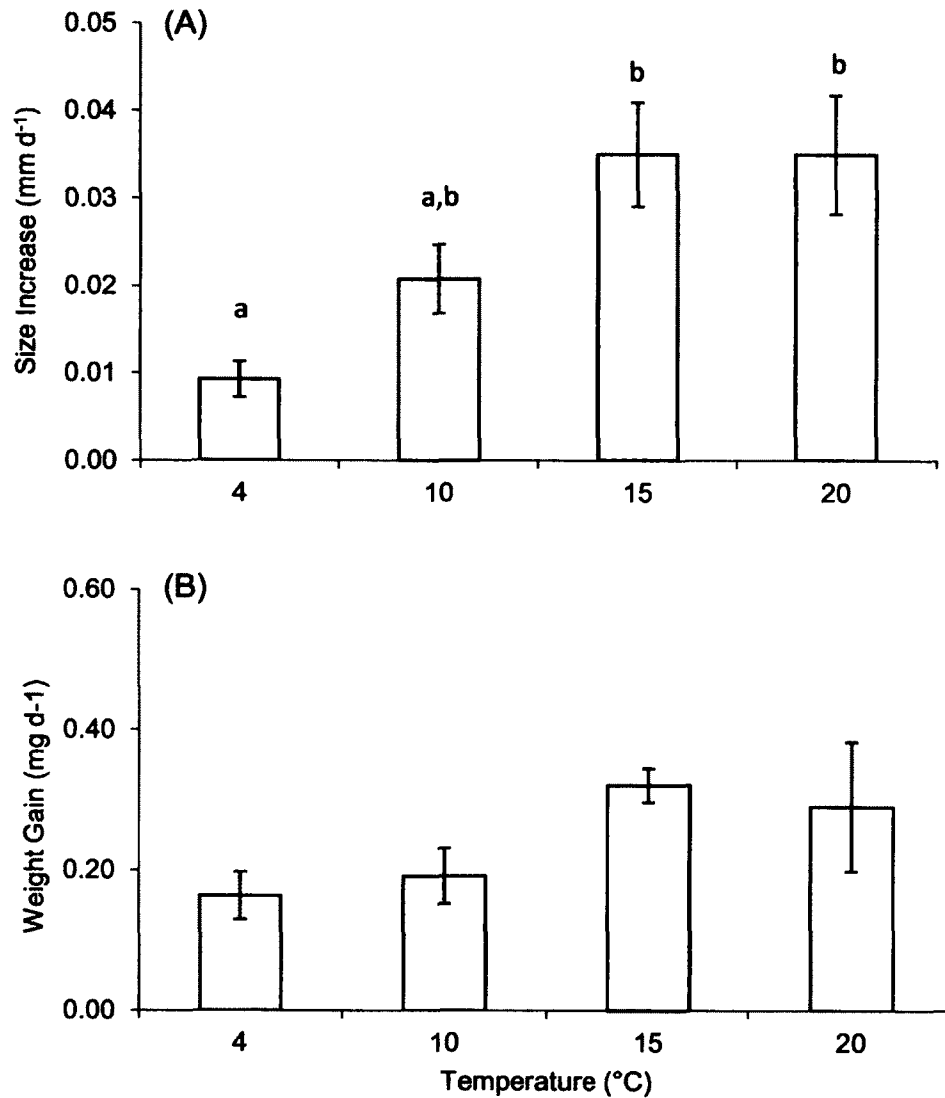


Figure 19: Mean percent daily growth rate of *C. obscura* ( $\pm$  SE). (A) Mean percent increase in length. (B) Mean percent daily weight increase. Letters represent homogeneous subsets.



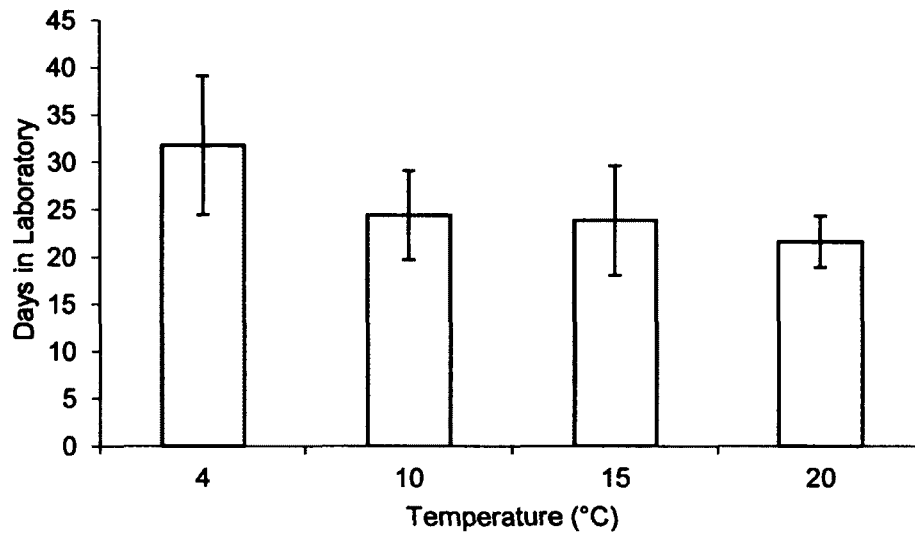


Figure 20: Mean maximum laboratory survival ( $\pm$  SE) of *C. obscura* at each temperature.

Table 6: Aspects of nudibranch spawning quantified in growth rate experiment. Mean # spawn calculated only with # nudibranchs that laid eggs.

	Treatment			
	4°	10°	15°	20°
<b># nudibranchs laid eggs</b>	4	13	22	13

Table 7: Capsule and ovum sizes, ovum/capsule ratios at each temperature ( $\pm$  SE) by temperature.

Treatment	Capsule ( $\mu\text{m}$ )	Ovum ( $\mu\text{m}$ )	Ovum/Capsule Ratio
10°C	102.12 $\pm$ 2.01	70.36 $\pm$ 1.26	0.692 $\pm$ .07
20°C	90.79 $\pm$ 1.47	68.26 $\pm$ .93	0.751 $\pm$ .09

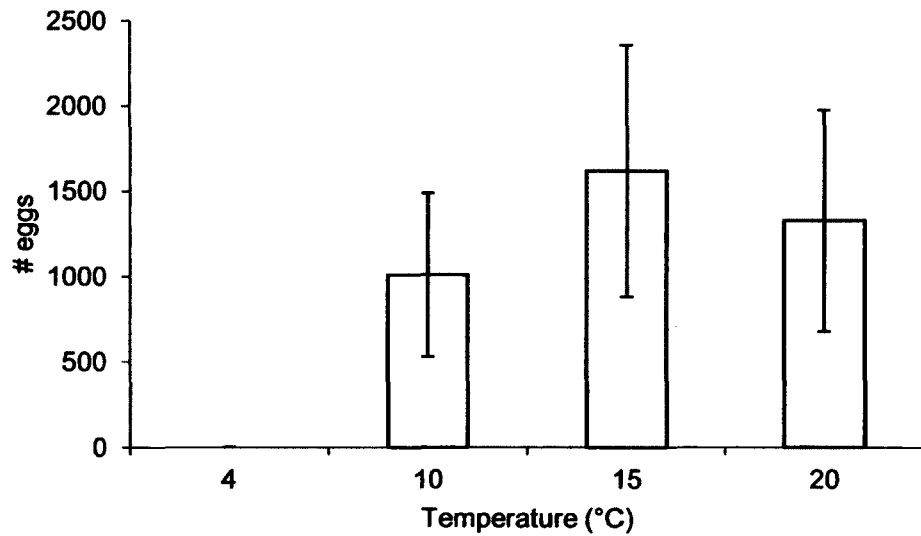


Figure 21: Mean number of eggs per spawn mass ( $\pm$  SE). No photographs were taken of spawn masses at 4°C.

## DISCUSSION

### **Abiotic Factors**

The abiotic factors measured at each site differed not only due to latitude (temperature), but also due to the location of the site within their bays or harbors relative to the Gulf of Maine and the layout of the marinas sampled (flow rate). Spring Point Marina (SPM) in South Portland, ME was the most northern site, but was not the site with the coolest sea surface temperatures (Figure 2, Figure 3). However, this site was also the most protected from the Gulf of Maine (Figure 1B) and could have a higher influence of solar warming due to lower flow during tidal exchange (Figure 4). Wentworth Marina (WWM) in New Castle, NH had the lowest temperatures out of all sites in 2010 (Figure 2), despite being south of SPM (Figure 1B). The flow rate at WWM was at the higher end due to its location in Portsmouth Harbor, though was probably not as high as flow rates of Beverly Port Marina (BPM) because of the presence of flow-reducing structures such as breakwaters and land barriers (Figure 1C). Beverly Port Marina (BPM) in Beverly, MA had the highest temperatures (Figure 2) and the highest flow rates (Figure 4) due to southern latitude and proximity to the Gulf of Maine without flow barriers (Figure 1D).

## **Biotic Factors**

Biotic factors such as kelp size, *Membranipora membranacea* percent cover, and nudibranch (*Corambe obscura* and *Onchidoris muricata*) abundances were different between sites, within sites, and between sampled years just as abiotic factors were. However, trends suggest that community members rely on abiotic factors and interactions with other species within the community for their settlement, growth, and reproduction (Table 4). Thus, they will be examined in the following sections.

## **Ecological Interactions**

### **Abiotic Factors**

The affect of abiotic factors on marine organisms is variable depending on species. Clearly, organisms must be able to withstand wide ranges of temperatures when their habitat is within the intertidal zone (Menge and Branch 2001), but those that live subtidally may have a smaller thermal range (Witman and Dayton 2001). Current, on the other hand, is more important to sessile species which require it for dispersal of larvae, nutrient/food transport, and chemical cue reception than for mobile organisms (Baynes and Szmant 1989, Eckman and Duggins 1993, Gaylord and Gaines 2000, Fingerut *et al.* 2011). In the Gulf of Maine fouling community surveyed, it appears that temperature and current affect the biota in different ways.

**Larval Density:** The density of larvae was highest at all sites at docks closest to shore despite lower flow rates (Figure 4). This could be due to larval

retention in low-flow areas (Chiswell and Roemmich 1998). Although the density of larvae was lower in high-flow areas, more larvae flow past potential settlement sites (Mullineaux and Butman 1991). If this is the case, the higher density of larvae in the protected areas may not be transported to a settlement substrate. Indeed, this study's estimate of larvae in flow suggests that exposed docks would have higher numbers of larvae flowing past the substrate (Figure 5B).

Only one sampling of larvae was completed during December, 2011 of this study. In the plankton tow, larvae found were nauplii, cyprids, and veligers, but if tows had been sampled during the survey season, it would be expected that there would be a higher abundance of veligers, cyprids, and cyphonautes larvae. For more accurate results, plankton tows should be made regularly throughout future studies.

*Saccharina latissima*: Kelp size relied heavily on temperature and was seen to have a significant inverse correlation with temperature (Table 4, Figure 7). Preference for lower temperatures by *S. latissima* is well documented (Bolton and Luning 1981, Lee and Brinkhuis 1986, Sjutun 1990, Davison *et al.* 1991, Bruhn and Gerard 1996). Optimal growth occurs between 10° and 15°C, while growth reduction was observed after 20°C and complete disintegration occurred after one week in culture studies at 23°C (Bolton and Luning 1982). This small range of optimal temperature greatly limits their geographical distribution to temperate and boreal environments. In the Gulf of Maine, these kelps began decreasing in size in July, when temperatures began to peak.

Current appeared to affect the morphology of surveyed kelps as well; kelps in lower flow situations had wider, shorter blades (SPM) and kelps in higher flow locations had narrower, longer blades (WWM and BPM; Figure 6). Similar morphological changes to current were found by Gerard (1987) and Coyer (2004). Specialized morphological characteristics such as flexibility and strong holdfasts allows kelps to thrive in high-current environments (Koehl and Wainwright 1977). Flexibility allows for tolerance to stress that algae require for survival (Davison and Pearson 1996).

*Membranipora membranacea*: Kelp percent cover by *M. membranacea* changed over the course of the field season and appeared to be correlated to temperature, though there was a lag time between peak temperatures and peak *M. membranacea* (Figure 11). This study showed that *M. membranacea* settles in late spring/early summer and most colonies senesce in winter, though some colonies overwinter. In addition, Saunders and Metaxes (2009) found that 84-87% of variation in growth rate of colonies of *M. membranacea* was due to the combination of colony size and temperature. The difference in *M. membranacea* abundance between surveyed years could be due to temperature as well. Saunders and Metaxes (2007) found that more growing degree days (thermal history) in the winter and spring months preceding *M. membranacea* settlement accounted for 81% of variation in settler abundance with earlier colonization and higher abundance during summer and fall. Winter temperatures of 2010 were generally lower and lasted a longer period of time than those temperatures in 2011. Because sampling did not start until August or September, 2010, it is

unclear when *M. membranacea* settled, but when comparing abundances during sampled months between years, it is clear that there was an overall higher percent coverage of *M. membranacea* on kelp blades in 2010 (Figure 11) than 2011. This suggests that the preceding winter might play a part in the lower percent cover of *M. membranacea* on blades in 2011 despite a favorable growing season, making this study's findings in accordance with those of Saunders and Metaxes (2007).

At the site with the clearest flow gradation (SPM), percent cover of *M. membranacea* on kelps was correlated with current, indicating that *M. membranacea* may be able to reach a higher percent cover with more flow because, as filter feeders, they can feed at a higher rate due to higher food availability (Pratt 2008). Pratt (2008) found that zooid ingestion rates are higher with increasing flow velocity, with decreased ingestion rates occurring at  $7 \text{ cm s}^{-1}$  for *M. membranacea*. The flow rate and larval densities at the docks furthest from shore further shows that more plankton will be flowing past these areas (Figure 5B). There was little to no correlation between bryozoan cover and flow rate at the sites with docks perpendicular to shore (WWM and BPM), however, WWM had a lower larval density than BPM, which could be why there is an overall higher percent cover of *M. membranacea* on kelp blades at BPM. Docks with intermediate flow rates at WWM and BPM often appeared to have the highest bryozoan percent cover, indicating better growth rates. In addition to findings by Pratt (2008), Eckman and Duggins (1993) found that higher flow rates ( $4.5 \text{ cm s}^{-1}$  and above) can cause shaking of tentacles, which may reduce particle

retainment and thus reduce growth in bryozoans. Water currents, in addition to temperature, clearly influence the overall amount of *M. membranacea* at each site.

*Corambe obscura*: Temperature was not highly correlated with the abundance of *C. obscura* per blade (Table 4). The veliger larvae of *C. obscura* are viable at temperatures ranging from 1.5 to 28°C (Perron and Turner 1977). Thus, it is likely that the lower temperatures found at WWM and SPM probably do not affect the mortality of *C. obscura*. The abundance of *C. obscura* between years increased from 2010 to 2011, which could be due to temperature differences between years during sample seasons (Figure 2, Figure 9). The low correlation between temperature and the temporal changes in both percent of encrusted kelps infested and the abundance of *C. obscura*, suggests that food availability is more influential than seasonal temperatures found in the Gulf of Maine on their settlement sites and abundance within the Gulf.

The abundance of *C. obscura* was higher at lower flows. Current is an important vector for chemical cue transmission to a larva from the water column (Turner *et al.* 1994, Hadfield and Koehl 2004). Nudibranchs are extremely specialized in their food preferences and their veliger larvae settle on or near the prey of the adult stage after cues are encountered (as reviewed in Harris 1973). Hadfield and Koehl (2004) found that the nudibranch *Phestilla sibogae* instantly responds to chemical cues by retracting the velar lobes and extending the foot, which causes them to sink to the coral substratum; however, once the chemical cue is lost, swimming is resumed (Hadfield and Koehl 2004). Veligers of *C.*



*obscura* swim strongly upwards after hatching (Perron and Turner 1977) which could be a behavioral adaptation for better dispersal and chemical cue reception. *C. obscura* requires a physical encounter, not just sensing chemical cues of prey (Perron and Turner 1977). Therefore, while flow is influential in transporting *C. obscura* larvae, low flow is likely better than high flow because it is easier for them to attach to the substrate and cast their larval shells.

*Onchidoris muricata*: Neither temperature or current was highly correlated to *O. muricata* abundance (Table 4). However, *O. muricata* was primarily found at SPM, which had the most observed colonies of *Electra pilosa* on kelps.

#### Interactions between species

It is clear that these community members respond not only to abiotic factors such as temperature and current, but also to biotic factors such as the presence of a settlement host (*M. membranacea*), chemical cues from prey items (nudibranchs), and the abundance of food. The results of this study indicate that biotic factors may, in fact, be more important than abiotic factors.

Kelps with higher percent cover of *M. membranacea* were larger at all sites in early summer (Figure 7), suggesting that *M. membranacea* preferably settles on larger hosts or simply have a higher probability of encountering a large kelp. This agrees with the findings of Berman *et al.* (1992). Size of kelps decreased with increasing percent cover of *M. membranacea* (Figure 7). This relationship could be due to the natural decrease in sizes of kelps during warmer months, but kelp blades did appear to decrease in size over a short period of time when they had large percent cover of bryozoans and decrease over a longer

period when they had little to no percent cover of *M. membranacea* (Figure 7). The negative interaction between invasive colonies of *M. membranacea* and kelps has been widely studied (Dixon *et al.* 1981, Lambert *et al.* 1992, Hurd *et al.* 1994, Hurd *et al.* 2000, Saier and Chapman 2004, Pratt 2008, Saunders and Metaxas 2008). In the northwest Atlantic, invasive *M. membranacea* colonies affect kelp life history, including decreased spore production (Saier and Chapman 2004), photosynthetic activity (Oswald *et al.* 1984), nitrogen intake (Hurd *et al.* 1994), and overall decrease in kelp canopy cover due to higher rates of defoliation (Lambert *et al.* 1992, Saunders and Metaxas 2008). As a result, encrusted kelps become unhealthy and are more susceptible to disintegration during warmer months when availability of nutrients is low (Gagne *et al.* 1982). The calcium carbonate colonies of *M. membranacea* also makes encrusted kelps more brittle and susceptible to breaking or tearing during winter months, especially at the stipe where the meristematic region is lost (Lambert *et al.* 1992).

The correlation between percent cover of *M. membranacea* and abundance of *C. obscura* was higher than those of both abiotic factors (current and temperature). Temporal changes in populations show that abundance of *C. obscura* does not increase with increasing temperatures; instead, their abundance increases after a short lag time in response to increase in percent cover of *M. membranacea*. Furthermore, the seasonal abundance pattern of *C. obscura* follows that of their prey (Figure 11). *C. obscura*'s specialization to *M. membranacea* is not surprising. Many nudibranchs are highly specialized to a specific prey type and have adapted not only their morphology, but also their

behavior (Harris 1973, Todd 1981). Species such as *M. membranacea* are ephemeral, which require nudibranch predators to trend towards shorter life-times, higher reproductive outputs, and planktonic larvae (Yoshioka 1986). These life history patterns are seen in related species which share the same genus, *Corambe*, on the California coast (Yoshioka 1986). Furthermore, these Californian species have adapted to settle on *M. membranacea* only at high densities and will delay settlement to do so (Yoshioka 1982). *C. obscura* in this study follows similar life-history patterns.

There was no correlation between abundance of *O. muricata* and percent cover of *M. membranacea* (Table 4), which is most likely due to their preference for *E. pilosa* (Pratt and Grason 2007). Indeed, the abundance of *O. muricata* was highly correlated to the number of *E. pilosa* colonies while no relationship was found between the abundance of *O. muricata* and percent cover of *M. membranacea* (Table 4).

#### Feeding preferences of *Onchidoris muricata* in the field

Field studies of *O. muricata*'s bryozoan preference on kelps are lacking. In fact, Pratt and Grason (2007) suggest that future work is needed to quantify which bryozoan *O. muricata* feeds upon in the field. More newly settled *O. muricata* were found on *E. pilosa* as opposed to *M. membranacea* in early and mid-August, 2010 and 2011 (Figure 12). The proportion of *O. muricata* found on *E. pilosa* decreased throughout the season, though slugs found after late August were juveniles and adults. 90% of newly settled slugs were found on *E. pilosa* in early August, which proceeded to drop to about 60% in September, 2010 and

22% in late August, 2011. Number of *O. muricata* on *E. pilosa* should decrease over time as it is overgrown by *M. membranacea* or zooid resources are depleted. In fact, overgrowth was observed during this study and after late August, slugs persisted on *M. membranacea* for the rest of the season, with the exception of November and December, 2010, in which the small number of slugs was found on *E. pilosa*, presumably when *M. membranacea* was being depleted and *E. pilosa* was more abundant. *O. muricata* clearly prefers to settle on *E. pilosa*, but will also settle on *M. membranacea*, albeit at a decreased rate. As *O. muricata* is an annual species that settles in June and July and overwinters (Todd 1978b), it is possible that *O. muricata* might be switching food sources over time once *E. pilosa* stocks are depleted. This observation of *O. muricata* on *M. membranacea* in the concurrent presence of *E. pilosa* was noticed by Harris and Mathieson (2000) as well. Harris and Mathieson (2000) also predicted that some veligers might begin accepting *M. membranacea* as a settlement cue, which does appear to be happening. However, these slugs still prefer their traditional Gulf of Maine prey, *E. pilosa*.

#### Field Morphology of *Corambe obscura*

The average size of *C. obscura* was similar at all sites (Figure 2). Slug size was smaller in 2010 compared to 2011, but in contrast, slug abundance increased from 2010 to 2011 (Figure 9A). These two trends could be related, as more reproduction is occurring and there is a higher turnover rate, making the average nudibranch smaller. This size difference between years could also be due to lower food abundance and possible food limitation. There was a lower

percent cover of *M. membranacea* and higher abundance of *C. obscura* in 2011 compared to 2010. A higher abundance of food and lower abundance of predators could mean that they are able to feed at a higher rate due to the smaller chance of becoming food-limited. The concern of food-limitation increases through time as expressed by Yoshioka (1986), which might be more of a concern with decreased percent cover of *M. membranacea* and increased abundance of *C. obscura* in 2011 as opposed to 2010.

No studies to date (Franz 1967, Perron and Turner 1977, Swennen and Dekker 1995) have found *C. obscura* to reach sizes larger than 7.5 mm, but in this study they were consistently found to be over this size limit. The largest observed slug found was 10.3mm. Perron and Turner (1977) found slugs no larger than 7mm, but were also working in Barnegat Bay, NJ where temperatures reach 30°C in the summer. In the Gulf of Maine, temperatures never or rarely reach 20°C in summer. This temperature discrepancy could support that nudibranchs living in warmer temperatures are smaller on average due to higher turnover rates.

Size frequency distributions indicate that there are multiple generations of *C. obscura* within the few months they are present (Figure 16 & 17). These nudibranchs have short survival times in which they lay many eggs, an advantage to a species which utilizes an ephemeral food source (Yoshioka 1986).

### **Temperature and biology of *Corambe obscura***

Temperature affected all aspects of *Corambe obscura* life history studied. Individual feeding rates of *C. obscura* ranged from 0.2 to 5 zooids hr<sup>-1</sup> (mean across all temperature treatments=1.87 zooids hr<sup>-1</sup>), with the highest mean amount of zooids consumed at 10°C and less at 15°C, 20°C, and 4°C, respectively (Figure 18). These numbers may be conservative, as no nudibranchs in the feeding trials laid eggs. The number of zooids consumed relative to temperature by *C. obscura* was similar to feeding rates of related species in the Pacific feeding on *M. membranacea* at 13.5°C, *Corambe steinbergae* (1.12 zooids hr<sup>-1</sup>) and *C. pacifica* (2.29 zooids hr<sup>-1</sup>) (Yoshioka 1986). The feeding rates of *C. obscura* are closer to those of *C. pacifica* than those of *C. steinbergae*. Yoshioka (1986) found that the higher feeding rates of *C. pacifica* compared to *C. steinbergae* were related to higher numbers of eggs per mass.

Laboratory studies indicate that *C. obscura* is most efficient at warmer temperatures with regards to growth and reproduction (Franz 1967, Perron and Turner 1977). Despite their lower feeding rates (Figure 18), slugs at 15°C and 20°C grew the fastest (Figure 19), produced the highest number of eggs (Table 6), and had the highest number of eggs per mass (Figure 21). These findings agree with those of Perron and Turner (1977), who found that *C. obscura* larvae grew and settled faster and that the egg to egg time was shorter at higher temperatures. While Perron and Turner (1977) primarily studied larval growth, larval preference for warmer temperature could be in adult nudibranchs as well. Unfortunately, slugs in this study were unable to be reared from spawn collected

in the field and thus results on egg to egg time at different temperatures are unavailable.

Lower temperature appeared to create trade-offs for some life history traits. Nudibranchs at 10°C fed at a higher rate and had the eggs with the largest capsules, indicating that they may be allocating more energy to fewer, more protected spawn masses than energy to growth. *C. obscura* produces eggs with one ovum per capsule, so the energy spent on capsule production may be high. Indeed, Perron (1981) found that capsules require 20-50% of reproductive energy in the genus *Conus*. However, why *C. obscura* at 10°C are allocating energy to capsules and not ova is unclear. Further studies could measure size of larvae through development until hatching at the treatment temperatures used in this study.

In this study that manipulated temperatures up to 20°C, egg capsule and ovum sizes at all treatments were about 10µm larger than those presented by laboratory studies by Perron and Turner (1977) that manipulated temperatures up to 25°C. Perron and Turner (1977) also had field *C. obscura* lay an average of 2,500 eggs per mass, while in this laboratory study there were never more than 2,300 eggs per mass at any temperature treatment. This could be due to the temperature differences between the Gulf of Maine and Barnegat Bay, NJ. Gulf of Maine temperature only briefly reached above 20° (Figure 2) while temperature was recorded to reach 30° in Barnegat Bay in August, 1976 (Perron and Turner 1977). This is further evidence that this nudibranch species prefers warmer temperatures, as they lay smaller eggs, more eggs per mass at 25°C

(Perron and Turner 1977), grow faster, and lay more spawn masses despite shorter survival times in this study.

In this study, *C. obscura* was only fed *M. membranacea*, while Perron and Turner (1977) had slugs feeding on *Einhornia crustulenta*. *M. membranacea* was not present until 1987, thus, there is the possibility that prey species may affect life history aspects of *C. obscura* in addition to temperature. Further studies may look at how the biology of *C. obscura* differs when feeding upon these different bryozoan species.

#### Overlap of nudibranch predators

It is clear that there are a variety of factors that contribute to the presence of these predatory nudibranchs. As mentioned previously, nudibranchs are highly specialized to their prey. Thus, the presence of an acceptable or preferable food source (*M. membranacea*) is a pre-determining factor to the population expansion and growth of *C. obscura* within the last few years. Now that populations of *C. obscura* are established, they may be undergoing physiological reactions to the increasing Gulf of Maine temperatures. Furthermore, *O. muricata* is associated with *M. membranacea*, often sharing kelp blades and *M. membranacea* colonies with *C. obscura*. The highest incidence of both nudibranchs occurring together on a blade was 33 *O. muricata* and 25 *C. obscura*. As previously mentioned, this could increase the threat of food limitation, especially if there is a small percent cover of *M. membranacea* with a high abundance of nudibranch predators.



These two nudibranchs are using the same food source. As partial predators, they consume colony zooids in patches, which could have implications on growth and reproduction of *M. membranacea* (Harvell 1984). Negative effects due to partial predation have been found by some workers (Harvell 1985, Todd and Havenhand 1989). Growth in encrusting bryozoans may be influenced by preferential predation on colony perimeters (Harvell 1984, 1985, Havenhand and Todd 1989). In this study, *C. obscura* was most often observed at colony centers. Thus, *C. obscura* may not be having a negative effect on *M. membranacea* growth by feeding on colony perimeters. Instead, the regeneration of zooids in the center that have been consumed by nudibranchs may be reducing energy allocated to colony growth in *M. membranacea* (Harvell 1984).

While not noted in this study, nudibranch predation can induce spine production in *M. membranacea* (Yoshioka 1982), subsequently reducing colony growth rates (Harvell 1986, Iyengar and Harvell 2002). Thus, short-term effects of decreased growth in *M. membranacea* directly relates to reduction in fecundity, as reproductive output is related to size of colonies (Harvell 1985). Long-term effects of decreased growth in *M. membranacea* colonies may reveal a reduction in fecundity as well as restrict their ability to prevent overgrowth by competitors, creating local patch disturbances and altering epifaunal assemblages (Todd and Havenhand 1989).

### Climate Change

The fact that temperature has an impact on these populations is clear, as evidenced by the increase in abundance of *C. obscura* (warm water preference)

increases and decrease of *O. muricata* (cool water preference) in 2011 compared to 2010 with increased sea surface temperature. Though the length of this study was limited to two seasons over two years, the difference between temperatures of 2010 and 2011, as well as the first observation of a higher abundance of *C. obscura* in 2009, gives insight as to what could be happening long-term with these species.

Climate change is the focus of many studies on invasions and range expansions and certainly should not be ignored (Davis *et al.* 1998, Hellmann *et al.* 2008, Sorte *et al.* 2010, Keith *et al.* 2011). *M. membranacea* has been present and increasing in abundance in the Gulf of Maine since 1987 (Berman *et al.* 1992), which is over two decades prior to the invasion of *C. obscura*.

Sea surface temperatures have risen since the introduction of *M. membranacea* (Dijkstra *et al.* 2011). Increasing temperatures could have facilitated persistence of *C. obscura* larvae in Gulf of Maine waters during years prior to this study, but not enough for them to establish a population if lower temperatures reduce fecundity as the results of this study show. During this study, temperatures in the Gulf of Maine have continued to increase in comparison to those presented up until 2005 by Dijkstra (2007). Additionally, before this study in 2008 and 2009, temperatures were lower on average than those of 2010 (Figure 2). These above average temperatures may be allowing *C. obscura* to establish permanent populations in the Gulf of Maine. *C. obscura* was found rarely past December on remaining *M. membranacea* colonies at the UNH Coastal Marine Lab Pier. With continuing increases in temperature that climate

change may bring in temperate waters, it is possible that *C. obscura* may begin to overwinter in higher numbers than found in this study and persist year-round, as they do in Barnegat Bay, NJ as observed by Perron and Turner (1977). Results indicate that these nudibranchs are capable of withstanding winter temperatures in this region, but laboratory results show that all aspects of growth and reproduction are reduced at lower temperatures (Figure 19 & 21). The caveat here is that *M. membranacea* does not typically persist in large abundances through winter in the Gulf of Maine, unless climate change increases their ability to subsist in cold temperatures as well.

On the other hand, *O. muricata* populations decreased between the two sampled years. Historically, *O. muricata* prefers cold water and is found to settle in summer and overwinter to begin reproducing in January (Thompson 1961, Todd 1978a, Bleakney 1996). Their decrease, despite the presence the food source *M. membranacea* offers, indicate that they may not be as abundant due to the higher 2011 temperatures compared to temperatures in 2010. Though winter temperatures in 2011 were lower than those of 2010, the small number of *O. muricata* found in December means that there were few left to reproduce. This reduction in abundance of *O. muricata* throughout the sampling season was interesting as well, as they should be overwintering (Figure 12). This could be due to predation, as living on flat-bladed *S. latissima* does not offer the protection that the folded blades of *Chondrus crispus* provide (Stachowicz and Whitlatch 2005).

This study was limited to two seasons of two years. In order to really assess the importance of temperature on settlement/abundance of these nudibranchs, surveys would need to continue for a longer period of time and for a longer field season. Future studies could also track specific kelps with and without bryozoan cover over time to track changes in their growth and the associated epifaunal community.

### **Conclusions**

Temperature and flow rate appear to be more important to community members such as kelps and *M. membranacea*. Laboratory studies and field observations suggest that temperature affects *C. obscura* life history aspects such as feeding rates, growth rates, and fecundity. Prey species appears to be the cause in the fluctuations in abundance and the seasonality of *C. obscura*. The high feeding rates, short life times, and large reproductive output of these newly established populations of *C. obscura* show high dependency on their ephemeral invasive food source.

In addition, while newly settled *O. muricata* are still found primarily on *E. pilosa*, juveniles and adults are associated less with the preferred native prey, *E. pilosa*, and are more with the invasive, *M. membranacea*. When *M. membranacea* was first studied in the Gulf of Maine it had no specialist nudibranch predators, but now native *O. muricata* and range expanded *C. obscura* overlap in habitat and invasive prey species. In the Pacific waters off the coast of California, *M. membranacea* has nudibranch predators which appear to

regulate its abundance (Harvell 1986). If these nudibranchs feed on overwintering *M. membranacea* colonies, perhaps they could regulate the abundance of this invasive bryozoan just as nudibranchs do on the west coast. Despite its brevity, this study gives insight into how abiotic and biotic factors interact within a small fouling community consisting of native, invasive, and range expanded species.

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