Fall 2008

Ecology, distribution, quantification, and impact of introduced, Asian Porphyra yezoensis f yezoensis Ueda and Porphyra yezoensis f narawaensis A Miura in the Northwestern Atlantic

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ECOLOGY, DISTRIBUTION, QUANTIFICATION, AND IMPACT OF INTRODUCED, ASIAN *PORPHYRA YEZOENSIS* F. *YEZOENSIS* UEDA AND *PORPHYRA YEZOENSIS* F. *NARAWAENSIS* A. MIURA IN THE NORTHWESTERN ATLANTIC

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THESIS

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the degree of

Master of Science

In

Plant Biology

September, 2008

This thesis has been examined and approved.

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31 July 2008

Date

DEDICATION

To Brita, my darling wife and best friend

ACKNOWLEDGEMENTS

I thank Dr. Arthur C. Mathieson, Dr. Christopher D. Neefus, and Dr. Larry Harris for their hard work in reviewing my thesis and making it worthy of publication by the University of New Hampshire. Your years of successful scientific writing have made you excellent editors and teachers.

I thank Dr. Mathieson and Dr. Neefus for taking me out to the intertidal during the coldest months of the year. Before I met you, I had never pictured the seacoast covered with snow.

I also thank the Sea Grant Foundation for funding my research, and the University of New Hampshire for funding my education and summer research efforts through teaching assistantships, the Summer TA Fellowship, and the COLSA Summer Fellowship. Without this support, this project would have been impossible.

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ECOLOGY, DISTRIBUTION, QUANTIFICATION, AND IMPACT OF INTRODUCED, ASIAN *PORPHYRA YEZOENSIS* F. *YEZOENSIS* UEDA AND *PORPHYRA YEZOENSIS* F. *NARAWAENSIS* A. MIURA IN THE NORTHWESTERN ATLANTIC

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Invasive species pose a threat to the balance of intertidal ecosystems. Recently, two forms of the non-native species, *Porphyra yezoensis* Ueda, were found at multiple sites between New York and Downeast Maine. A 2007 New England survey confirmed the presence of *P. yezoensis* f. *yezoensis* at nine sites, including two beyond its reported distribution. *Porphyra yezoensis* f *narawaensis* A. Miura was found at four sites in Long Island Sound. To assess the ecological impact of f. *yezoensis* and f. *narawaensis* on Northwest Atlantic macroalgal communities, monthly density and biomass data were gathered in 2008 from seven southern New England sites along 20 m transect lines. *P. yezoensis* f. *yezoensis* was not detected at two historic sites. The f. narawaensis has expanded to Cape Cod. Fucoid algae epiphytized by *P. yezoensis* demonstrated no stature reduction. A *Porphyra* species of cryptic origins, *P.* spp. *'stamfordensis,'* may be competing with *P. yezoensis*.

INTRODUCTION

Human consumption of *Porphyra* (nori) as food has occurred in Asia for over 1,000 years (Xia and Abbott, 1987). *Porphyra* is valued for its cholesterol regulating agent, taurine (Tsujii et al., 1983) and its high protein content (29-35% dry weight) which is 1.7 times higher by weight than beef (Arasaki and Arasaki, 1983). *Porphyra* is also an excellent source of vitamin A, being 67 times higher than found in eggs, and vitamin C, having 1.5 times more than in oranges (Xia and Abbott, 1987).

Porphyra has been a staple of healthy diets in Asia for centuries (Mumford and Miura, 1989). In China, *Porphyra* is eaten in several ways including: sushi; lightly fried and flavored with soy sauce, sugar, or sesame oil; in soups; with pork in dumplings; or stir fried with other vegetables and meat (Xia and Abbott, 1987).

Porphyra also has important medical and scientific uses in that it contains the phycobilin red pigment r-phycoerythrin, which is utilized as a fluorescent tag for labeling antibodies, proteins, and nucleic acids. Phycobiliprotein dyes can be used in applications such as immunofluorescence microscopy, microarrays, and flow cytometry.

The widespread production of *Porphyra* as a food stuff and fluorescent tag was not possible until its complete life history was understood. For hundreds of years before, farmers recognized the diploid stage of *Porphyra* (Figure 1), they 'farmed' the blades by rock cleaning and, to increase production, bamboo 'planting'(Tseng, 1984). Based upon experience, early Chinese and Japanese nori farmers readied their rocks rods at times of year they expected the arrival of *Porphyra* 'seeds' (Tseng, 1984). Heavy reliance on the abundance of nature without fully understanding the developmental processes of *Porphyra* kept Asian farmers from producing industrial levels of nori.

Kathleen M. Drew's 1955 discovery of '*Conchocelis rosea*' as a microscopic life history phase of *Porphyra umbilicalis* Kütz removed the largest obstacle to the successful phycoculture of various *Porphyra* species. With the understanding that the highly resilient, shell boring, diploid sporophytic conchocelis stage was the source of 'seed' for the valuable haploid gametophytic blade phase of *Porphyra,* large scale production of nori began in earnest in Asia in the late 1950s (Tseng, 1984). By placing nets seeded with conchospores from the cultured conchocelis into coastal waters, Asian nori farmers were able to boost production to unprecedented annual values, which, by the 1990s, neared US $1.5 billion (FAO, 1997; Hanisak, 1998).

Not only have Asian nori farmers learned how to maximize the production of their native seaweeds, but they have developed, since the 1960s, fast growing cultivars of their most desirable *Porphyra*, including *P. tenera* Kjellman and *P. yezoensis* (Patwary and van der Meer, 1992). *Porphyra yezoensis* f. *narawaensis* A. Miura, which is now found in the northwest Atlantic, was developed from a single strain in the late 1960s at a nori farm in Narawa in the Chiba Prefecture of Japan (Niwa and Aruga 2003). Cultivars derived from this strain are highly prized in Japan for rapid growth, lengthy vegetative period, blade size (up to 1 m in length). When used in the production of hoshi-nori, its texture and flavor are deemed superior (Miura 1984). The smooth, dark-green to black, rectangular sheets can be eaten alone or as a wrapper for sushi containing vinegared rice, thinly sliced vegetables, and fish. By the late 1980s, because of their growth characteristics and quality, forma narawaensis cultivars were nearly the only ones grown in Japanese nori-culture (Miura and Aruga 1987). Also at this time, Miura and Aruga (1987) determined that nori farming along the Japanese coast was so extensive as to be nearly saturated.

Because the production of nori in Asia was highly lucrative, scientists and speculators in the United States and Canada became interested in bringing commercial nori-culture to North America. In the late 1970s, *Porphyra* cultivation began in western North America under the impetus of Thomas Mumford, Jr. and J.E. Merrill at the University of Washington and the Washington State Department of Natural Resources (Merrill, 1981; Mumford, 1990). Merrill, having studied for a year under Miura in Tokyo, pushed for *Porphyra* cultivation in Washington State for two reasons: the coastal waters of Washington were nearly ideal year-round, whereas in Japan only the winter months were suitable for blade development; the sushi industry had begun to flourish in the US, driving up imports (Mumford, 1990). After extensive consultation and assistance from Japanese nori-culture experts, Merrill determined that *Porphyra* cultivation, using established technology and techniques, was possible in coastal Washington (Merrill, 1981). A Washington Department of Natural Resources study followed, which determined that the US could 'enter and compete in the market for products of the red seaweed *Porphyra*' (Kramer et al., 1982).

Nori farming at several sites in Washington US began in the early 1980s, using some native North American species and several cultivars imported from Japan (Mumford, 1987). Researchers and businessmen opted to use species from Japan, including *Porphyra yezoensis* f. *narawaensis*, because there was an established, global market for this species. They believed the cultivars posed little risk of permanent introduction to the region due to two factors: they believed that, in Washington, the combination of coastal water temperatures and day lengths would not allow the conchocelis to reproduce; and they believed the area had likely been inoculated with Japanese *Porphyra* conchocelis, through the shells imported for oyster culture, for fifty years without establishment of the species (Mumford and Hansen, 1987; Conway et al., 1975).

Utilizing the techniques of modern Asian nori-culture, several private companies grew *Porphyra yezoensis* with some success in the late 1980s, including New Channel Nori in the San Juan Islands that produced the equivalent of nearly 500,000 nori sheets processed by Canada West Nori (Mumford, 1990). Because of the successes of the few establish nori-farming firms in Washington, Mumford estimated that the industry could have been well developed in that area by the year 2000.

Although the cultivation of *Porphyra* in western North America showed promise, unanticipated political and ecological obstacles interfered with the establishment of the industry. Individual coastal land owners and special interest groups fought against the permitting of nori farms based on ecological concerns (the potential introduction of new species and resulting impacts). They also argued that the floats and nets used in nori-culture had a negative impact on coastal views and, therefore, property values. The grass roots pressure swayed the legislative process and resulted in severe permitting difficulties (Mumford 1990). When permits were given, it was determined that floating debris was a greater problem than anticipated. The region's unique hydrogeographic characteristics caused drifting logs, branches, plastics, and seaweeds to become entangled in the

Porphyra floats, which led to production inefficiencies and, in some cases, required the construction of expensive barrier systems (Mumford 1990).

Despite the setbacks in the nori farming attempts in western North America, scientists and entrepreneurs in New England attempted to cultivate *Porphyra* for economic purposes in the 1990s. Initially, Coastal Plantations International attempted to grow *Porphyra yezoensis* f. *narawaensis* in Downeast Maine for its potential use as a food product and for phycobilin pigment production. It was hoped the industry would be a financial boon to the struggling economy of Washington County, Maine (Levine, 1998). Again, permits were approved for the culture and outplanting of this non-native species due to the belief that photoperiod and water temperatures would not allow sexual reproduction or permanent establishment of the species (Watson et al., 1998). Attempts to successfully farm the commercial Japanese cultivars failed due to nutrient limitations and a lack of understanding of the seasonality of *P. yezoensis* in New England. The gametophytic blade phase of this species only appears in the late winter and early spring months in New England, but Coastal Plantations International attempted to grow the blades during the summer months believing temperatures and light levels were superior at that time (Yarish, personal communication). Their initial failures did not end the attempts to grow nori in Maine.

Because *Porphyra* species have been determined to be highly efficient in the uptake of nutrients commonly found in eutrophic waters, it was proposed that they could be used as bioremediators in areas of established fish farms (Chopin and Yarish, 1998). Uptake and growth observations using native *Porphyra* species (*P. purpurea* (Roth) C. Agardh and *P. umbilicalis*) and non-native *P. yezoensis* were made in natural habitats, on nets, and in integrated aquacultural systems. Comparisons were made between ambient and tissue P and N levels. *Porphyra* species reduced P and N to non-harmful levels, and it was estimated that between 22 and 27 nori nets would be needed per ton of finfish produced per year to offset the P and N (Chopin and Yarish, 1999), with *P. yezoensis* and *P. purpurea* deemed the best bioremediators tested. Further assessment of the bioremediation of other native species, including *P. leucosticta, P. amplissima, P. linearis*, was proposed along with a cultivar improvement program (Yarish et al., 1999).

While, to date, commercial scale nori farming has been largely unsuccessful in North America, *Porphyra yezoensis* has become established in regions of the continent's coast. Extensive field collections, herbarium specimens, and molecular evaluations have confirmed the occurrence and the distribution of two distinct *P. yezoensis* genotypes in the northwestern Atlantic (Bray, 2006; Mathieson et al., 2008; Neefus et al., 2008). One of the two genotypes has an ITS-1 sequence identical to a GenBank sequence from a specimen of *P. yezoensis* f. *yezoensis* that was collected from the wild near Nanaehama, Hakodate, Hokkaido Japan (Neefus et al., 2008). The distribution of this forma extends from Maine to New York. The ITS-1 sequence of the second forma is identical to more than a dozen recently developed commercial cultivars of *P. yezoensis* f. *narawaensis;* Its distribution is more limited and extends from Hammonassett State Park near Madison, Connecticut, in the west, to Westport, Massachusetts, in the east (Figure 2). While f. *narawaensis* occurred within the range of f. *yezoensis*, Bray (2006) reported that at sites where f. narawaensis occurred, f. yezoensis was absent. Such patterns suggested that competition favored the commercial cultivar (Bray, 2006, Neefus et al. 2008).

The modes of introduction of alien species have been studied extensively due to the sometimes devastating ecological and economic effects recognized since the early 1900s (Ostenfeld, 1908; Elton 1958; Carlton 1999). It has been determined that no region of the world is without established alien marine species (Carlton, 1979), including 260 alien marine macroalgal species (Hewitt et al., 2007). Because introduced macroalgal species are not easily eradicated or controlled once established, much effort has been directed at identifying vectors of transport and release. The modes of transport and inoculation of alien marine species into new regions have been detailed by many and include wooden-hull boring; fouling of and subsequent transport of fishing nets, relocation of oil rigs, and untreated metal ship hulls, recreational boat hulls; dry ballast (intertidal rocks and sand); ballast water uptake and release; attachment to sea chests or propellers, intentional transfer of maricultural organisms (including shellfish, finfish, and seaweeds); accidental transfer of organisms associated with maricultural organisms; improper disposal of live, frozen, or dried seafood; accidental release from aquaculture; improper release of aquarium stock; and the improper disposal of seaweeds used as packing material for live bait (Elton 1958, Carlton 1996, Weigle et al., 2005).

Because *Porphyra yezoensis* is a resilient organism with a complex life history that includes sexual and multiple forms of asexual reproduction, it could be transported from its point of origin to new regions by most of the above mentioned modes. Hewitt et al. (2007) delineated the likelihood of encounter and the survival constraints associated with the common modes of alien transport, which included ease of uptake in ballast water, association with a target species (oysters) or habitat (subtidal conchocelis), ability to survive the shear stresses of transport on the exterior of a vessel, survival of desiccation, darkness, crushing stress, and exposure to climate change. The conchocelis stage of *P. yezoensis* is likely to encounter and survive the uptake transport modes of most dispersal vectors.

Though one might point to nori-culture in America as the source for the establishment of *Porphyra yezoensis* f. *narawaensis* in the northwestern Atlantic, evidence suggests that it is not the vector to blame. Although f. *narawaensis* cultivars were imported and out-planted into the waters of Cobscook Bay in Downeast Maine, this genotype has not subsequently been discovered north of Long Island Sound (Bray, 2008). Because the water temperature and light regimes are markedly different north and south of the Cape Cod, and because hydrogeographic mixing and boat traffic north to south across this barrier are minimal, Coastal Plantation's nori farms in Maine are not the likely source of f. *narawaensis* populations in New England (Neefus et al. 2008). Also, because Coastal Plantations International did not attempt to cultivate f. *yezoensis* and because there are herbarium specimens of f. yezoensis from New England that pre-date the CPI's operation, they cannot be its source of introduction in the region (Bray, 2006).

Although *Porphyra yezoensis* has the potential to be distributed to new regions by many of the known transport vectors. Both forms of *P. yezoensis* were likely transported to New England as shell boring conchocelis associated with organisms imported for use in mariculture (Bray 2006). Clokie and Boney (1980) found a close association between conchocelis infected shells in the subtidal zone and high density of *Porphyra* blades in the intertidal zone in the Firth of Clyde, Scotland. The earliest voucher specimens of *P.* yezoensis f. yezoensis were collected in the region in the 1960s (Bray, 2006), around the time another Asian algal species *Codium fragile* ssp *fragile* (Suringar) Hariot was introduced with oysters brought from Peconic Bay, Long Island, NY (Galstoff, 1962). It is believed that f. *narawaensis* was introduced to New England, in the 1980s, at about the time the cultivars were developed for widespread use in Japan (Neefus et al. 2008).

The establishment of the two forms of *Porphyra yezoensis* in the northwestern Atlantic is significant in that only a small percentage of macroalgae are ever found beyond their points of origin (260 of thousands). In Williamson and Fitter's (1996) treatise on invaders, they proposed that only one in ten species are ever introduced to new regions via anthropomorphic transport vectors. Of these introduced species, only one in ten survive the transportation and the new environment for long enough to become established in the new region. Once established, one in ten of these introduced aliens becomes invasive (destructive environmentally and/or economically) in the new region. As *P. yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis* have been successfully transported and established in New England, according to Williamson and Fitter's estimation, the species has a ten percent probability of becoming invasive in this new region.

To predict future invading organisms Nyberg and Wallentinus (2005) delineated the traits common to successful invaders and produced of a list of thirteen characteristics indicative of invasive potential. The traits were based on the summaries given by Boudeouresque and Verlaque (2002), Ribera Siguan (2002), and Wallentinus (2002). and included: current geographical distribution (organisms found in roughly half of the world's regions were more likely to be invaders than those found in few or nearly all regions); probability of being transported; survival time out of water; salinity survival range; temperature survival range; tolerance to pollutants; reproductive flexibility;

growth strategy (stress tolerant, competitive, ruderal) including surface area to volume; defense mechanisms against grazing and infestation; thallus size (larger organisms being more likely to negatively impact new environments); morphology (crust and mat forming increases negative impact); and life span.

Using these criteria, Nyberg and Wallentinus (2005) evaluated 113 algal species introduced to Europe and an equal number of equivalent native European taxa. Species were awarded scores between 0 and 1 for each criterion, with the overall score being the average across the thirteen traits. The authors deemed the results of the evaluation reliable in that fifteen of the twenty-six invasive species were listed in the twenty highest ranked taxa. In this study, *Porphyra yezoensis* ranked 16th among the 77 red algal species evaluated. Although this ranking was high compared to other red algal species, *P. yezoensis* was not considered to have the potential of being highly invasive.

While hypothetical species-trait risk assessments can be useful for determining an organism's overall invasiveness potential, it has been common to find that a species invasive to one region is not invasive in another. An example of this phenomenon is *Codium fragile* ssp. *fragile* which has had a significant negative impact on the western Atlantic coast, while at the same time has had a minimal effect on the east Atlantic Ocean (Chapman, 1999; Schaffelke and Hewitt, 2007), though both regions are abiotically similar. Disturbance in the receiving community (through nutrient, substrata, or water temperature disruption, macroalgal removal through grazing or disease, and ecosystem "meltdown" caused by high levels of other invaders) has been the key to nearly all the successful macroalgal invasions in which the inoculation mechanism is known (Valentine et al., 2007), with a notable exception being the invasion of the Mediterranean by

Caulerpa taxifolia (M. Vahl) C. Agardh. *Sargassum muticum* (Yendo) Fensholt and *C. fragile* ssp. *fragile* both require a disturbance of native canopy-forming algae in order to become established (Johnson, 2007). The same was found to be true for *Undaria pinnatifida* (Harvey) Suringar in Tasmania (Johnson, 2007). These introduced species have also been agents of habitat modification in disturbed areas, whereas they have remained background species at other undisturbed sites. Resistance to invasion has been highest in regions with extensive seagrass or macroalgal cover (Ceccchereli and Cinelli, 1999). Therefore alien macroalgal species do not typically outcompete native species unless the growth of native assemblages is limited by disturbance.

The fact that alien macroalgal species require environmental disturbance to become invasive may explain why some species may become invasive in a particular location and not at another. Initial short term studies of the effect of introduced *Caulerpa taxifolia* on the density of the seagrass *Cymodocea nodosa* (Ucria) Ascherson in the Mediterranean pointed to a reduction of *Cymodocea* shoots, whereas long term studies demonstrated that the two organisms coexisted without future shifts in the competitive balance (Ceccherelli and Cinelli, 1997). Harris and Tyrell's (2001) twenty five year study of the northwestern Atlantic demonstrated a shift in abundance from kelp to a *C. fragile* and red algal dominated assemblage. The same ecosystems have reverted in recent years with kelp abundances increasing and *Codium* levels decreasing to the point where it may no longer be damaging particular communities (Harris, personal communication). Although few studies have examined sites prior to, or in the early stages of, invasion (Schaffelke and Hewitt, 2007) it has been observed that aliens often remain background species with little impact for some time before expanding to the point of becoming invasive (Stockwell et al., 2003).

Although there are no published reports of *Porphyra yezoensis* f. *yezoensis* or *P. yezoensis* f. *narawaensis* becoming invasive following introduction into new regions, evidence from their home range suggests that the commercial cultivars of f. *narawaensis* have the potential to cause ecological damage. The cultivars were developed to grow rapidly, efficiently absorb nutrients, and to proliferate through the production of neutral spores (Miura 1984). While these qualities have been highly beneficial to the nori industry, they have had some negative consequences on the Japanese coast. In areas of heavy nori-culture, f. *narawaensis* has migrated from the coastal bay nets, on which it was seeded, to the open coast where it has become firmly established. The cultivar has subsequently displaced and even caused the extinction of other native Japanese macroalgal species (Miura and Aruga 1987).

The impact of *Porphyra yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis* in the northwestern Atlantic has been unclear, but their presence had been noted with concern. The Connecticut Aquatic Nuisance Species Working Group (2005) included *P. yezoensis* as a Management Class 4 species, which means 'it is established in the waters of Connecticut and may have the potential to cause impacts, but current knowledge is insufficient to determine if control actions are warranted.' The management actions for such organisms include the prevention of further introduction, the interruption of the export pathways from Connecticut, further research to evaluate invasive potential and ecosystem impact, and continued monitoring of existing populations to determine rates of spread.

In accordance with these management recommendations, the current study set out to look for changes in the distribution of *Porphyra yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis* throughout New England and to monitor existing southern New England populations of f. *yezoensis* and f. *narawaensis* during the growing season, through monthly measurements of density and biomass at sites where the organism was previously collected (Bray 2006). To determine the possible ecological impacts of f. *yezoensis* and f *narawaensis,* density and biomass measurements were also taken for all macroalgal taxa growing in close proximity to either form. Because both forms of *P. yezoensis* often grow epiphytically on long-lived fucoid algae (Miura 1988; Bray 2006), this study also attempted to determine the impact of *P. yezoensis* on host organisms. Therefore, stature measurements of host organisms were compared to those of non-host organisms of the same species found in the same locations.

While previous studies had done much to define the range, seasonality, and population locations of *Porphyra yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis* (Bray, 2006; Mathieson et al., 2008) in the northwest Atlantic, little effort had been given to ecological quantification. It is hoped that the current study will provide valuable baseline data for further comparisons and long term monitoring of this introduced species.

Through the course of this study a *Porphyra* species of cryptic origins, *Porphyra* spp. *'stamfordensis'* (Bray 2006), was also detected at several sites. Because *P.* spp. *'stamfordensis'* may have been introduced this decade, and it was discovered in high density and biomass at several sites, special attention has been given to its collection data.

Material and Methods

Rapid Assessment Survey

In the winter of 2006-2007, sites from Lubec, ME to western Connecticut were surveyed for *Porphyra yezoensis* f *yezoensis* and *P. yezoensis* f *narawaensis* using rapid assessment techniques. Likely population locations (channels, breachways, narrow tidal rapids, boat ramps, marinas, etc.) were visited briefly and visually scanned for *Porphyra* species. Possible *P. yezoensis* blades were collected for molecular analysis. The sites thus examined were Rocky Neck State Park, Niantic, CT; Niantic Boat Valet, Niantic, CT; Black Point, Narragansett, RI; Village Inn Beach, Narragansett, RI; Mackerel Cove, RI, the Westport Boat Ramp, Westport, MA; Pope's Island Marina, Fairhaven, MA; Buzzard's Bait Bridge, Wareham, MA; Victory Rd Park, S. Boston, MA; Morrissey Boat Ramp, S. Boston, MA; Carson Beach, S. Boston, MA; Lead Hazard Bridge, Marblehead, MA; Marblehead Neck, MA; Salem Willows, MA; Goose Cove, Gloucester, MA; Dover Point, Newington, NH; Seapoint, Kittery,ME; Leeman Hwy, Brunswick, ME; Great Island, Harpswell, ME; Orr Island, Harpswell, ME; Cundy's Harbor, ME; Machiasport, ME; Cutler, ME; Pikeland, Lubec, ME; Lubec Town Dock, Lubec, ME (Figure 10). For comparative purposes, it was decided that only sites in and surrounding the known distribution of f. *narawaensis* would be further examined in this study.

Field Procedures for Quantification

During the winter-spring growing season (December 2007 through May 2008), *Porphyra yezoensis* sites, documented by Bray (2006), were monitored monthly (Figure 2, Table 1). Once *P. yezoensis* blades appeared (initial month of appearance varied by location), a twenty meter transect line was established and twenty sample quadrats (0.5 m x 0.5 m) were established along this line in the low intertidal zone at each site. The quadrats were used to determine occurrence and density of all macroalgal taxa. An attempt was made to establish an equal number of quadrats in areas containing *P. yezoensis* and areas devoid of *P. yezoensis*, but similar in substrata, wave exposure, temperature, salinity, slope, currents, and nutrients. However, after close inspection of collected materials in the laboratory, it was determined that most "non-*P. yezoensis*" quadrats contained some small epiphytic *P. yezoensis* blades that were undetectable in the field. Quadrats were digitally photographed for percent cover calculations, but due to the small size of most *P. yezoensis* blades, this technique was ineffective.

A destructive macroalgal sample (0.1 m x 0.1 m) was collected from a random location from within each of the larger (0.5 m x 0.5 m) quadrats during each month. To randomly select the destructive sampling area, the large quadrats were divided into 25 sectors (10 cm x 10cm) being five sectors across by five sectors down. Prior to sampling, a ten-sided die was rolled twice to determine the coordinates of the sample. The first roll determined the across value, and the second determined the down value. With rolls of 6 or above (the zero reading equaling ten), the proper sectors were determined by subtracting 5 from the rolled value. Therefore, a roll of 8 was actually a coordinate of 3. Once the coordinates were determined, a paint scraper was used to remove the algae from the substrata. Each destructive sample was placed in its own labeled plastic bag and transported, untreated, to a processing lab in the Spaulding Life Science building at the University of New Hampshire.

Collection processing

In the lab, the contents of each bag from destructive sampling were examined for *Porphyra* specimens. A subsample of *Porphyra* was removed, floated in seawater, and pressed on labeled herbarium sheets. Using a razor, 2 cm x 2 cm sections were cut from a selection of blades to use for molecular identifications. Each piece removed was placed in its own labeled 1.7 ml tube, along with silica beads. The remainder of the destructive sample in each bag was frozen at -20°C freezer for between 1 to 4 weeks before further processing. Upon removal from the freezer each destructive sample was placed in an aquarium net and rinsed in warm water to thaw and remove sediments. The samples were then floated in tap-water in a 28 x 43 cm pan. Species were sorted and counted on dry trays. Identifications of macroalgae were made based upon macroscopic and microscopic characters using keys to the marine algae of the northwestern Atlantic (Sears, 2002; Bohnsack-Villalard, 1995). Once counted, the individuals of each taxon where clumped together, squeezed until damp dry, and fresh weight (FW) was determined to the nearest hundredth of a gram (Mettler Toledo PR503 Delta Range). Biomass of each taxon (g FW/m^2) and density counts (individuals/ m^2) were estimated by multiplying the measured values by 100. Voucher specimens of each taxon from each collection were pressed and will be deposited in the Albion R. Hodgdon Herbarium (NHA) at the University of New Hampshire.

Prior to weighing, fucoid algae were segregated into those with and without epiphytic loads of *Porphyra yezoensis*. The individual lengths of all intact fucoid algae from both groups were measured from the holdfast to the tip. Likewise, the lengths of a representative subset of *Porphyra* were measured from each destructive sample during the months of greatest luxuriance (April and May).

Molecular Methods

The *Porphyra* samples that were dried for molecular analysis were ground in labeled 1.7 ml microcentifuge tubes using disposable plastic pestles, a few grains of molecular grade sand, and 300 ml of Gentra Puregene® Cell Lysis Solution (D-5002). The DNA was extracted with a Gentra Puregene ® Isolation Kit as per the manufacturer's instructions. Samples were incubated in a 65°C heatblock for one hour inverting 10 times at 30 minutes and cooled to room temperature before 100 µl of Protein Precipitation Solution (Gentra D-5003) was added. Samples were inverted 150 times and chilled at -20°C for 45 minutes before they were centrifuged for 15 minutes at 13,000 rpm. The supernatant was then poured into at new 1.7 ml microcentifuge tube containing 300 µl of 100% isopropanol and inverted 50 times before centrifugation for 10 minutes at 13,000 rpm. The alcohol was decanted and replaced with 300 µl of 70% ethanol before inversion and 5 minutes of centrifugation at 13,000 rpm. The alcohol was decanted, and the sample was air dried for 60 minutes before 50 µl of DNA Hydration Solution (Gentra D-5004) was added. After briefly mixing, the samples were incubated in a 65°C heatblock for one hour and centrifuged for 5 minutes.

Polymerase chain reactions were carried out in 50 µl volumes containing 4 µl extracted DNA, 10 µl Taq buffer (Promega GoTaq® Flexi Green), (0.2 mM) Mg^{2+}, 1 µl dNTPs, 1 µl each (20 mM) primer, and 0.25 µl Taq polymerase (GoTaq® Flexi). The segment of DNA amplified was 1481 bp in length extending from position 67 of *rbc*L through the *rbc*L-*spc*S intergenic spacer to the beginning of the small subunit. The evaluation was done using the F67 and rbc-spc primers (Teasdale et al., 2000).

The PCR products were separated by electrophoresis on a Cyber-Safe® treated low-melt agarose gel (0.8%) in nTBE Buffer (0.5x). On a UV lightbox, the desired DNA bands were excised using microscope slide covers and transferred to 1.7 ml tubes, incubated at in a 65°C heatblock for five minutes, and then transferred to 37°C heatblock. To each tube, 1.5 µl of agarase (Sigma A6303, 50 units/ml) were added, and the mixture was incubated overnight.

Concentrations of DNA were quantified using an Invitrogen™ Quant-iT™ dsDNA BR Assay Kit (Q32851) and an Invitrogen™ Qubit™ fluorometer (Q32857) as per the manufacturer's instructions, and appropriate volumes of DNA and primers were sent to Hubbard Genomic Center (UNH) for clean-up and sequencing reactions using Applied Biosystems BigDye Terminator Cycle Sequencing Kits (v1.1 and v3.1). The DNA samples were resolved by capillary electrophoresis on an ABI3130 DNA Analyzer.

Resulting sequences were trimmed in Chromas (version 2.2, Technelysium, Pty. Ltd., Tewantin, Queensland, Australia). Sequence assembly, alignments were made and proofed using Seq Man II (version 7.1 for Windows, DNAStar, Inc., Madison, Wisconsin). Comparative alignments and GenBank searches were performed using MegAlign (version 7.1 for Windows, DNAStar, Inc., Madison, Wisconsin).

<u>Site Descriptions</u>

Seven study sites visited monthly from December 2007 through May 2008:(1) Lighthouse Point, New Haven, CT; (2) Guilford Marina, Guilford, CT; (3) Rocky Neck

State Park, Old Lyme, CT; (4) Charlestown Breachway, Charlestown, RI, (5) Black Point, Narragansett; (6) Westport, MA; and (7) Falmouth Heights, MA (Table 1, Figures 2-9). Transect/Quadrat sampling was conducted monthly beginning at each site with the initial appearance of *Porphyra yezoensis* blades.

Light House Point, New Haven, CT (Figure 3), also known as Morris Point from colonial times and Five Mile Point (due to the fact that it is located five miles from the center of New Haven), marks the eastern end of New Haven Harbor. Its tidal amplitudes range from lows of -1 ft to highs of 7.6 ft above Mean Low Water (MLW). Because the location is moderately exposed, it experiences low to moderate wave action. Its granitic boulder and sandy substrata support the growth of fucoid algae, *Chondrus crispus* Stackhouse, *Ulva* spp., and multiple *Porphyra* species. The rocky point lies beside a wide sand beach designated for public swimming and sunbathing (http://www.cityofnewhaven.com/Parks/ParksInformation/lighthousepoint.asp). As an indication of the level of pollution in the harbor, the New Haven Board of Health frequently monitors the area waters in the summer for unhealthy levels of bacteria, and resulting beach closures are not uncommon (East Shore Ranger, Terry McCool, personal communication).

The Guilford Marina, Guilford, CT (Figure 4), site is located in shallow Guilford Harbor sheltered by Faulkner's Island. Its tidal amplitudes range from lows of -.8 ft to highs of 5.6 ft. The Marina was designated a Connecticut Clean Marina in 2007 by the Department of Environmental protection for its efforts to control pollutants from fuels and litter along with efforts to properly clean boat hulls (http://www.ct.gov/Dep/cwp/view.asp?A=2712&Q=329898). The Marina is home to slips and moorings for upwards of thirty residential and recreational boats. The study site is located on a wide, manmade retaining wall comprised of granitic boulders located at the mouth of the marina. The boulders predominantly support the growth of fucoid algae and associated epiphytes. Swans frequent the study site.

The Rocky Neck State Park, Niantic, CT site (Figure 5) is located on an exposed point on the western edge of the park. Tidal amplitudes range from lows of -0.5 ft to highs of 3.6 ft. The granitic and basaltic bedrock substrata support the growth of barnacles, fucoid and ulvoid algae, *Chondrus crispus*, and multiple *Porphyra* species. Wave action at this site can be heavy with an apparently strong current running away from the point. For example, a sample bag accidentally dropped into the water, was immediately carried straight away from shore and was out of sight in minutes. Ducks and geese frequent the study site.

The Charlestown Breachway, site in Charlestown, RI (Figure 6) is located along the inside of a manmade jetty channel that was constructed in the middle of a miles-wide stretch of sand beach on the southwestern coast of Rhode Island. The breachway was originally a natural feature of the coastline that connected the Atlantic Ocean to the Pawaget, Ninigret, and Charlestown Ponds. Because nature's breachway was sandy and tended to fill in with sand and other sediments, the people of the Charlestown region, during the late 1800s and early 1900s, pushed for the construction of a permanent breachway and jetties composed of 400 pound field stones stacked as retaining walls. The labor required to build the breachway was extensive and used horses, railways, and rail carts. The construction was done in hopes of preserving the common practice of cultivating and harvesting oysters in the ponds (http://www.riparks.com/charlestownhistory.htm). The large fieldstone walls currently support the growth of fucoid and ulvoid algae, along with multiple species of *Porphyra*. The breachway is heavily used for saltwater fishing in spring and summer, and it serves as the point of ocean access for the Ocean House Marina that has slips and dry dock storage space for more than fifty recreational boats. Tidal amplitudes at this site range from lows of -.05 ft to highs of 3.7 ft.

The Black Point, Narragansett, RI site (Figure 7) is highly exposed and wave action is extreme due to an abrupt granitic bedrock ledge. Due to the pounding of the waves, fucoid algae are nearly absent from this site, and ulvoid algae and *Porphyra* species are found growing attached to blue mussels (*Mytilus edulis* L.), barnacles (*Semibalonus balanoides* L.), and, in low areas, *Chondrus crispus. Scytocyphon lomentaria* (Lyngbye) J. Agardh is also abundant at this site. The tidal amplitudes at Black Point range from lows of -0.5 ft to highs of 4.6 ft. While boat traffic close to this site is unlikely, the Block Island ferry terminal lies within miles.

The Westport, MA site (Figure 8) lies in a completely sheltered estuarine environment at the western edge of Buzzards Bay. The site is near the confluence of the eastern and western branches of the Westport River. Collections were made along a transect line placed on a short manmade jetty comprised of large field stones that support the growth of *Fucus vesiculosis* L., *Ascophyllum nodosum* (L.) Le Jolis, and ulvoid algae along with a few *Porphyra* species. The jetty lies within twenty yards of a seasonally operated seafood restaurant on the west and an oft used public boat landing on the east. Multiple marinas and marine businesses lie within a mile of this location. Tidal amplitudes at this site range from -0.3 ft lows to 4.3 ft highs. Currents along the tip of the jetty can be dangerously strong at points in the tidal cycle.

The Falmouth Heights, MA study site on Cape Cod (Figure 9) lies in a short (50 m), narrow (15 m) manmade fieldstone-walled channel that drains from Little Pond into Vineyard Sound at low tide. The boulders and sandy substrata support the growth of fucoid and ulvoid algae, *Chondrus crispus*, and several *Porphyra* species. Currents in the channel are moderate. Wave action is minimal. East and west of the channel lie miles of sandy beach with heavy public use in summer months. Tidal amplitudes range from lows of -0.2 ft to highs of 1.7 ft.

Several other sites where *Porphyra yezoensis* had been previously reported by Bray (2006) were visited monthly for collecting, but were not used for macroalgal community quantification in most cases, because significant *P. yezoensis* populations never appeared. These sites were from west to east: Hammonasset State Park, Madison, CT; Niantic Boat Valet, Niantic, CT; and Fort Rodman, New Bedford, MA. These sites were not examined as thoroughly as the main study sites for a few reasons. Due to profound lack of *Porphyra* of any kind, the New Bedford, MA site was omitted. Although the Fort Taber site (also known as Fort Rodman) in New Bedford, MA was historically reported to support populations of *P. yezoensis*, no such populations were found in this study. Only five blades, of other *Porphyra* species, were found in rapid surveys from January through March. The Niantic, CT boat valet site was not selected for this quantification study because of the high densities of the morphologically similar *Porphyra* spp. *'stamfordensis'* and seemingly low densities of *P. yezoensis* f *yezoensis.*

The site was left out because visually separating the two species was difficult if not impossible without reproductive markings, which neither species displayed regularly.

The Hammonassett State Park site was not used for quantification because the *Porphyra yezoensis* populations were located in a precarious position far out on a jetty surrounded by deep water.

Results

Rapid Assessment Survey

Table 2 summarizes all of the *Porphyra* species collected through the winter 2006-2007 rapid assessment survey. *Porphyra yezoensis* f. *yezoensis* was confirmed at more sites, 9 of 25, than was *P. yezoensis* f. *narawaensis,* 4 of 25 (Figure 10). *Porphyra* ssp. *'stamfordensis'* was not confirmed at any of the 25 survey sites.

During the survey, *Porphyra yezoensis* f. *yezoensis* was collected at two sites outside of its previously published distribution. In May of 2007, voucher specimens of f. *yezoensis* were collected at the town dock in Lubec, ME, more than 60 miles north of the distributional limits reported by Bray (2006). In April of 2007, voucher specimens of f. *yezoensis* were collected at the Niantic Boat Valet, Niantic, CT. This is the only known population of *P. yezoensis* f. *yezoensis* that exists within the distributional range of *P. yezoensis* f. *narawaensis* in the Northwest Atlantic.

Quantification Study

Table 3 summarizes all of the macroalgal species obtained through destructive quadrat sampling along the line transects of each of the seven study sites. The greatest number of taxa (fourteen) was recorded for the New Haven, Rocky Neck, Charlestown, and Black Point sites. Each of these locations had seasonal populations of *Porphyra yezoensis* throughout the study period (February-May), but none supported populations of both *P. yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis.*

Two sites with fewer number of taxa, Guilford (8 species), and Falmouth Heights (10 species), had seasonal populations of *Porphyra* spp. *'stamfordensis'* throughout the study period. No *P. yezoensis* specimens were collected from Guilford, and very few from Falmouth Heights (only in March and April). The collections of *P. yezoensis* f. *narawaensis* from Falmouth Heights represent the first records east of Westport, MA for this genotype.

Of the macroalgal species listed for each site, those commonly found growing epiphytically on *Fucus* included: *P. yezoensis* f. *narawaensis, P. yezoensis* f. *yezoensis, P. leucosticta* Thuret, *P. olivii* Orfanidis, Neefus & Bray, *P.* spp. *'stamfordensis', Ulva intestinalis* L., *Polysiphonia stricta* (Dillwyn) Greville, *Elachista fucicola* (Velley) J. E. Areschoug, *Ulothrix flacca* (Dillwyn) Thuret, and *Pylaiella littoralis* (L.) Kjellman.

The monthly density values (individuals/m^2) for each species collected on the twenty quadrats from each site are summarized in Appendix A. Counts of minute epiphytic species (*Elachista fucicola, Pylaiella littoralis, Blidingia minima* (Nägelli ex Kützing) Kylin, *Bangia fuscopurpurea* (Dillwyn) Lyngbye, *Ulothrix flacca)* were not included in the species density enumerations, as it was difficult to accurately document in a reasonable amount of time. *Porphyra* species and *Ulva intestinalis,* growing epiphytically or epibiotically (on *Mytilus edulis* and *Semibalanus balanoides* at Black Point) in dense clusters, typically had the highest counts per month at each site.

The monthly biomass data (g FW/m^2) for each species on the twenty quadrats from each site were also summarized (Appendix B). Unlike the density data, all species were included in the biomass recordings. For each site, excluding Black Point, biomass yields were highest for fucoid algal species [*Ascophyllum nodosum* (Westport), *Fucus spiralis* (Falmouth Heights), *Fucus vesiculosis* (all other sites)]. Because only one frond of *Fucus vesiculosis* was collected at Black Point during the study, *P. yezoensis* f. *narawaensis* supplied the bulk of that site's biomass.

Seasonality and abundance in both *Porphyra yezoensis* forms were estimated using monthly means from each site (Figures 11 and 12). *Porphyra yezoensis* f. *yezoensis* exhibited an earlier peak density period (February) at New Haven than the f. *narawaensis* populations at Rocky Neck, Charlestown Breachway, Black Point, and Falmouth Heights (March to April). The mean population density of *P. yezoensis* at peak periods was more than twice as high for the f. *yezoensis* at New Haven (10,150 blades per $m^2 \pm 1796.6$ SE) than for f. *narawaensis* at Black Point (5003 blades per $m^2 \pm 1119.6$ SE). The Falmouth Heights site contained a population of f. *narawaensis* that had a low density (15 blades per $m^2 \pm 10.9$ and 15 SE) during April and May.

Figures 13 and 14 summarize mean monthly biomass at each site during February to May. *Porphyra yezoensis* f. *yezoensis* biomass peaked earlier (February) at New Haven compared with *P. yezoensis* f. *narawaensis* at the other sites (March at Rocky Neck and Charlestown Breachway, April at Black Point and Falmouth Heights). The peak biomass was more than twice as great for the Charlestown Breachway *P. yezoensis* f. *narawaensis* populations (511.3 g/ $m^2 \pm 441.7$ SE) compared with *P. yezoensis* f. *yezoensis* populations from New Haven (237.3 g/ $m^2 \pm 40.2$ SE). *Porphyra yezoensis* f. *narawaensis* populations at Falmouth Heights had a mean biomass of only 7.15 g/ $m^2 \pm$ 5.4 SE at peak in April.

Because significant populations of *Porphyra* spp. *'stamfordensis'* occurred at several study sites, its seasonality and abundance was also estimated (Figure 15) and mean monthly values were enumerated for each site. The taxon was collected on transects from February through May at four sites. Peak population biomass yields occurred in February at Charlestown (5.15 g/ $m^2 \pm$ 2.57 SE), while maximum values occurred in March at Guilford (147.3 g/ $m^2 \pm$ 59.4 SE), Falmouth Heights (108 g/ $m^2 \pm$ 20.26 SE) and Wesport (262.8 g/ $m^2 \pm$ 61.5 SE).

The maximum biomass contribution of the dominant *Porphyra* species to the total macroalgal community biomass is summarized in Table 4. Due to the absence of large fucoid algae at Black Point, *Porphyra yezoensis* f. *narawaensis* biomass contribution was substantially higher (81%) than at all other sites: New Haven—1%, Rocky Neck—2%, Charlestown—2%. *Porphyra* spp. *'stamfordensis'* was a small contributor of biomass to all of the communities it occupied (Guilford—1%, Westport—1%, Falmouth Heights—2%).

To evaluate the impact of epiphytic *Porphyra* loads on long lived fucoid algae, the percentage of epiphytized plants were calculated during March and April (Figure 16). Both the highest and lowest values were recorded for *Porphyra* spp. *'stamfordensis'* populations at Falmouth Heights (67%) and Guilford (16%), respectively. The values for *P. yezoensis* f. *yezoensis* at New Haven was greater (48%) than those found at both sites occupied by *P. yezoensis* f. *narawaensis*—i.e. Rocky Neck (36%) and Charlestown (34%).

The mean frond lengths for *Fucus* with and without epiphytic *Porphyra yezoensis* were enumerated during March and April (Figure 17). ANOVA revealed that epiphytized *Fucus* plants were longer than those without *Porphyra* loads (P value <0.01). The difference was most clearly demonstrated at New Haven, Charlestown, and Westport (P values each <0.01).

Table 5 summarizes mean frond length of *Porphyra yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis* during March and April (i.e. peak values). The mean blade lengths were < 5 cm for each site. The longest mean blade length (4.38 cm ±1.5 cm) was recorded for the *P. yezoensis* f. *narawaensis* at Black Point, and the shortest mean blade length (2.40 cm ± 0.91 cm) was recorded for the f. *yezoensis* at New Haven. The range of individual blade lengths for *P. yezoensis* f. *yezoensis* varied from < 0.5 cm to 9 cm, while *P. yezoensis* f. *narawaensis* ranged from < 0.5 cm to 10 cm.

The mean frond lengths for all other *Porphyra* species at each site were also determined during peak periods of March and April (Table 6). Again the mean blade lengths for each species at different sites were all less than 6 cm. The longest mean blade length (5.33 cm ± 4.72 cm) was recorded for *Porphyra leucosticta* from the Charlestown Breachway, while the shortest values (2.54 cm ± 1.63 cm) were recorded for *P. olivii* at New Haven. Mean blade lengths for *Porphyra* spp. *'stamfordensis'* ranged from 3.51 cm ± 3.00 cm at Guilford to 4.42 cm ± 3.10 cm at Westport.

Discussion

As *Porphyra yezoensis* is an introduced species in the northwestern Atlantic, coastal managers have been wary of its potential negative impact on native macroalgal communities (Anonymous, 2005). To assess the extent its introduction, a coastal survey was conducted by Bray (2006) to determine the distribution both f. yezoensis and f. *narawaensis.*

The survey methods employed were designed to rapidly assess presence and absence of f. *yezoensis* and f. *narawaensis* in channels, breachways, narrow tidal rapids, boat ramps, marinas, etc. along the New England Coast. These methods revealed the presence of dozens of *P. yezoensis* populations from New York to Downeast Maine (Bray 2006).

During the winter/spring of 2007, I conducted another rapid assessment survey of *Porphyra* species along the New England Coast (Table 2; Figure 10). This study revealed the presence of *P. yezoensis* f. *yezoensis* at 9 of 25 sites, including two collections (Lubec, ME and Niantic, CT) of f. *yezoensis* outside of the distribution reported by Bray (2006).

The voucher specimens of f. *yezoensis* from Lubec, ME are the first collections of this form north of Bar Harbor, ME. This marks a range expansion of 60 miles. Although this area was not surveyed by Bray (2006), it was extensively monitored for escapes in the winter and spring of 1998 and 1999 following the region's nori culture attempts (Watson et al., 2000), and no form of *P. yezoensis* was found. Thus, it is likely that *P. yezoensis* f. *yezoensis* has expanded to this region within the last decade.

The voucher collections of f. *yezoensis* from Niantic, CT mark the first discovery of a population of f. *yezoensis* within the distribution of f. *narawaensis* in New England. Because the distribution of f. *yezoensis* in the Northwest Atlantic is interrupted by f. *narawaensis*, which arrived later, it has been proposed that the distribution of f. *yezoensis* was once continuous in the region (Bray, 2006; Neefus, personal communication). The f. *yezoensis* in Niantic, CT is either a holdover population that has been long established in the region, or it has recently arrived. Because there are no collection records from the Niantic Boat Valet site prior to 2007, one can only speculate as to the history of the population at this location. Because of the sheltered nature of this site, I suspect this is a holdover population still residing in this location. Because competitive exclusion favoring f. *narawaensis* has been suggested (Bray, 2006), it is likely that the Niantic, CT site has never been successfully inoculated with f. *narawaensis.*

To quantify the level of establishment of *Porphyra yezoensis* f. *yezoensis*, *P. yezoensis* f. *narawaensis*, and *P.* spp. *'stamfordensis'* in New England, and to assess the macroalgal communities they occupy, I conducted monthly biomass and density assessments of all macroalgal taxa, growing within transects, at the established study sites from New Haven, CT to Falmouth Heights, MA, during the season of maximum blade growth in New England (February-May).

The study intended to measure f. *yezoensis* populations at four sites (New Haven, CT; Guilford, CT; New Bedford, MA; and Falmouth Heights) and f. *narawaensis* populations at four others (Rocky Neck State Park, Niantic, CT; Charlestown, RI; Black Point, Narragansett, RI; and Westport, MA). The lack of detection of f. *yezoensis* or f. *narawaensis* at Guilford, CT is interesting in that the site lies at the distributional convergence of both forms. It is also important to note that *P.* spp. *'stamfordensis'*, which has likely been introduced recently, was the dominant *Porphyra* species at this site. Because there have been no previous collection records of any kind from this location, we do not know if either form of *P. yezoensis* was ever established in this site. But with the proximity of the marina and heavy recreational boat traffic, it is unlikely that this site has only been inoculated with *P.* spp. *'stamfordensis'*. If competition with either form of *P. yezoensis* has occurred at this site, it appears to have favored *P.* spp. *'stamfordensis'*.

That *P. yezoensis* f. *narawaensis* was not collected at Westport, MA in 2008 is curious in that it had been collected at the site, along with *P.* spp. *'stamfordensis'*, by Bray (2006). Again, competition, at least in blade recruitment, has favored *P.* spp. *'stamfordensis.'* at this site.

The absence of f. *yezoensis* and the presence of both f. *narawaensis Porphyra* spp. *'stamfordensis'*, at the Falmouth Heights site is of great interest. Both f. *yezoensis* and *P.* spp. *'stamfordensis'* had been collected at this site previously (f. *yezoensis* in April 2004 and *P.* spp. *'stamfordensis'* in January of 2005) by Bray (2006), and f. *narawaensis* had not. *Porphyra* spp. *'stamfordensis'* was the dominant *Porphyra* species at this site throughout the 2008 study period, with f. *narawaensis* being first detected in April, at low density (300 total blades across two quadrats). The appearance of f. *narawaensis* was months behind its emergence at all other f. *narawaensis* sites in this study. That successful gametophytic blade recruitment of f. *narawaensis* followed the peak density period of *P.* spp. *'stamfordensis'* at this site suggests a competitive advantage for *P.* spp. *'stamfordensis'* during its months of peak production. It is likely that the recently introduced f. *narawaensis* has lower conchocelis density at this stage of its introduction than does the established *P.* spp. *'stamfordensis'* and is therefore releasing fewer conchospores than its competitor.

That f. *yezoensis* was not detected at Falmouth Heights in 2008, following the arrival of f. *narawaensis*, is further evidence of competitive exclusion favoring the cultivar. Further investigation of the site's short, narrow, shallow channel, which connects Little Pond to the Atlantic Ocean, could reveal much about the nature of competition between *P. yezoensis* f. *yezoensis*, *P. yezoensis* f. *narawaensis*, and *P.* spp. *'stamfordensis'*, especially if one could locate and observe the conchocelis phase of each throughout the year, or if one conducted laboratory culture experiments.

The lack of detection of f. *yezoensis* populations at New Bedford, MA and Falmouth Heights, MA, and the lack of detection of f. *narawaensis* at Westport, MA, is puzzling. If their absence was not the result of sampling error, it is possible that the forms have been completely eradicated from these locations. Another possibility is that the forms continue to exist at these locations in the perennating conchocelis phase, and no gametophytes successfully recruited into the intertidal zone this year due to: spore release during and ebb versus flood tide; rain or ice event that interfered with spore attachment; or the conchocelis many not release spores every year. The total absence of *P. yezoensis* at these locations is doubtful in that the conchocelis stage of *Porphyra* species is quite resilient and can remain viable for years under refrigeration without the addition of nutrients or exposure to sunlight (C. Yarish, personal communication).

But some evidence suggests that the conchocelis of the *P. yezoensis* forms may no longer reside at these sites. Given the right conditions, a very small amount of conchocelis can give rise to an incredible number of progeny in a limited time period. For example, in a study of free-living *P. leucosticta* conchocelis, He and Yarish (2006) found that 1 g dry weight of conchosporangia could release over 20 million conchospores at peak production. With that level of fecundity it seems that if there were conchocelis reproducing in these locations, as has happened in the past, some of the millions of conchospores would have successfully recruited.

Although thorough collections at some previously identified *Porphyra yezoensis* sites did not detect the expected populations, the current studies were useful in measuring the presence, biomass, and density of entire macroalgal communities growing in close association f. *yezoensis*, f. *narawaensis*, and *P.* spp. *'stamfordensis'*. In doing so, baseline data was assembled for future comparative studies, which may be able to detect further changes in these macroalgal communities across time. Such comparisons are of great importance in assessing the effect of an introduced species on its host community.

The biomass and density data is of critical importance at the present time in documenting the autecology of different *Porphyra* populations (Figures 10 and 11). That is, peak blade production in *P. yezoensis* f *yezoensis* occurred earlier (February) than in *P.* spp. *'stamfordensis'* (March) and *P. yezoensis* f *narawaensis* (March to April). The differential timing of production in the forms of *P. yezoensis* may reflect the genetic difference between the two. It is also possible that the trends seen in peak production time are not based on genetic differences between the forms, but rather are the result of biotic or abiotic differences between the various sites. Comparative examination of blade development in the two *P. yezoensis* forms, under controlled laboratory conditions, could better resolve this issue. If there is a genetic basis for the differential production timing in the two forms of *P. yezoensis*, and blade recruitment space was a limiting factor, f. *yezoensis* would hold an advantage as a preemptor of space in recruitment competition with both *P.* spp. *'stamfordensis'* and *P. yezoensis* f. *narawaensis*.

The mean blade lengths of both forms of *P. yezoensis* were determined during the months of greatest luxuriance (March and April). The mean blade length of either form of *Porphyra yezoensis* was less than 5 cm at each site (Table 5). Considering that cultured nori blade lengths routinely exceed 60 cm and can reach lengths of up to 1.0 m (Miura and Aruga, 1987), the size of the *P. yezoensis* blades growing along Long Island Sound are very short. That the longest individual *P. yezoensis* blade recorded in the study was a mere 10 cm, only 10% of the maximum expected length, indicates that conditions for growth at these sites varies greatly from those in Asian nori-culture in which the blades are grown subtidally in protected bays and are thus protected from the stresses of wave action and exposure at low tide. The reduced stature of *P. yezoensis* in New England may result from exposure to the above stressors, lower nutrients, or a shorter growing season. In addition, the reduced stature observed could have been caused by grazing. Although little has been published on ingestion of *P. yezoensis* by grazing organisms (Noda et al., 2003), ducks, geese, or swans were observed in each of the study sites. However, consumption of *P. yezoensis* blades by these animals was never observed.

Although the average blade length of *Porphyra yezoensis* was short compared to Bray's (unpublished data, 2006) descriptions (f. *yezoensis* mean length of 8.9 cm $\pm$ 0.89 SE and f. *narawaensis* mean length of 15.6 cm $\pm$ 3.5 SE) and the lengths described for this species in nori-culture, they were similar to average blade length calculations for all other *Porphyra* species recorded in this study (Table 6). Two species (*P. olivii, P.* spp. *'stamfordensis'*) had mean blades lengths of less than 5 cm, and the mean blade length of *P. leucosticta* was less than 6 cm. The mean lengths were longer for two of these species in Bray's (unpublished data, 2006) study (*P.* spp. *'stamfordensis'* = 7.6 cm $\pm$ 0.98 SE and *P. leucosticta* = 7.3 cm $\pm$ 1.2 SE). Discrepancies in length descriptions between the current study and that conducted by Bray are likely the result of sampling differences due to collection purpose and technique, with Bray's study selecting conspicuous, therefore larger, blades.

As a measure of impact, data collected in this study were used to determine the population sizes of both forms of *Porphyra yezoensis* in comparison to other macroalgal species in their host communities. The biomass of all macroalgal taxa was measured, and the mean percent contribution of *P. yezoensis* was calculated for each site. The percent contribution of both forms of *P. yezoensis* biomass was minimal (1% to 4%) for each site with significant *Fucus* populations. Even when *P. yezoensis* density was highest (greater than 10,000 blades per m^2 for f. *yezoensis* at New Haven), the biomass of the short, thin blades contributed little to the total community. It has been argued that only large, canopy forming, or turf forming macroalgae can become damaging, and therefore invasive, upon introduction to a host community. With their large thalli, these organisms modify the habitats in which they grow through space preemption and light blocking.

Although *Porphyra yezoensis* blades are not long enough to dwarf most macroalgae, they can block sunlight penetration to the organisms on which they grow epiphytically. As *P. yezoensis* commonly grows attached to long lived fucoid algae, which are keystone species in many macroalgal communities, this study sought to determine if such epiphytic growth was harmful to these host plants. Therefore, the percent of *Fucus* with epiphytic *Porphyra* was determined for each site (Figure 16). During the peak months of growth (March and April), nearly half (48%) of all *Fucus* plants from New Haven bore loads of *P. yezoensis* f *yezoensis*, and roughly one-third (34% and 36%) of the *Fucus* plants from Charlestown and Rocky Neck bore loads *P. yezoensis* f *narawaensis*. Although these loads were substantial, it is also clear that *P. yezoensis* has yet to saturate its preferred substratum at these sites. With 52% to 66% of all *Fucus* fronds completely uncolonized, *P. yezoensis* populations have not likely reached maximal levels.

While the epiphytic *Porphyra yezoensis* loads were substantial, negative impact could not be assumed. Lengths of *Fucus* plants bearing *P. yezoensis* were compared to those free of epiphytic *Porphyra*. Because it was reasoned that plants bearing loads of epiphytic *P. yezoensis* would get less light, and possibly less nutrients than those without, it was hypothesized that load bearing plants would be shorter than non-load bearing plants. However, my findings were the opposite (Figure 17).

The observed greater mean lengths for *Fucus* plants bearing loads of *P. yezoensis* are not likely caused by the presence of these epiphytes. Rather their blades are likely found more often attached to longer *Fucus* plants because the longer plants have a greater surface area on which the blades can recruit, and/or longer *Fucus* plants are older and more worn, which may enhance their susceptibility to epiphytes.

Despite the statistical significance of the relationship between epiphytic *Porphyra yezoensis* and *Fucus* length, this study was not totally comprehensive as other epiphytic organisms (*Elachista fuciola, Ulva intestinalis, Ulothrix flacca,* and *Pylaiella littoralis*) grew along with, or in the absence of, *P. yezoensis* on the measured *Fucus* fronds. Thus, the true effect, if any, of epiphytic *Porphyra* growth would be difficult to determine.

Another measure commonly used to assess the impact of an introduced organism on its host community is to compare the species richness of affected communities to the richness of unaffected but otherwise ecologically similar communities. Although the some study sites that possessed substantial populations of *P. yezoensis* varied markedly on some environmental parameters (salinity, waved action, exposure to tidal currents, substrata) from sites that did not contain populations of *P. yezoensis*, Table 3 shows that the *P. yezoensis* sites were home to more macroalgal species (14 species at New Haven, Rocky Neck, Charlestown, and Black Point) compared to the *P.* spp. *'stamfordensis'* dominated sites (11 at Westport and 8 at Guilford). Perhaps these higher species counts are an indication that both forms *P. yezoensis* exist as a background species at their sites and have not yet acted to exclude other macroalgal species. However, conclusions about the impact of f. *yezoensis*, f. *narawaensis*, and *P.* spp. *'stamfordensis'* on the diversity of the study sites are only speculative due to the absence of pre-invasion data.

In summary, the current study was effective at establishing baseline structure data for seven macroalgal communities from New Haven, CT to Falmouth Heights, MA. A single season snapshot of density and biomass data was recorded for populations of the introduced Asian red algal species *Porphyra yezoensis* at these seven sites. The present data set will be useful to coastal managers conducting future comparative assessments of the macroalgal assemblages at these locations. The density and biomass data were useful for determining peak production times for both *P. yezoensis* forms and *P.* spp. *'stamfordensis'* across the study sites, as well as for evaluating the contribution of this species to these communities. The epiphytic load of *P. yezoensis* on *Fucus* was determined for each site, and the effect of said epiphytes on *Fucus* stature was examined. Species counts for sites with and without current blade phase populations of *P. yezoensis* were compared. None of these evaluations revealed a clear negative impact of *P. yezoensis* on its host macroalgal communities.

The main difficulty with conducting impact assessments of introduced species is that most studies are conducted post invasion (Schaffelke and Hewitt, 2007). The present study is certainly an example of this phenomenon. The best way to conduct an impact assessment study is to thoroughly examine and catalog the algal community at a particular location both *before* and after an introduction. Failing this, many researchers have attempted to study concurrent and seemingly similar sites to compare the structure of communities with and without invaders. Because it is unclear if the uncolonized sites are uncolonized because they are abiotically or biotically different from colonized sites, some studies have suggested that the lack of pre-invasion data significantly limits the ability of a researcher to make inferences about the impact of the introduced species (Taylor 2002). Many researchers have also attempted to make post-invasion impact assessments through manipulation of the invaded environment. In the bulk of these studies, the introduced species is removed and the site is treated as uncolonized. However, some researchers have proposed that such techniques are flawed in that removal of the introduced organism from a site may reset the assemblage to an earlier successional stage rather than to pre-invasion condition (Edgar et al., 2004). Therefore, reliable impact inferences are limited.

The effectiveness of impact studies is also impaired due to limited time, with most studies lasting from weeks to, at most, a few years (Schaffelke and Hewitt, 2007). While this time scale is practical from the standpoint of research effort, it does not allow for the lag time between introduction and full blown invasion. Many invasive marine species initially exist at low levels for a period before increasing in number and expanding into new territory (Stockwell et al., 2003). The lag time may be caused by adaptation to environmental controls such as competition and herbivory. Also, density dependent survivorship thresholds might need to be reached before expansion can occur.

Studies of brief duration may also overestimate the impact of introduced species. Because grazers may initially avoid the ingestion of an introduced species, populations may expand rapidly. Over time, however, herbivore preferences have been seen to shift (Stimson et al., 2001). Such a shift reduces the competitive advantage and negative impact of the introduced organism on its host community.

Regardless of the duration of the impact assessment studies, some have argued that the invasiveness risk is minimal for most marine macroalgal organisms. Of the 260 introduced species worldwide, only 17 have been considered at all with only 4 of these (*Caulerpa taxifolia, Undaria pinnatifida, Codium fragile* ssp. *fragile,* and *Sargassum muticum*) being highly studied (Johnson, 2007). Hence the impact of most introduced seaweeds is minimal or their impacts are often unclear. Because alien species that actively modify habitats have a much higher negative impact on new environments than organisms that do not (Wallentinus and Nyberg 2007), the impact of introduced marine animals are undoubtedly greater than the impact of algal species.

While the impact of both forms of *Porphyra yezoensis* on their host communities in New England is currently unclear, the data gathered from this study will provide a baseline for further monitoring of their impacts on macroalgal assemblages. Although this study revealed that *P. yezoensis* had seemingly disappeared from three sites where it had previously been observed (f. *narawaensis* from Westport, MA, and f. *yezoensis* from both New Bedford, MA and Falmouth Heights, MA), the range of f *narawaensis* had expanded east nearly 100 miles to Falmouth Heights, on Cape Cod (Figure 18). Range expansion of introduced species is a concern, as it indicates the ability of this species to continue to spread throughout New England, inhabiting new communities, with potential negative effects.

Also of note, *Porphyra* spp. *'stamfordensis'*, a species of unknown origin, was found to inhabit five of the seven study sites, and it was the dominant species at three sites. Given that this species was first detected at Hammonassett State Park by Neefus in 2004 (Bray, 2006), and nothing more is known about its introduction to the region, continued monitoring and impact assessment of this species should be coupled with these same efforts for *P. yezoensis.*

While *Porphyra yezoensis* f. *yezoensis*, *P. yezoensis* f. *narawaensis*, and *P.* spp. *'stamfordensis'* are established and possibly invasive in New England, attempts to eradicate them would be difficult, if not impossible, at this time. Physical removal of all gametophytic blades would be implausible due to their abundance and small size. Chemical treatment of the infected shores would likely have little effect on the subtidal-dwelling, and blade-producing conchocelis stages of these organisms and would likely be devastating to native species.

Efforts to reduce the further spread of these species would be difficult and costly. The curtailing of recreational boat traffic, fishing, and shipping in affected regions is unreasonable, at this time, in light of the fact that negative impacts of these species have yet to be observed in New England.

TABLES

Table 1 GPS coordinates of study sites

Sites	Coordinates
New Haven Light	N 41°14.820' W 072°54.180'
Guilford Marina	N 41°16.250' W 072°39.9310'
Rocky Neck	N 41°17.820' W 072°14.760'
Black Point	N 41°23.848' W 071°27.750'
Charlestown Breachway	N 41°21.360' W 071°38.340'
Westport	N 41°30.840' W 071°04.080'
Falmouth Heights	N 41°32.700' W 070°35.279'

Table 2 Winter 2006-2007 rapid assessment survey results - *Porphyra* species by site

	P. yezoensis f yezoensis	*P. yezoensis* f narawa*ensis*	*P.* spp. *'stamfordensis'*	*P.* spp. *'collinsii'*	*P.* leucosticta	*P.* tsengii	*P.* purpurea	*P.* spatulata	*P.* amplissima	*P.* umbilicalus	*P.* linearis
Rocky Neck State Park, Niantic, CT		X			X						
Niantic Boat Valet, Niantic, CT	X										
Black Point, Narragansett, RI		X			X						
Village Inn Beach, Narragansett, RI		X			X						
Mackerel Cove, RI				X				X			
Westport Boat Ramp, Westport, MA		X?		X							
Pope's Island Marina, Fairhaven, MA	X?		X?								
Buzzard's Bait Bridge, Wareham, MA	X										
Victory Rd Park, S. Boston, MA							X				
Morrissey Boat Ramp, S. Boston, MA	X										
Carson Beach, S. Boston, MA	X							X			
Lead Hazard Bridge, Marblehead, MA							X				
Marblehead Neck, MA					X					X	X
Salem Willows, MA										X	
Goose Cove, Gloucester, MA	X									X	X
Dover Point, Newington, NH	X						X			X	
Seapoint, Kittery,ME											X
Leeman Hwy, Brunswick, ME						X					
Great Island, Harpswell, ME							X			X	
Orr Island, Harpswell, ME	X						X				
Cundy's Harbor, ME	X										
Machiasport, ME							X				
Cutler, ME							X		X		
Pikeland, Lubec, ME									X		
Lubec Town Dock, Lubec, ME	X								X		

The '?' symbol means species identitification was based on morphology alone.

Table 3 Species present on transect at seven sites during the study.

Winter/Spring Presence by Site	New Haven	Guilford	Rocky Neck	Charlestown	Black Point	Westport	Falmouth H
Porphyra yezoensis f narawaensis A. Miura			x	x	x		x
Porphyra yezoensis f yezoensis Ueda	x						
Porphyra spp. *'collinsii'*		x	x				
Porphyra leucosticta Thuret					x		
Porphyra olivii Orfanidis, Neefus & Bray	x						
Porphyra spp. *'stamfordensis'*	x	x		x		x	x
Porphyra suborbiculata Kjellman							x
Fucus spiralis Linnaeus							x
Fucus vesiculosus Linnaeus	x	x	x	x	x	x	
Ulva lactuca Linnaeus	x	x	x	x	x	x	x
Ulva intestinalis Linnaeus	x	x	x	x	x	x	x
Chondrus crispus Stackhouse	x		x	x	x		
Petalonia fascia (O. F. Müller) Kuntze	x	x		x	x		
Porlysiphonia stricta (Dillwyn) Greville	x	x	x	x	x		x
Scytosiphon lomentaria (Lyngbye) J. Agardh	x		x	x	x		x
Dumontia contorta (S. G. Gmelin) Ruprecht						x	x
Elachista fucicola (Velley) J. E. Areschoug	x		x	x	x	x	
Blidingia minima (Nägelli ex Kützing) Kylin				x	x		
Ulothrix flacca (Dillwyn) Thuret	x	x	x		x	x	x
Cystoclonium purpureum (Hudson) Batters			x		x	x	
Bangia fuscopurpurea (Dillwyn) Lyngbye	x		x	x	x	x	
Pylaiella littoralis (Linnaeus) Kjellman	x		x	x		x	
Chaetomorpha linum (O. F. Müller) Kützing			x				
Codium fragilessp fragile (Suringar) Hariot				x			
Ascophyllum nodosum (Linnaeus) Le Jolis						x	
Total taxa in transect	14	8	14	14	14	11	10

Table 4 Maximum percent biomass contribution for dominant *Porphyra* species at different sites.

Site	Contribution	Porphyra species
New Haven	4%	*P. yezoensis* f *yezoensis*
Guilford	1%	*P.* spp. *'stamfordensis'*
Rocky Neck	2%	*P. yezoensis* f *narawaensis*
Charlestown	2%	*P. yezoensis* f *narawaensis*
Black Point	81%	*P. yezoensis* f *narawaensis*
Westport	1%	*P.* spp. *'stamfordensis'*
Falmouth Heights	2%	*P.* spp. *'stamfordensis'*

Table 5 Mean blade length of *Porphyra yezoensis* fronds at different sites.

Porphyra yezoensis Mean Blade Length (cm)					
	March	**April**	**Overall Average**	**S.D.**	**N**
New Haven	2.05	2.85	2.40	0.91	427
Rocky Neck	4.13	4.45	4.24	1.94	386
Charlestown	3.79	4.08	3.88	1.27	349
Black Point	4.51	4.21	4.38	1.50	501

Table 6 Mean blade length of different *Porphyra* taxa at different sites.

Site	**Species**	**Mean**	**SD**	**N**
New Haven	*P. olivii*	2.54	1.63	162
Guilford	*P.* spp. *'stamfordensis'*	3.51	3.00	213
Rocky Neck	*P. leucosticta*	3.69	2.46	250
Charlestown	*P. leucosticta*	5.33	4.72	103
Westport	*P.* spp. *'stamfordensis'*	4.42	3.10	315
Falmouth Heights	*P.* spp. *'stamfordensis'*	3.53	2.47	492

FIGURES

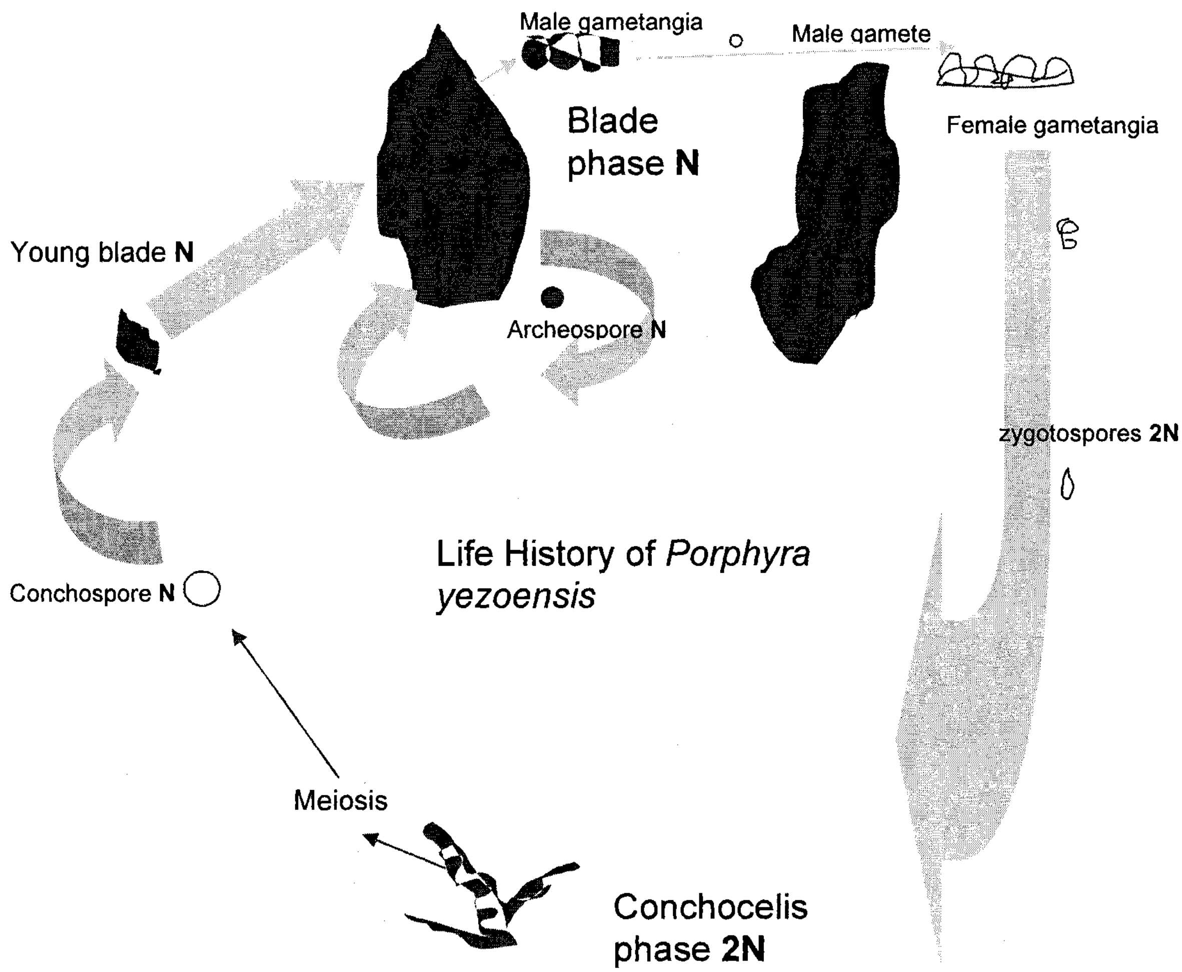

Figure 1 Life history phases of *Porphyra yezoensis*. Terminology from Holmes and Brodie (2005).

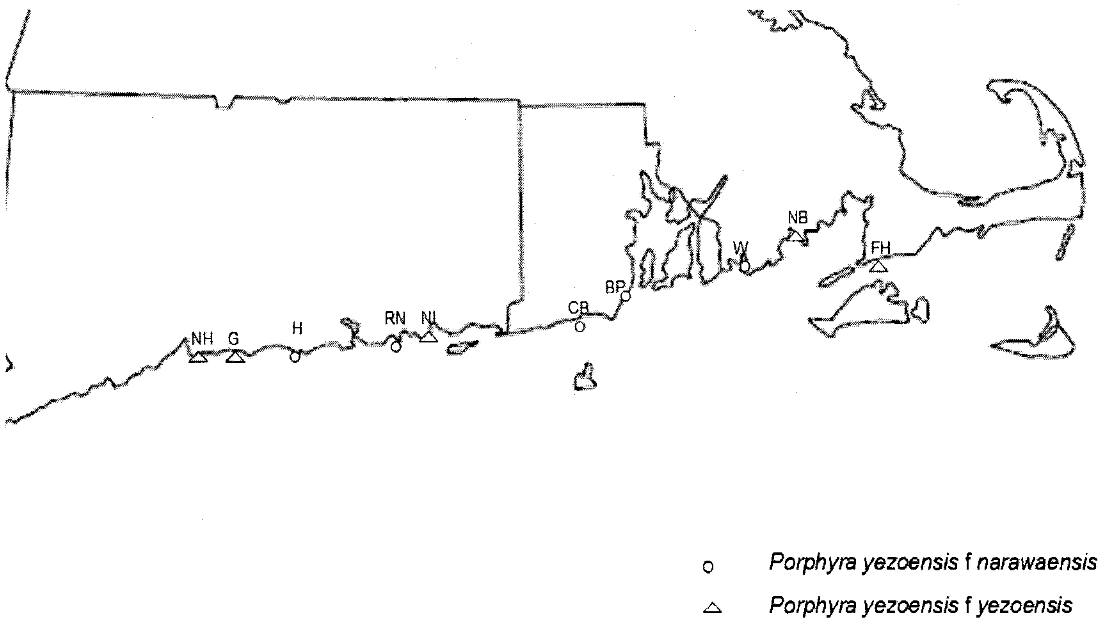

Figure 2 Study sites with previously confirmed *Porphyra yezoensis* populations. Sites from west to east are New Haven (NH), Guilford (G), Hammonassett State Park (H), Rocky Neck State Park (RN), Niantic Boat Valet (NI), Charlestown Breachway (CB), Black Point (BP), Westport Boat Ramp (W), New Bedford (NB), and Falmouth Heights (FH).

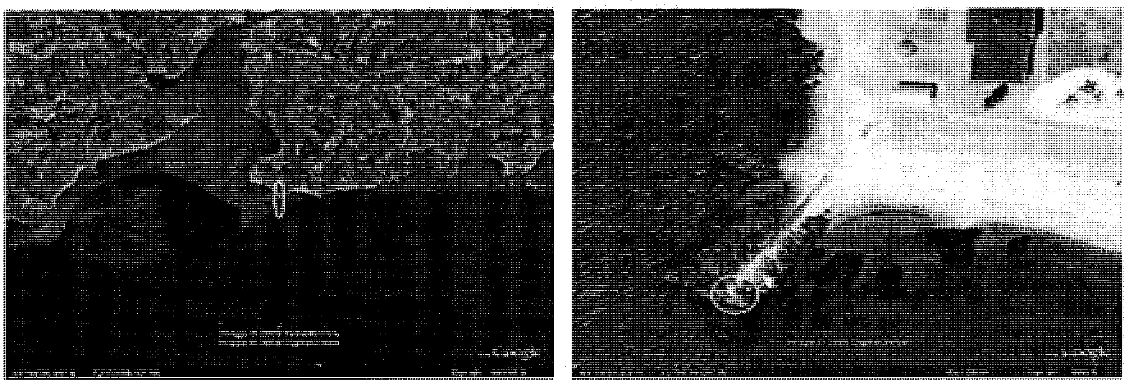

Figure 3 Wide and close aerial views of New Haven Light study site. Image courtesy of Google Earth ™ mapping service.

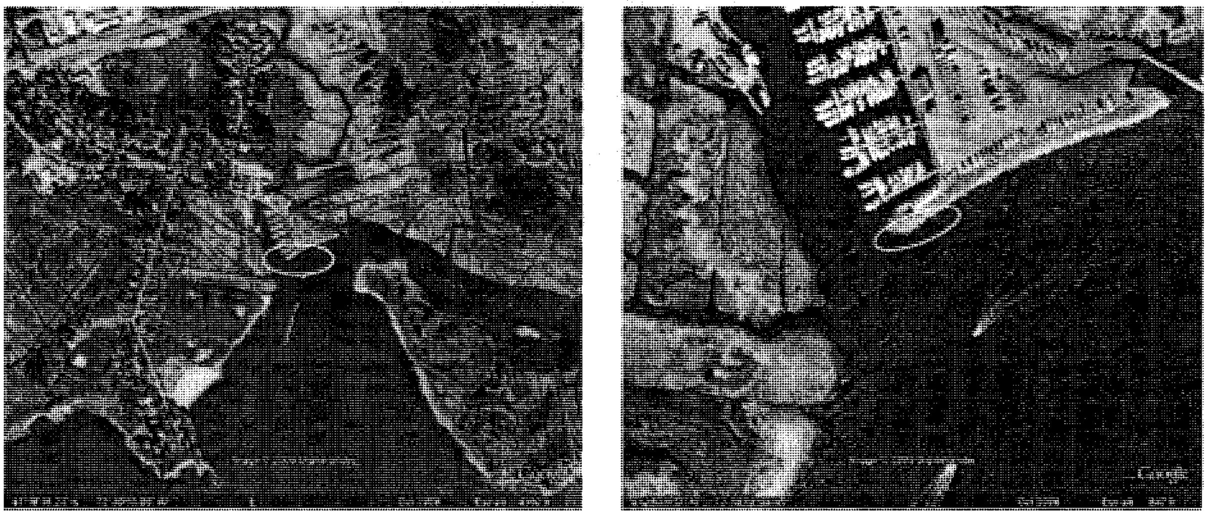

Figure 4 Wide and close aerial views of the Guilford Marina study site. Image courtesy of Google Earth ™ mapping service.

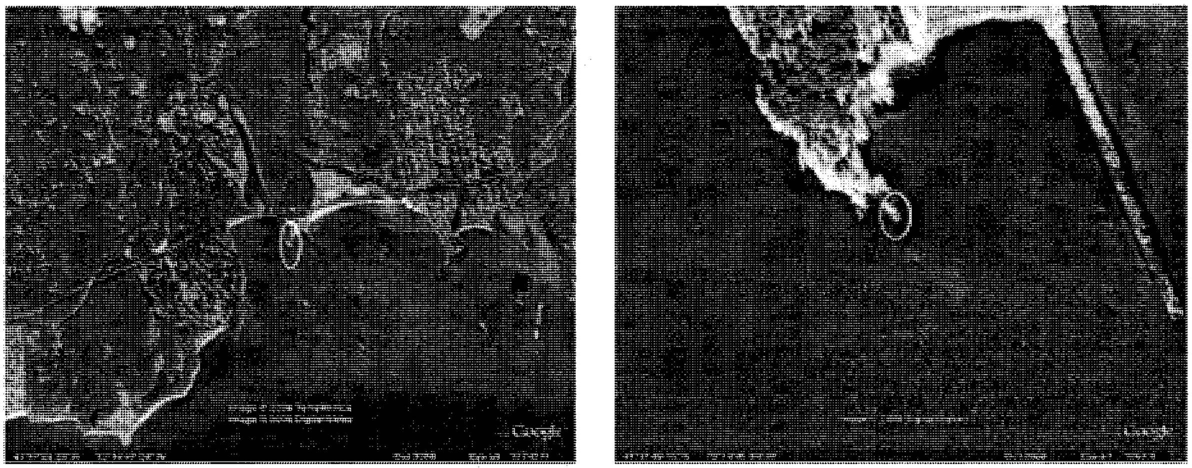

Figure 5 Wide and close aerial views of the Rocky Neck State Park study site. Image courtesy of Google Earth ™ mapping service.

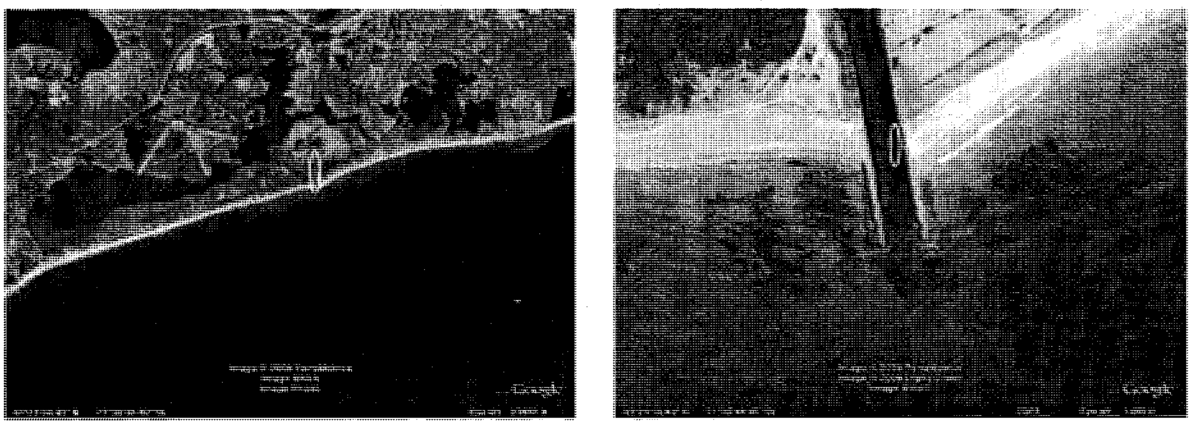

Figure 6 Wide and close aerial views of the Charlestown Breachway study site. Image courtesy of Google Earth ™ mapping service.

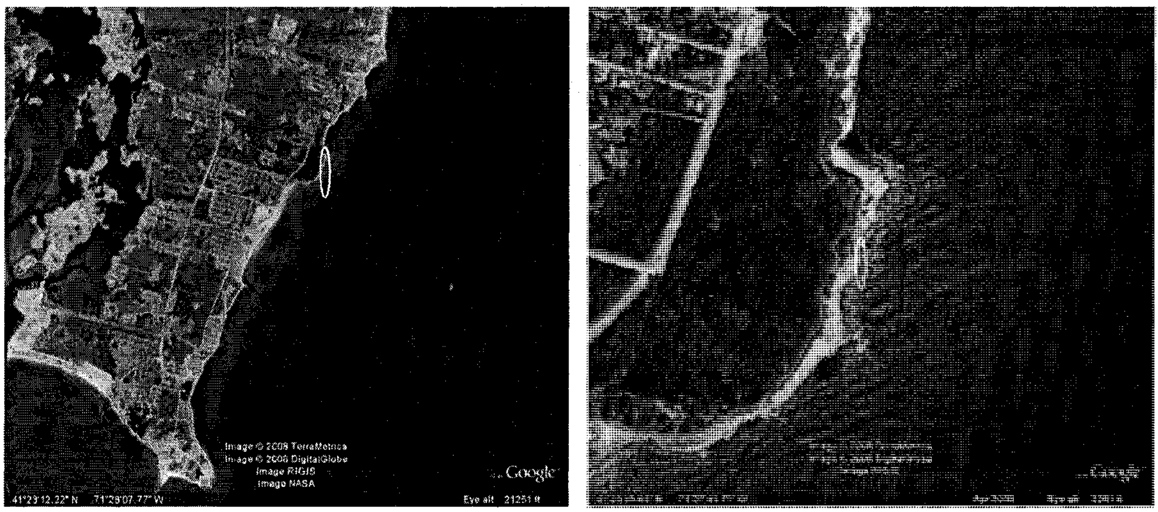

Figure 7 Wide and close aerial views of the Black Point study site. Image courtesy of Google Earth ™ mapping service.

Figure 8 Wide and close aerial views of the Westport Boat Ramp study site. Image courtesy of Google Earth ™ mapping service.

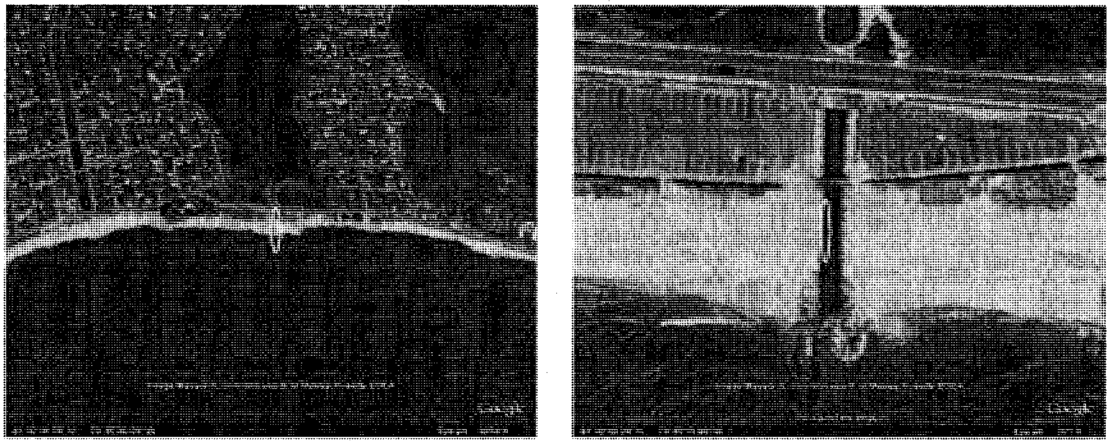

Figure 9 Wide and close aerial views of the Falmouth Heights study site. Image courtesy of Google Earth ™ mapping service.

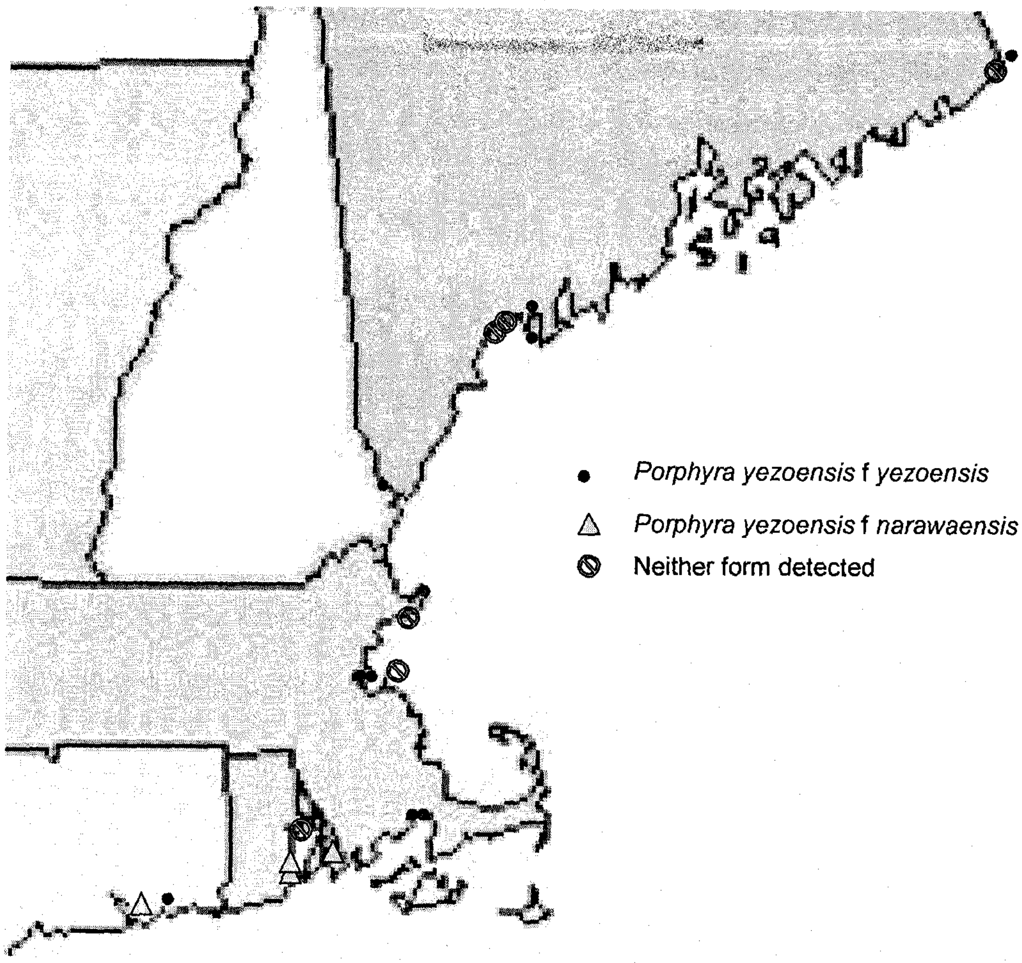

Figure 10 Winter 2007 rapid assessment survey results- *Porphyra yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis* presence/absence by site

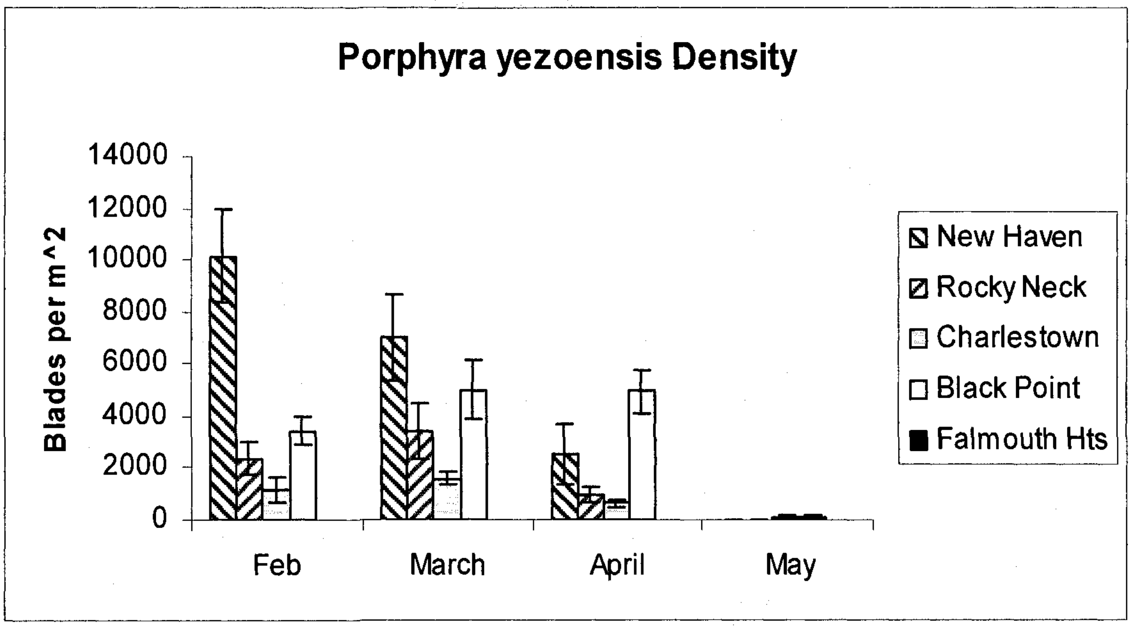

Figure 11 Mean monthly *Porphyra yezoensis* density by site.

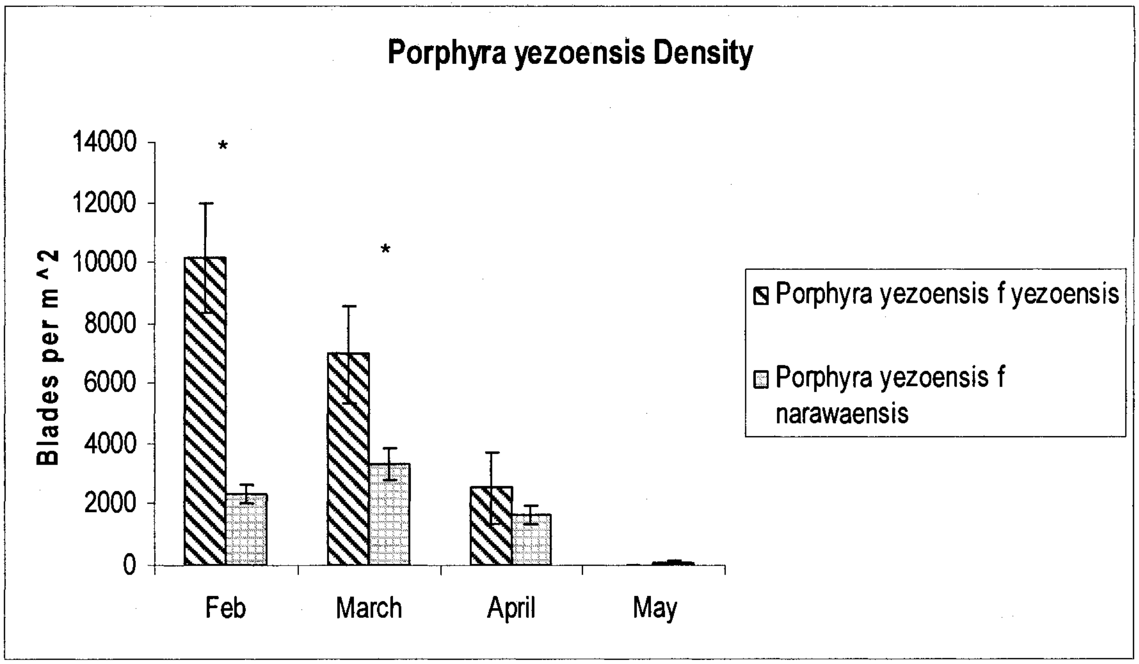

Figure 12 Monthly mean density of *Porphyra yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis*. Asterisks indicate significant differences between the two forms ($p < 0.05$).

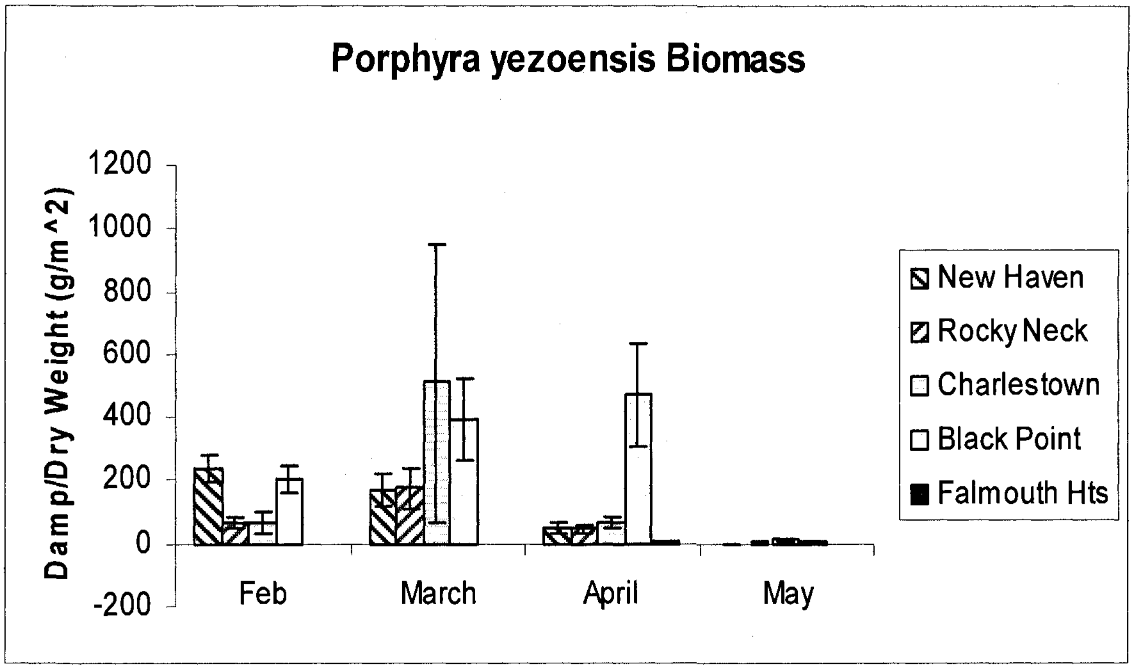

Figure 13 Mean monthly *Porphyra yezoensis* biomass by site.

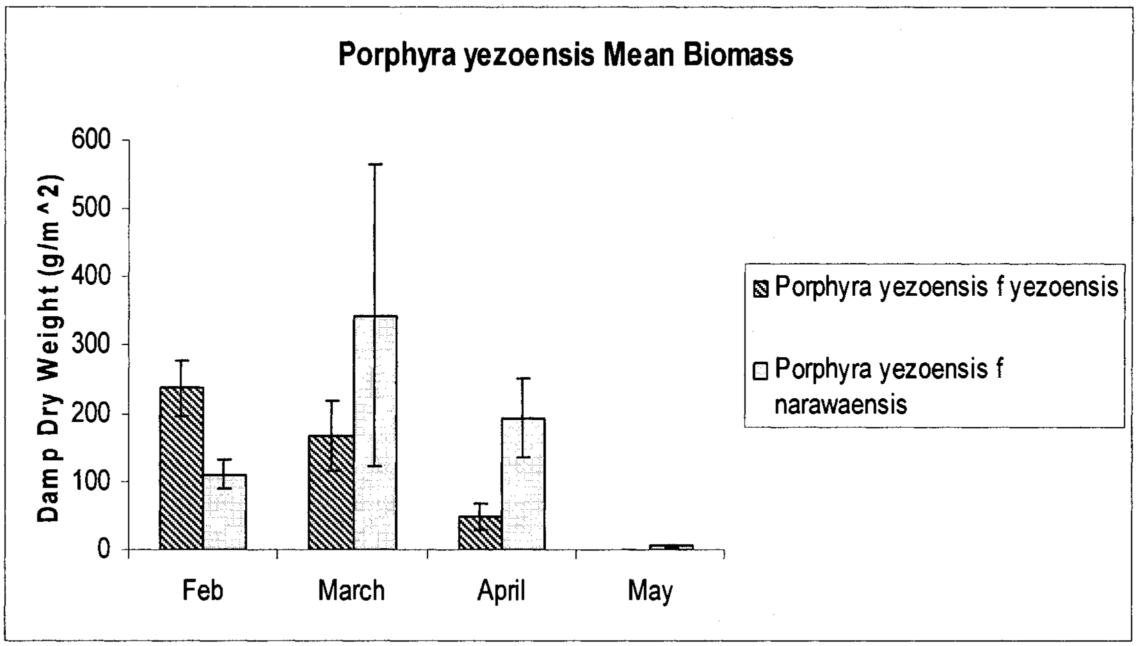

Figure 14 Mean monthly biomass of *Porphyra yezoensis* f. *yezoensis* and *P. yezoensis* f. *narawaensis*

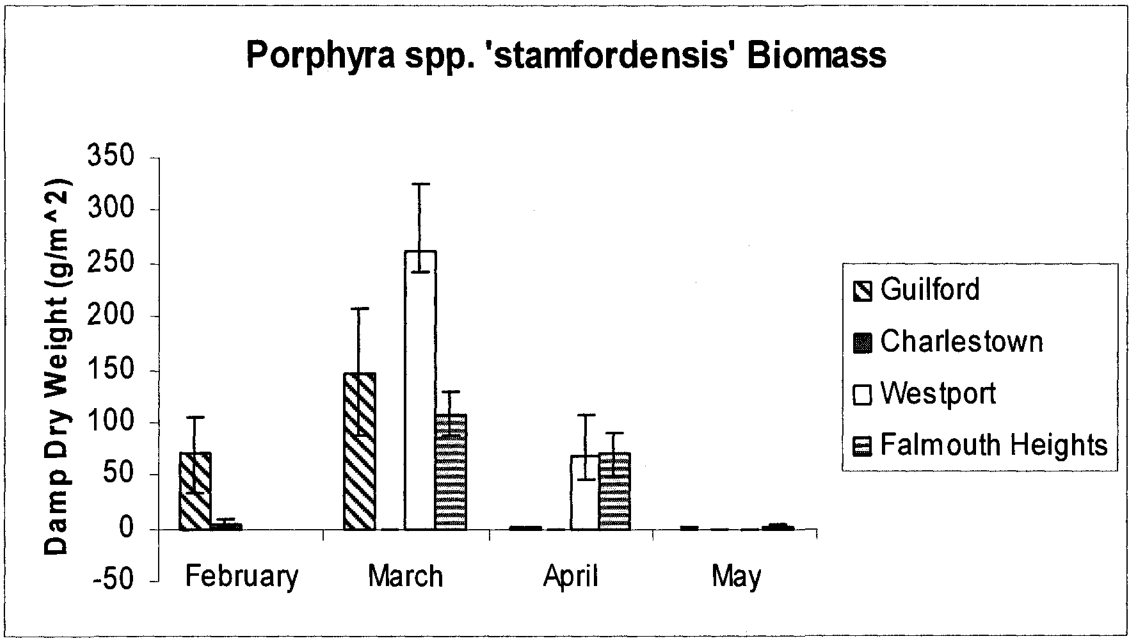

Figure 15 Mean monthly *Porphyra* spp. *'stamfordensis'* biomass by site.

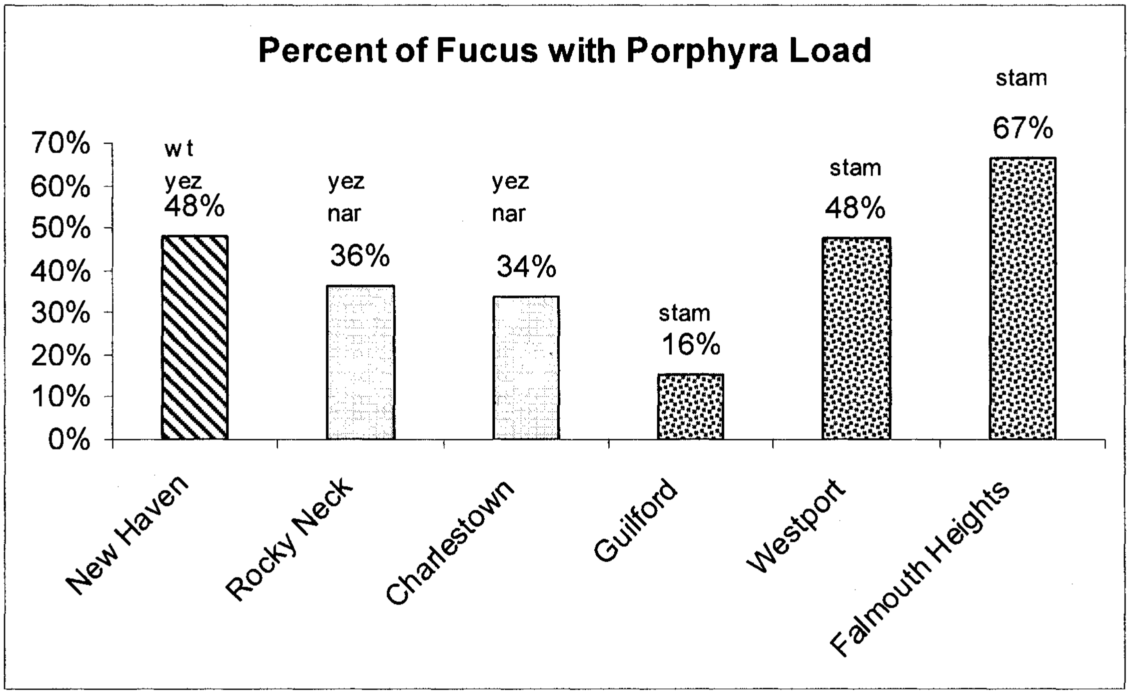

Figure 16 Percentage of *Fucus* plants bearing epiphytic *Porphyra* loads. Calculations were made using all *Fucus* fronds collected in March and April. Abbreviations represent: *Porphyra yezoensis* wild type, *P. yezoensis* f *narawaensis*, and *P.* spp. *'stamfordensis'*.

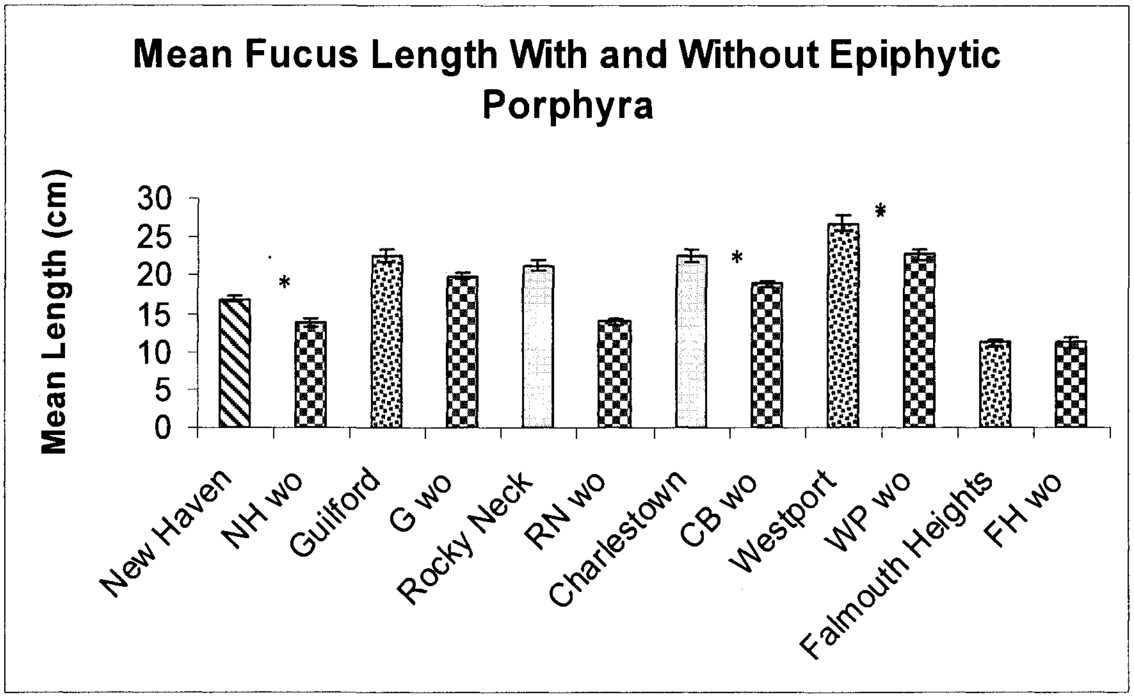

Figure 17 Mean *Fucus* length with and without epiphytic *Porphyra* loads. The checkered bars represent mean lengths of *Fucus* plants without epiphytic loads. *Porphyra yezoensis* f *yezoensis* is represented by striped bars, *P.* spp. *'stamfordensis'* by dotted bars, and *P. yezoensis* f *narawaensis* by cross hatched bars. An asterisk between two bars represents a significant length difference as calculated by Tukey's test.

Figure 18 *Porphyra* species collected by site in the current study. Sites from west to east are New Haven (NH), Guilford (G), Hammonassett State Park (H), Rocky Neck State Park (RN), Niantic Boat Valet (NI), Charlestown Breachway (CB), Black Point (BP), Westport (W), and Falmouth Heights (FH).

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Appendix A: Monthly density by site

New Haven Light, New Haven, CT

Destructive Sampling Count per m^2 February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f yezoensis	4900	12000	22000	14000	21000	10300	2300	7700	3300	900	23000	30000	5700	4900	7300	7500	2700	7000	4500	12000	**10150**	**8034**
Porphyra olivii	2000	5000	6000	3000	10000	1900	500	0	0	0	0	9800	0	0	5200	1000	0	0	0	0	**2220**	**3272**
Fucus vesiculosis	2000	300	1000	0	1000	1600	700	1200	1900	1100	1000	0	900	700	300	500	200	100	200	500	**760**	**599**
Ulva lactuca	400	400	600	200	800	0	100	200	0	0	400	0	200	700	700	100	100	300	600	100	**295**	**265**
Ulva intestinalis	0	4100	1500	0	6000	3600	40000	0	1200	0	500	1300	1500	700	0	0	100	2800	600	1500	**3270**	**8798**
Chondrus crispus	0	600	500	200	1300	0	0	100	100	0	300	1500	0	0	600	0	100	300	700	0	**315**	**439**
Petalonia fascia	0	200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	400	**35**	**98.8**

Destructive Sampling Count per m^2 March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f yezoensis	300	3000	12000	5200	200	2900	3800	500	2400	4800	300	9000	1100	9000	11000	3000	11000	10000	24000	26000	**6975**	**7346**
Porphyra olivii	1800	17000	3000	0	2100	0	0	1200	0	0	1900	4000	17000	9000	1500	2400	6000	9000	16000	10000	**5095**	**5887**
Fucus vesiculosis	1100	900	1200	1400	800	600	1400	1600	1700	2000	1100	2300	100	1000	800	1100	900	600	400	1000	**1100**	**529**
Ulva lactuca	200	0	2000	0	0	300	300	800	2200	0	800	0	100	300	200	0	0	0	300	0	**375**	**639**
Ulva intestinalis	800	21000	3000	1400	700	500	900	0	1900	0	0	1000	300	1400	500	200	200	3200	600	400	**1900**	**4587**
Chondrus crispus	0	0	100	0	0	0	0	0	0	0	0	0	0	300	0	0	200	0	300	0	**45**	**99.9**
Scytosiphon lomentaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	**5**	**22.4**

Destructive Sampling Count per m^2 April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f yezoensis	0	800	2400	2200	600	1100	1100	22000	12000	0	200	600	900	200	300	2200	1100	600	2000	600	**2545**	**5255**
Porphyra olivii	700	500	0	1200	0	0	500	0	0	300	300	500	0	0	100	400	0	0	0	0	**225**	**326**
Fucus vesiculosis	800	700	400	300	500	600	500	400	100	700	700	400	900	400	400	300	200	500	200	500	**475**	**210**
Ulva lactuca	0	0	0	0	0	0	200	0	0	0	0	0	0	0	200	0	0	0	800	100	**65**	**184**
Ulva intestinalis	18200	11100	9800	7200	2300	6200	3300	14200	4300	8200	1400	1300	2300	600	400	7200	100	42100	2100	0	**7115**	**9652**
Chondrus crispus	0	0	0	0	0	0	100	0	0	0	0	0	0	0	100	0	100	0	100	0	**20**	**41**
Petalonia fascia lit	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	**5**	**22.4**
Scytosiphon lomentaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	**5**	**22.4**

Destructive Sampling Count per m^2 May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	0	0	0	200	100	0	0	0	0	200	0	0	0	100	100	0	100	0	0	100	**45**	**68.63**
Fucus vesiculosis	500	500	300	300	400	100	300	200	300	200	200	400	100	300	100	100	200	300	200	400	**270**	**126.1**
Ulva lactuca	100	0	0	0	0	0	0	0	1500	2100	0	2200	100	0	1500	0	0	0	0	0	**375**	**759.4**
Ulva intestinalis	500	200	400	0	400	0	0	2700	2300	500	800	0	0	100	0	4700	300	0	0	0	**645**	**1213**

Guilford Marina, Guilford, CT

Destructive Sampling Count per m^2 February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	0	800	3500	1400	1100	3600	0	0	0	3200	100	2000	1000	6800	1400	7000	5100	6900	900	1600	**2320**	**2415**
Fucus spiralis	1200	1600	1800	0	900	1700	1100	2300	2300	2500	900	2500	900	1600	1500	1700	1600	1300	1200	1800	**1520**	**618.7**
Ulva intestinalis	0	0	0	0	32000	200	100	0	0	0	0	0	0	0	0	0	13000	23000	30000	1E+05	**9915**	**23682**

Destructive Sampling Count per m^2 March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	300	700	200	1100	28000	200	1800	3500	4000	100	3900	1300	2600	1000	0	5300	4500	3600	200	0	**3115**	**6110**
Porphyra spp. 'collinsii'	0	0	0	0	0	0	0	0	400	0	0	0	0	0	0	0	0	0	0	0	**20**	**89.44**
Fucus vesiculosis	1000	1400	2400	1800	2500	1500	1100	1200	1400	500	1900	300	1100	1100	0	1100	1800	400	1200	700	**1220**	**657.4**
Ulva lactuca	0	0	1800	0	0	900	0	0	0	0	0	0	0	0	0	0	0	100	0	0	**140**	**439.4**
Ulva intestinalis	3500	200	300	7900	47000	0	500	2200	3300	0	0	200	2800	900	0	3800	1700	12900	0	0	**4360**	**10543**
Petalonia fascia	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**	**22.36**

Destructive Sampling Count per m^2 April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	0	100	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	0	0	0	**15**	**36.63**
Porphyra spp. 'collinsii'	1800	0	900	300	200	0	0	1200	0	0	600	0	1200	0	200	1400	0	0	600	0	**420**	**573.6**
Fucus vesiculosis	2300	900	600	1700	900	1200	1500	1100	1100	1100	1000	1100	1500	1700	900	1300	900	1400	900	800	**1195**	**396.7**
Ulva intestinalis	2000	0	100	0	0	0	300	7700	0	2300	6200	2700	43000	0	2700	34000	0	0	100	0	**5055**	**11733**

Destructive Sampling Count per m^2 May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	0	0	300	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**15**	**67.1**
Fucus vesiculosis	400	500	500	200	300	500	100	400	100	100	100	1000	100	400	500	500	400	200	400	200	**345**	**221**
Ulva lactuca	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	200	0	0	0	**15**	**48.9**
Ulva intestinalis	2000	0	0	0	0	0	0	0	0	300	0	0	0	0	0	12000	0	0	0	0	**715**	**2694**

Rocky Neck State Park, Niantic, CT

Destructive Sampling Count per m^2 February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	2100	1500	400	6900	100	300	500	1300	7700	8300	2600	4200	3500	100	4900	900	800	1200	300	0	**2380**	**2666**
Porphyra leucosticta	2200	6100	0	800	1100	0	0	400	100	0	300	0	800	0	0	0	0	0	0	0	**590**	**1411**
Fucus vesiculosis	1300	700	1200	1200	900	900	2100	600	600	600	1200	1700	500	1200	1400	1500	2100	1300	1900	800	**1185**	**496**
Ulva lactuca	0	0	0	0	0	100	100	1000	0	0	0	0	0	0	0	200	0	0	100	100	**80**	**224**
Ulva intestinalis	0	0	1100	0	0	500	200	2600	100	1200	100	0	0	800	100	2700	0	0	0	0	**470**	**835**
Chondrus crispus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	200	**10**	**44.7**
Scytosiphon lomentaria	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	**5**	**22.4**
Chaetomorpha linum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1400	**70**	**313**

Destructive Sampling Count per m^2 March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	100	3400	1900	9600	5000	600	3200	800	0	9000	1400	3700	0	1200	2700	1100	100	600	20000	3000	**3370**	**4771**
Porphyra leucosticta	3700	0	200	7600	300	2700	1400	7300	0	39000	600	200	300	600	0	0	0	0	0	0	**3195**	**8741**
Fucus vesiculosis	1500	2400	1500	700	2400	1600	1300	1100	0	500	700	700	600	700	1100	600	1200	800	1100	1400	**1095**	**602**
Ulva intestinalis	0	0	0	0	2000	0	0	0	0	0	100	1600	100	600	0	0	0	300	6000	0	**535**	**1401**

Destructive Sampling Count per m^2 April

Quadrat	20	19	18	17	16	15	**14**	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	700	300	200	1200	0	900	0	3600	5400	1400	500	2600	500	500	0	500	0	1200	200	200	**995**	**1385**
Porphyra leucosticta	1000	2100	1000	1900	0	1000	0	1100	0	400	800	300	0	200	0	0	0	0	100	100	**500**	**656**
Fucus vesiculosis	800	700	700	100	800	200	1200	200	600	1000	600	300	700	600	300	1000	200	200	600	800	**580**	**316**
Ulva lactuca	0	0	0	200	0	0	0	200	0	100	100	0	0	0	0	0	0	0	0	0	**30**	**65.7**
Ulva intestinalis	0	0	0	3700	0	100	0	100	0	0	0	0	0	0	0	0	0	0	0	0	**195**	**826**

Destructive Sampling Count per m^2 May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	300	0	100	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	**25**	**71.6**
Porphyra leucosticta	400	500	0	0	300	0	0	0	0	100	800	200	0	100	0	0	0	0	0	0	**120**	**219**
Fucus vesiculosis	300	200	500	300	400	500	700	300	500	400	500	600	500	900	300	500	600	500	300	400	**460**	**164**
Ulva lactuca	0	200	100	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	**20**	**52.3**
Ulva intestinalis	100	0	0	0	0	0	0	0	0	0	0	0	0	0	900	0	0	0	0	0	**50**	**201**
Chondrus crispus	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**	**22.4**

Charlestown Breachway, Charlestown, RI

Destructive Sampling Count per m^2 February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	0	900	0	300	300	0	500	0	800	1100	100	9000	2200	1000	0	2000	1100	900	3300	100	**1180**	**2039**
Porphyra spp. 'stamfordensis'	800	0	0	100	0	600	0	400	0	300	0	0	0	0	200	0	0	0	0	0	**120**	**231**
Fucus vesiculosis	0	600	300	300	900	0	900	0	100	300	700	700	1000	400	900	1200	1200	1000	400	1700	**630**	**470**
Ulva lactuca	1600	1700	1800	2900	400	300	200	1300	0	0	100	0	0	0	0	100	0	0	0	0	**520**	**849**
Ulva intestinalis	9000	24000	1200	8000	2500	0	200	1200	48000	40000	100	4500	25000	66000	0	60000	5000	1100	200	200	**14810**	**21613**
Chondrus crispus	0	0	0	0	0	1600	0	500	0	0	0	0	0	0	0	0	0	0	0	0	**105**	**369**
Petalonia fascia	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	**5**	**22.4**
Porlysiphonia stricta	0	2000	0	0	0	3000	600	0	0	0	0	0	0	0	0	300	0	0	0	0	**295**	**785**
Scytosiphon lomentaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	**5**	**22.4**

Destructive Sampling Count per m^2 March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	1000	2500	2300	1000	2400	400	800	3700	3000	900	300	0	200	1300	0	2300	3500	2400	1700	2100	**1590**	**1158**
Porphyra leucosticta	100	0	0	0	0	100	0	0	0	0	1300	4700	3500	0	600	0	0	300	0	0	**530**	**1275**
Fucus vesiculosis	1300	700	1800	2000	900	1000	1800	1800	3000	1500	700	900	1100	500	1000	900	600	700	1300	1200	**1235**	**607**
Ulva lactuca	300	0	0	3200	600	0	1500	0	0	0	300	0	300	0	0	0	0	0	0	0	**310**	**768**
Ulva intestinalis	42000	0	30000	15000	15000	2000	17000	9000	6000	4000	6200	0	16200	700	0	3300	5300	0	700	500	**8645**	**11207**

Destructive Sampling Count per m^2 April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	1000	200	0	1900	400	800	100	1300	0	1200	0	700	0	100	700	800	200	2800	800	100	**655**	**732**
Porphyra leucosticta	500	500	400	0	800	400	0	900	0	200	0	0	0	100	1000	300	700	0	0	300	**305**	**335**
Fucus vesiculosis	300	200	100	500	200	300	200	400	400	300	1000	500	300	400	300	700	700	900	900	200	**440**	**264**
Ulva lactuca	0	200	0	0	0	0	0	0	200	0	0	0	200	0	0	0	0	0	0	0	**30**	**73.3**
Ulva intestinalis	100	700	0	300	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**55**	**167**

Destructive Sampling Count per m^2 May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	300	0	0	0	0	100	0	0	0	100	100	800	0	0	1400	0	0	0	0	0	**140**	**350**
Porphyra leucosticta	400	0	200	0	0	0	0	0	0	0	100	0	1100	0	0	0	2400	0	0	0	**210**	**576**
Fucus vesiculosis	100	500	100	300	200	300	400	200	100	100	100	100	100	200	300	200	200	300	200	400	**220**	**120**
Ulva lactuca	0	0	400	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**20**	**89.4**
Ulva intestinalis	100	100	300	4100	0	18000	0	0	0	100	0	3300	400	0	0	0	1200	0	100	0	**1385**	**4072**

Black Point, Narragansett, RI

Destructive Sampling Count per m^2 February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	1000	6700	2400	1100	2900	3000	3400	4000	5600	7900	9300	1300	4900	5400	2400	3100	1200	900	800	1700	**3450**	**2471**
Porphyra leucosticta	0	0	0	300	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**15**	**67.1**
Ulva lactuca	1300	1000	800	1800	2400	0	400	0	0	400	200	1000	100	1500	0	600	1100	0	2200	5700	**1025**	**1335**
Ulva intestinalis	1100	0	1200	800	0	50000	200	200	32000	400	2600	0	2000	1800	16000	2000	2600	40000	4100	800	**7890**	**14834**
Chondrus crispus	0	0	0	100	0	0	0	0	0	0	0	0	0	300	0	700	0	0	0	0	**55**	**167**
Petalonia fascia	0	0	0	0	0	0	0	0	0	0	0	7500	0	800	0	500	1600	42000	900	500	**2690**	**9403**
Scytosiphon lomentaria	0	0	100	0	0	300	0	200	0	0	300	0	500	300	500	500	1000	0	1300	300	**265**	**359**

Destructive Sampling Count per m^2 March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	5200	1600	6600	3600	1300	1400	2200	1200	1700	2000	10000	22000	11000	2160	1600	4000	7000	8500	3500	3500	**5003**	**5007**
Porphyra leucosticta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	500	0	0	**25**	**112**
Ulva lactuca	1800	0	0	400	500	0	1200	1200	0	0	0	0	500	100	3700	0	2000	1500	1500	500	**745**	**977**
Ulva intestinalis	2000	13000	0	0	0	100	0	500	100	2300	5200	2600	2000	200	0	7000	500	1500	4500	2000	**2175**	**3224**
Chondrus crispus	0	0	0	0	0	0	0	200	0	200	0	0	0	0	0	0	0	0	0	0	**20**	**61.6**
Petalonia fascia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	800	0	200	3500	500	0	**250**	**792**
Porlysiphonia stricta	0	0	0	0	0	0	0	0	0	700	0	0	0	0	500	500	0	0	0	500	**110**	**229**
Scytosiphon lomentaria	500	500	0	700	1300	0	1100	700	300	800	400	0	3000	200	700	1000	2500	2000	1000	1500	**910**	**819**

Destructive Sampling Count per m^2 April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	16000	4000	5400	12000	10000	700	4000	1400	1600	3100	5100	5200	2300	3300	4100	5800	5400	4100	2400	2300	**4910**	**3772**
Ulva lactuca	2000	0	0	0	0	1000	0	0	0	0	0	0	0	0	0	2100	0	0	0	0	**255**	**653**
Ulva intestinalis	0	300	100	0	0	0	100	0	0	200	0	1000	0	100	100	0	100	2800	0	100	**245**	**642**
Scytosiphon lomentaria	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**	**22.4**

Destructive Sampling Count per m^2 May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra yezoensis f narawaensis	0	100	0	0	0	300	0	0	0	100	0	100	0	0	0	400	0	0	800	700	**125**	**240**
Porphyra leucosticta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	200	400	**30**	**97.9**
Fucus vesiculosis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	**5**	**22.4**
Ulva lactuca	0	1200	1200	800	100	0	500	700	100	600	400	700	800	0	800	700	3800	2300	1400	2000	**905**	**928**
Ulva intestinalis	0	0	0	0	1600	3100	1000	0	600	0	1700	2100	0	6000	11200	0	0	0	8000	0	**1765**	**3112**
Petalonia fascia	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	**5**	**22.4**
Scytosiphon lomentaria	0	200	300	200	200	0	300	100	300	0	100	100	100	600	0	100	100	0	0	0	**135**	**153**

Westport Boat Landing, Westport, MA

Destructive Sampling Count per m^2 March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	0	2400	2800	13000	4000	700	18000	27000	10800	27000	1400	1200	3400	400	1800	4400	1300	3900	100	200	**6190**	**8541**
Fucus vesiculosis	0	400	200	500	300	400	900	1300	1000	600	1200	700	400	100	800	400	300	300	100	200	**505**	**369**
Ulva lactuca	100	0	0	0	0	0	12000	0	0	0	0	0	0	0	0	20	0	0	0	0	**606**	**2682**
Ulva intestinalis	0	0	700	0	400	1100	0	7000	0	0	0	5200	1400	1500	300	2700	100	5100	0	300	**1290**	**2081**
Ascophyllum nodosum	600	200	0	200	0	500	100	0	0	100	0	0	0	0	0	0	100	0	3600	100	**275**	**801**

Destructive Sampling Count per m^2 April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	100	0	100	0	0	0	1500	7200	3200	0	100	0	0	0	500	0	0	0	0	0	**635**	**1725**
Fucus vesiculosis	500	500	200	400	400	200	700	100	900	500	200	400	1000	400	500	500	0	200	0	0	**380**	**278**
Ulva lactuca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	100	0	**10**	**30.8**
Ulva intestinalis	0	0	0	0	0	0	0	800	21100	0	0	0	0	0	100	0	0	0	0	0	**1100**	**4711**
Ascophyllum nodosum	0	0	100	0	100	0	0	100	0	0	0	0	0	1	0	0	100	0	300	200	**45.1**	**82.5**

Destructive Sampling Count per m^2 May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Fucus vesiculosis	200	100	100	400	200	100	300	400	700	400	300	100	0	300	0	0	0	0	0	0	**180**	**194**
Ascophyllum nodosum	0	0	0	0	0	0	0	0	0	0	0	0	300	0	300	300	400	200	200	400	**105**	**154**

Falmouth Heights, MA

Destructive Sampling Count per m^2 March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	1900	3700	1100	4100	5100	2600	4800	3800	500	1300	1300	2300	2000	2700	2200	1500	1000	800	11000	3600	**2865**	**2343**
Porphyra suborbiculata	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	400	0	600	0	0	**55**	**157**
Fucus spiralis	300	100	200	600	300	300	300	700	200	700	3300	800	700	500	500	400	500	600	900	1800	**685**	**716**
Ulva lactuca	0	0	400	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	100	**30**	**92.3**
Ulva intestinalis	4200	3100	16000	5000	3100	4200	700	1600	300	1200	1300	1900	300	1300	1700	2900	1300	2300	41000	3700	**4855**	**9144**
Scytosiphon lomentaria	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**	**22.4**

Destructive Sampling Count per m^2 April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	1000	400	1300	1600	1300	1500	1800	1000	100	1400	300	100	2600	2000	200	3000	100	2600	200	0	**1125**	**945**
Porphyra yezoensis f narawaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	200	**15**	**48.9**
Fucus spiralis	400	200	200	300	300	600	300	600	100	500	500	200	400	500	600	300	200	200	200	100	**335**	**166**
Ulva lactuca	0	0	0	0	700	0	0	100	0	0	0	0	0	0	0	0	0	200	0	0	**50**	**161**
Ulva intestinalis	0	0	0	100	0	0	0	500	0	0	0	500	600	0	500	0	200	0	0	0	**120**	**214**

Destructive Sampling Count per m^2 May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD+-**
Porphyra spp. 'stamfordensis'	0	0	0	0	100	600	0	0	0	0	100	0	0	0	400	0	0	0	0	0	**60**	**157**
Porphyra yezoensis f narawaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	300	0	0	0	**15**	**67.1**
Fucus vesiculosis	300	500	200	200	200	400	100	0	300	600	400	100	300	200	200	300	100	300	200	200	**255**	**143**
Ulva lactuca	0	0	0	800	0	0	0	0	0	0	0	0	0	0	0	0	0	0	700	100	**80**	**231**
Ulva intestinalis	0	0	0	300	100	0	0	0	0	300	3000	100	0	0	0	0	6200	0	1200	100	**565**	**1499**

Appendix B: Monthly biomass by site

New Haven Light, New Haven, CT

Destructive Sampling Damp/Dry weight (g/m^2) February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	Mean	SD
Porphyra yezoensis f yezoensis	115	201	400	69	325	245	46	186	417	14	651	563	98	226	167	106	104	250	89	474	**237.3**	**180**
Porphyra olivii	40	60	30	15	150	25	20	0	0	0	0	170	0	0	110	15	0	0	0	0	**31.75**	**52**
Fucus vesiculosis	7800	1320	3775	4238	3503	4970	1060	5867	10050	8583	9427	0	6228	5460	3300	5120	3262	4003	909	3930	**4640**	**2799**
Ulva lactuca	16	14	13	57	11	0	1	4	0	0	14	0	1	32	13	1	1	6	13	11	**10.4**	**14**
Ulva intestinalis	0	7	23	0	16	6	58	0	1	0	3	11	1	0	0	0	1	22	3	10	**8.1**	**14**
Chondrus crispus	0	550	470	277	1656	0	0	14	132	0	588	2750	0	1	880	0	272	683	1271	0	**477.2**	**712**
Petalonia fascia	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	25	**2.05**	**6**
Elachista fuciola	10	130	140		58	62	72	14	60		95	53	53	32	1	32	23	29	15	55	**46.7**	**39**

Destructive Sampling Damp/Dry weight (g/m^2) March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	Mean	SD
Porphyra yezoensis f yezoensis	1	24	123	113	5	26	214	500	53	64	3	70	10	183	161.5	13.8	174	113	740	770	**168.1**	**231**
Porphyra olivii	24	68	65	0	48	0	0	5	0	0	19	53	225	111	11.5	13.8	42	22	240	20	**48.37**	**69**
Fucus vesiculosis	13358	9292	10189	13870	9991	1960	12830	23300	13030	19180	15755	18049	1501	10700	6936	16164	7818	6463	4269	12310	**11348**	**5652**
Ulva lactuca	14	0	43	0	0	15	7	15	151	0	29	0	4	4	6.4	0	0	0	8	0	**14.82**	**34**
Ulva intestinalis	1	47	9	1	7	1	3	0	1	1	0	1	10	11.2	4	3.1	1	12	4	3	**6.015**	**10**
Chondrus crispus	0	0	52	0	0	0	0	0	0	0	0	0	0	305	0	0	225	0	535	0	**55.85**	**140**
Scytosiphon lomentaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	**0.2**	**1**
Elachista fuciola	0	0	0	8	0	3	3	9	96	19	1	9	0	0	41	0	10	0	0	228	**21.35**	**54**
Ulothrix flacca	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.15**	**0**
Bangia fuscopurpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.3**	**0**
Pylaiella littoralis	49	105	135	0	77	1	1	0	13	0	12	0	24	0	1	6.9	10	8	12.4	14	**23.47**	**38**

Destructive Sampling Damp/Dry weight (g/m^2) April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f yezoensis	0	14	63	63	5	12	22	320	21	0	4	9	10	4	6	27	121	11	236	20	**48.4**	**85**
Porphyra olivii	15	5	0	30	0	0	10	0	0	5	1	16	0	0	1	8	0	0	0	0	**4.55**	**8**
Fucus vesiculosis	5072	7075	8100	5228	7749	9386	5655	5695	3371	11205	16781	7701	7395	5077	7561	9410	5470	12218	4442	8040	**7632**	**3112**
Ulva lactuca	0	0	0	0	0	0	6	0	0	0	0	0	0	0	29	0	0	0	161	6	**10.1**	**36**
Ulva intestinalis	270	224	110	74	19	120	23	164	33	261	30	7	15		27	34	17	477	66	0	**98.55**	**125**
Chondrus crispus	0	0	0	0	0	0	35	0	0	0	0	0	0	0	201	0	301	0	298	0	**41.75**	**99**
Petalonia fascia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78	0	0	0	0	0	**3.9**	**17**
Scytosiphon lomentaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	**0.55**	**2**
Elachista fuciola	0	0	3	0	3	112	40	40	45	0	30	26	0	61	0	0	8	0	0	0	**18.4**	**29**
Ulothrix flacca	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	**0.35**	**2**
Pylaiella littoralis	119	53	128	0	8	42	49	0	0	148	21	51	143	1	1	19	0	5	0	0	**39.4**	**52**

Destructive Sampling Damp/Dry weight (g/m^2) May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra spp. 'stamfordensis'	0	0	0	33	2	0	0	0	0	1	0	0	0	1	1	0	3	0	0	0	**2.05**	**7**
Fucus vesiculosis	5840	4586	2283	2517	6268	2734	3337	2969	2424	3351	2808	5290	1018	2179	5189	3025	4590	1755	3354	6932	**3622**	**1610**
Ulva lactuca	5	0	0	0	0	0	0	0	109	98	0	34	1	0	0	0	0	0	0	0	**12.35**	**32**
Ulva intestinalis	11	1	3	0	6	0	0	41	18	2	6	0	0	1	39	134	0	0	0	0	**13.1**	**31**
Porlysiphonia stricta	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.05**	**0**
Elachista fuciola	0	0	0	0	1	0	0	0	1	3	1	0	0	0	0	1	0	0	0	0	**0.35**	**1**
Bangia fuscopurpurea	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	**0.65**	**3**

Guilford Marina, Guilford, CT

Destructive Sampling Damp/Dry Weight (g/m^2) February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra spp. 'stamfordensis'	0	14	90	0	13	114	0	0	0	109	5	28	7	0	31	94	158	693	8	17	**69.05**	**155**
Fucus spiralis	8830	16250	16820	9170	8430	12692	13020	14690	15120	15360	8630	16250	10180	10160	11695	13070	23550	13380	13049	11517	**13093**	**3642**
Ulva intestinalis	0	0	0	0	49	1	2	0	0	0	0	0	0	0	0	0	24	56	4	17	**7.65**	**17**
Elachista fuciola	1	1	1	2	1	5	5	1	3	8	26	33	3	410	0	7	80	0	1	38	**31.3**	**91**
Ulothrix flacca	8	13	22	29	25	5	20	0	7	68	6	6	1	0	119	0	0	0	0	0	**16.45**	**29**

Destructive Sampling Damp/Dry Weight (g/m^2) March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra spp. 'stamfordensis'	2	49	2	32	1110	4	46	210	55	3	165	17	53	47	0	488	298	364	1	0	**147.3**	**266**
Porphyra spp. 'collinsii'	0	0	0	0	0	0	0	0	144	0	0	0	0	0	0	0	0	0	0	0	**7.2**	**32**
Fucus vesiculosis	19490	15276	53190	23822	19060	17780	10700	20900	13200	8153	19547	17622	21636	23435	0	25085	32232	11705	12400	10827	**18803**	**10752**
Ulva lactuca	0	0	63	0	0	14	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**3.9**	**14**
Ulva intestinalis	13	1	1	60	360	0	1	8	12	0	0	1	19	6	0	51	9	242	0	0	**39.2**	**93**
Petalonia fascia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.05**	**0**
Elachista fuciola	0	0	0	0	0	16	0	3	9	0	12	4	22	1	0	1	0	0	0	0	**3.4**	**6**
Ulothrix flacca	0	0	0	0	0	0	0	0	0	0	1	7	0	0	0	0	0	0	0	1	**0.45**	**2**
Pylaiella littoralis	0	0	0	18	520	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**26.9**	**116**

Destructive Sampling Damp/Dry Weight (g/m^2) April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra spp. 'stamfordensis'	0	1	0	17	0	0	0	0	0	1	4	0	0	0	0	0	0	0	0	0	**1.15**	**4**
Porphyra spp. 'collinsii'	55	0	13.5	0	1	0	0	26	0	0	30	0	32	0	1	27	0	0	5	0	**9.525**	**16**
Fucus vesiculosis	21386	8210	12060	27754	9495	21240	14716	12470	19400	17700	6440	8364	11660	15390	12780	11800	12800	6470	20996	10100	**14062**	**5732**
Ulva intestinalis	1	0	1	0	0	0	4	38	0	3	27	6	196	0	22	180	0	0	2	0	**24**	**57**
Elachista fuciola	1	0	3.8	4	1	1	1	6	1	1	1	0	2	1	4	1	1	0	30	0	**2.99**	**7**

Destructive Sampling Damp/Dry Weight (g/m^2) April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra spp. 'stamfordensis'	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.2**	**1**
Fucus vesiculosis	11831	4820	7980	1424	13979	6054	1470	7062	619	5725	3166	10617	1889	4600	7970	4679	11499	6860	4456	1733	**5922**	**3838**
Ulva lactuca	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	**0.55**	**2**
Ulva intestinalis	11	0	0	0	0	0	0	0	0	20	0	0	0	0	0	229	0	0	0	0	**13**	**51**
Porlysiphonia stricta	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.2**	**1**
Elachista fuciola	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.05**	**0**

Rocky Neck State Park, Niantic, CT

Destructive Sampling Damp/Dry Weight (g/m^2) February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	107	34	13	260	1	12	3	55	226	215	62	81	101	1	116	4	7	19	24	0	**67.05**	**81**
Porphyra leucosticta	113	243	0	17	47	0	0	9	1	0	9	0	17	0	0	0	0	0	0	0	**22.8**	**58**
Fucus vesiculosis	13950	6980	10630	12290	6146	2667	5367	5821	2496	1657	8675	4123	3650	4650	1060	2886	5270	2190	2622	3328	**5323**	**3587**
Ulva lactuca	0	0	0	0	0	4	4	13	0	0	0	0	0	0	0	4	0	0	2	1	**1.4**	**3**
Ulva intestinalis	0	0	1	0	0	1	1	7	1	31	1	0	0	1	1	9	0	0	0	0	**2.7**	**7**
Scytosiphon lomentaria	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	**0.2**	**1**
Elachista fuciola	97	71	0	18	6	1	0	101	17	7	1	0	12	46	0	3	41	0	0	6	**21.35**	**33**
Ulothrix flacca	0	3	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**0.4**	**1**
Chaetomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	**0.15**	**1**
Bangia fuscopurpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	**0.2**	**1**
Pylaiella littoralis	0	0	0	0	0	0	0	0	0	0	0	1	16	0	0	0	0	0	0	0	**0.85**	**4**

Destructive Sampling Damp/Dry Weight (g/m^2) March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	5	233	65	775	324	24	154	68	0	240	54	186	12	66	64	11	1	23	1120	89	**175.7**	**285**
Porphyra leucosticta	141	0	1	660	2.1	404	104	705	0	1070	34	4	0	12	0	0	0	0	60	0	**159.9**	**305**
Fucus vesiculosis	14380	10170	10150	5850	22020	22100	8273	12120	0	6414	9372	8574	6459	13674	9370	1787	8672	6100	15350	1123	**9598**	**5917**
Ulva lactuca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	260	0	**13**	**58**
Ulva intestinalis	0	0	0	0	0	0	0	0	0	0	1	4	1	1	0	0	0	1	80	0	**4.4**	**18**
Elachista fuciola	0	0	0	26	80	56	3	20	0	100	20	24	60	23	21	0	1	0	3760	0	**209.7**	**836**
Ulothrix flacca	0	1	0	0	0	0	3	0	0	10	0	0	0	0	0	0	0	1	0	1	**0.8**	**2**
Bangia fuscopurpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	**0.65**	**3**
Pylaiella littoralis	2100	0	1060	0	5	0	119	58	0	10	7	0	6	206	35.2	0	0	0	0	0	**180.3**	**510**

Destructive Sampling Damp/Dry Weight (g/m^2) April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	25	36	8	110	0	38	0	323	143	44	6	95	3	27	0	5	0	36	3	7	**45.45**	**77**
Porphyra leucosticta	20	71	50	322	0	16	0	60	0	9	5	21	0	11	0	0	0	0	1	9	**29.75**	**72**
Fucus vesiculosis	8296	0	1181	5617	9597	2286	7240	4120	5850	7696	7525	2942	4783	4720	5084	24716	4551	554	4761	3728	**5762**	**5143**
Ulva lactuca	0	0	0	13	0	0	0	3	0	1	3	0	0	0	0	0	0	0	0	0	**1**	**3**
Ulva intestinalis	0	0	0	28	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**1.5**	**6**
Elachista fuciola	0	5	13	12	0	0	0	12	0	4	0	8	0	0	0	0	0	0	1	0	**2.75**	**5**
Ulothrix flacca	0	1	0	0	0	0	0	0	0	0	1	3	1	0	0	1	0	1	1	0	**0.45**	**1**
Bangia fuscopurpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	**0.3**	**1**

Destructive Sampling Damp/Dry Weight (g/m^2) May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	3	0	3	0	0	0	0	0	0	2	0	8	0	0	0	0	0	0	0	0	**0.8**	**2**
Porphyra leucosticta	9	21	0	0	7	0	0	0	0	0	8	2	0	17	0	0	0	0	0	0	**3.2**	**6**
Fucus vesiculosis	7021	744	3331	5877	2658	6708	10154	1894	4895	5335	8139	7065	3661	6557	1194	4586	3707	2233	5437	2555	**4688**	**2482**
Ulva lactuca	0	8	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**0.6**	**2**
Ulva intestinalis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	**0.7**	**3**
Chondrus crispus	96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**4.8**	**21**
Porlysiphonia stricta	1	0	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2.7**	**12**
Elachista fuciola	0	0	1	1	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	**0.6**	**2**
Cystoclonium purpureum	0	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	**1.6**	**7**
Pylaiella littoralis	0	0	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**3**	**13**

Charlestown Breachway, Charlestown, RI

Destructive Sampling Damp/Dry Weight (g/m^2) February

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	0	43	0	13	5	0	3	0	38	80	13	688	35	6	0	152	41	11	122	1	**62.55**	**153**
Porphyra spp. 'stamfordensis'	44	0	0	1	0	21	0	24	0	5	0	0	0	0	8	0	0	0	0	0	**5.15**	**11**
Fucus vesiculosis	0	7766	4444	4130	19362	0	22300	0	1593	8514	7966	9182	15888	7285	10444	18420	16084	10915	5837	23500	**9682**	**7382**
Ulva lactuca	271	185	67	180	3	4	12	730	0	0	1	0	0	0	0	7	0	0	0	0	**73**	**173**
Ulva intestinalis	168	73	5	48	26	0	1	12	68	55	1	9	49	235	0	203	56	2	1	1	**50.65**	**71**
Chondrus crispus	0	0	0	0	0	3005	0	352	0	0	0	0	0	0	0	0	0	0	0	0	**167.9**	**672**
Petalonia fascia	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**0.05**	**0**
Porlysiphonia stricta	0	85	0	0	0	165	4	0	0	0	0	0	0	0	0	6	0	0	0	0	**13**	**40**
Elachista fuciola	0	4	12	0	29	35	1	73	4	3	0	0	0	0	0	0	0	1	1	0	**8.15**	**18**
Codium fragilessp tomentosoides	237	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0	**13.85**	**53**

Destructive Sampling Damp/Dry Weight (g/m^2) March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	34	124	133	111	88	10	20	185	67	19	9	0	65	39	0	8900	194.5	46	75	106	**511.3**	**1975**
Porphyra leucosticta	150	0	0	0	0	1	0	0	0	0	42	266	254	0	41	0	0	9	0	0	**38.15**	**83**
Fucus vesiculosis	32490	9300	6490	23790	23960	15140	24480	26090	21780	21260	18625	22848	23027	12561	24900	18800	10015	18234	26488	25470	**20287**	**6656**
Ulva lactuca	84	0	0	173	31	0	59	0	0	0	22	0	16	0	0	0	0	0	0	0	**19.25**	**43**
Ulva intestinalis	150	0	113	118	19	6	55	35	9	13	21	0	126	5	0	23	17	0	4	1	**35.75**	**49**
Elachista fuciola	0	0	1	2	0	1	2	1	2	0	7	0	0	0	0	0	0	0	0	0	**0.8**	**2**
Ulothrix flacca	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.3**	**1**
Bangia fuscopurpurea	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.05**	**0**

Destructive Sampling Damp/Dry Weight (g/m^2) April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	68	8	0	159	42	92	4	153	0	118	0	270	0	1	42	55	22	204	41	1	**64**	**79**
Porphyra leucosticta	552	36	379	0	53	12	0	310	0	28	0	0	0	1	45	15	58	0	0	6	**74.75**	**153**
Fucus vesiculosis	1816	6885	757	8926	1718	7597	7275	10349	9689	6084	8671	2413	9930	8899	8887	9535	10296	14807	23915	7993	**8322**	**5064**
Ulva lactuca	0	6	0	0	0	0	0	0	8	0	0	0	9	0	0	0	0	0	0	0	**1.15**	**3**
Ulva intestinalis	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.2**	**1**

Destructive Sampling Damp/Dry Weight (g/m^2) May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	24	0	0	0	0	1	0	16	0	17	11	116	0	0	25	0	0	0	0	0	**10.5**	**26**
Porphyra leucosticta	20	0	49	0	0	0	0	0	0	0	1	0	14	0	0	0	310	0	0	0	**19.7**	**69**
Fucus vesiculosis	11404	14562	528	1365	2477	7465	13720	3976	2432	1014	916	2310	1807	4304	8863	2313	6234	7228	1195	2697	**4841**	**4354**
Ulva lactuca	0	0	85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**4.25**	**19**
Ulva intestinalis	1	1	2	32	0	309	0	0	0	1	0	59	1	0	0	0	0	0	1	0	**20.35**	**69**
Blidingia minima	0	0	0	0	4	0	0	10	51	0	0	0	0	0	0	0	0	0	0	0	**3.25**	**11**

Black Point, Narragansett, RI

Destructive Sampling Damp/Dry Weight (g/m^2) February

Quadrats	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	54	583	141	108	160	110	152	214	93	323	620	38	469	360	208	180	35	100	21	86	**202.8**	**178**
Porphyra leucosticta	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.3**	**1**
Ulva lactuca	76	71	27	99	105	0	33	0	0	6	9	27	8	122	0	26	60	0	72	327	**53.4**	**76**
Ulva intestinalis	22	0	98	9	0	169	0	1	117	4	17	0	40	17	150	13	60	540	49	.25*100	**65.3**	**126**
Chondrus crispus	0	0	0	31	0	0	1	0	0	0	0	0	0	235	0	230	0	0	0	0	**24.85**	**71**
Petalonia fascia	0	0	0	0	0	0	0	0	0	0	0	73	0	16	0	17	52	810	9	8	**49.25**	**180**
Porlysiphonia stricta	0	0	0	0	0	169	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**8.45**	**38**
Scytosiphon lomentaria	0	6	0	0	0	1	0	18	0	0	7	0	66	26	21	120	116	0	52	21	**22.7**	**37**
Elachista fuciola	10	0	2	0	0	0	0	15	0	1	0	0	0	0	0	0	0	0	0	0	**1.4**	**4**

Destructive Sampling Damp/Dry Weight (g/m^2) March

Quadrats	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	377	138	436	319	120	177	202	65	89	112	1080	2650	640	203	140	215	365	275	145	86.5	**391.7**	**582**
Porphyra leucosticta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	**0.4**	**2**
Ulva lactuca	128	0	0	7	23	0	97	103	0	0	0	0	155	8	0	0	145	22.5	62.5	12.5	**38.18**	**55**
Ulva intestinalis	1	280	0	0	0	1	0	12	1	66	62	30	21	2.5	45	145	10	19.5	35.5	28	**37.98**	**67**
Chondrus crispus	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	**0.95**	**4**
Petalonia fascia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	0	25	49.5	7.2		**5.235**	**13**
Porlysiphonia stricta	0	0	0	0	0	0	0	0	0	23	0	0	0	0	8	5	0	0	0	1	**1.85**	**5**
Scytosiphon lomentaria	5	6	0	43	133	0	143	133	7	46	37	0	188	48	131	200	230	23.5	97.5	43.3	**75.72**	**75**
Ulothrix flacca	0	0	1	0	0	9	0	0	6	0	0	0	0	0	0	0	0	0	0	0	**0.8**	**2**
Bangia fuscopurpurea	5	0	6	4	0	14	0	0	15	0	0	9	0	0	0	0	0	0	0	0	**2.65**	**5**

Destructive Sampling Damp/Dry Weight (g/m^2) April

Quadrats	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	1160	263	885	620	3280	34	199	250	96	268	357	351	94	180	292	206	352	347	100	52	**469.3**	**718**
Ulva lactuca	1800	0	0	0	0	128	0	0	0	0	0	0	0	0	0	33	0	0	0	0	**98.05**	**402**
Ulva intestinalis	0	10	7	0	0	0	0	0	0	1	0	13	0	0	1	0	0	68	0	1	**5.05**	**15**
Scytosiphon lomentaria	0	0	0	0	40	10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**2.55**	**9**
Ulothrix flacca	0	0	0	10	0	0	0	0	0	1	0	0	1	0	0	0	0	0	14	1	**1.35**	**4**

Destructive Sampling Damp/Dry Weight (g/m^2) May

Quadrats	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra yezoensis f narawaensis	0	17	0	0	0	7	0	0	0	4	0	5	0	0	0	14	0	0	53	10	**5.5**	**12**
Porphyra leucosticta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	16	**1.85**	**6**
Fucus vesiculosis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	185	**9.25**	**41**
Ulva lactuca	0	190	266	161	9	0	95	217	170	263	58	78	82	0	162	48	681	450	643	170	**187.2**	**197**
Ulva intestinalis	0	0	0	0	145	165	37	6	36	0	70	72	0	13700	312	0	0	0	248	0	**739.6**	**3052**
Petalonia facia	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	**0.45**	**2**
Cystoclonium purpureum	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	**0.65**	**3**
Scytosiphon lomentaria	0	59	110	56	70	0	225	0	127	0	5	26	10	449	0	51	214	0	0	0	**70.1**	**113**

Westport Boat Landing, Westport, MA

Destructive Sampling Damp/Dry Weight (g/m^2) March

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra spp. 'stamfordensis'	0	168	84	310	374	16	790	820	597	650	35	55	266	64	55	335	115	513	7	1	**262.8**	**275**
Fucus vesiculosis	0	12378	3556	18817	15000	1960	25300	26600	12220	29710	29958	11254	11225	2095	2131	13586	4816	3413	8000	30326	**13117**	**10386**
Ulva lactuca	1	0	0	0	0	0	0	0	0	0	0	0	17	0	4	5	1	0	0	0	**1.4**	**4**
Ulva intestinalis	0	0	1	10	2	1	10	10	0	0	0	40	0	39	0	12	0	11	80	1	**10.85**	**20**
Cystoclonium purpureum	0	0	0	0	0	0	0	0	0	0	0	0	0	605	0	0	0	0	0	0	**30.25**	**135**
Elachista fuciola	0	0	0	0	0	0	30	0	65	10	0	0	0	0	156	0	0	0	0	0	**13.05**	**37**
Ulothrix flacca	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	**0.4**	**1**
Pylaiella littoralis	0	36	122	210	964	122	500	1900	157	0	0	5	509	55	160	129	1284	97	740	226	**360.8**	**505**
Ascophyllum nodosum	8550	5800	0	8830	0	9500	2991	0	0	11730	24	0	0	0	0	0	8480	0	19300	14929	**4507**	**5994**

Destructive Sampling Damp/Dry Weight (g/m^2) April																						
Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra spp. 'stamfordensis'	3	0	23	0	0	0	149	683	450	0	3	0	0	0	25	0	0	0	0	0	**66.8**	**178**
Fucus vesiculosis	19726	13579	15076	19466	12426	2786	16051	703	22525	13322	8895	7691	14435	8442	7723	12785	0	3416	0	0	**9952**	**7095**
Ulva intestinalis	0	0	0	0	0	0	0	16	506	0	0	0	0	0	10	0	0	1	0	0	**26.65**	**113**
Cystoclonium purpureum	0	0	0	1	0	0	0	0	0	5	0	0	0	0	0	2	0	0	0	0	**0.4**	**1**
Elachista fuciola	0	0	0	0	0	0	0	0	10	0	5	0	0	0	0	0	0	1	0	0	**0.8**	**2**
Pylaiella littoralis	3	56	28	333	156	204	213	400	504	91	81	150	455	71	210	177	379	0	93	46	**182.5**	**154**
Ascophyllum nodosum	0	0	214	0	1182	0	0	1765	0	0	0	0	0	297	0	0	9341	0	7324	4042	**1208**	**2643**

Destructive Sampling Damp/Dry Weight (g/m^2) May																						
Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Fucus vesiculosis	221	3735	1385	3127	1790	2762	2936	1597	7539	748	853	915	0	3904	0	0	0	0	0	0	**1576**	**1950**
Cystoclonium pupureum	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	**0.45**	**2**
Bangia fuscopurpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	66	0	**3.3**	**15**
Ascophyllum nodosum	0	0	0	0	0	0	0	0	0	0	0	0	2570	0	2840	3546	2355	1714	5618	1835	**1024**	**1617**

Falmouth Heights, MA

Destructive Sampling Damp/Dry Weight (g/m^2) March																						
Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	**Mean**	**SD**
Porphyra spp. 'stamfordensis'	23	155	58	214	123	95	235	213	17	73	69	99	9	86	101	38	90	12	370	80	**108**	**91**
Porphyra suborbiculata	0	0	0	0	0	0	0	0	0	0	0	124	0	2	0	49	0	3	0	0	**8.9**	**29**
Fucus spiralis	14160	5878	4565	17.05	81	5774	980	6768	11320	6040	10254	6537	7172	4815	18113	10696	4095	9979	3489	4149	**6744**	**4598**
Ulva lactuca	0	0	7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	**0.6**	**2**
Ulva intestinalis	8	8	94	7	0	7	76	6	1	1	4	3	1	5	5	18	5	7	95	9	**18**	**31**
Scytosiphon lomentaria	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.05**	**0**
Bangia fuscopurpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	**0.2**	**1**

Destructive Sampling Damp/Dry Weight (g/m^2) April

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	Mean	SD
Porphyra spp. 'stamfordensis'	19	25	95	90	33	138	77	10	3	14	7	20	316	103	2	252	0	167	11	0	**69.3**	**89**
Porphyra yezoensis f narawaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	103	**7.15**	**24**
Fucus spiralis	4544	2940	2755	1143	3509	11558	3604	0	2156	7482	0	9138	2293	3678	21146	4073	21857	1132	10505	2977	**5825**	**6255**
Fucus vesiculosis	0	0	0	0	0	0	0	3549	0	0	0	0	0	0	0	0	0	0	0	0	**177.5**	**794**
Ulva lactuca	0	0	0	0	22	0	0	6	0	0	0	0	0	0	0	0	0	17	0	0	**2.25**	**6**
Ulva intestinalis	0	0	0	1	0	0	0	2	0	0	0	1	5	0	8	0	7	0	0	0	**1.2**	**2**
Porlysiphonia stricta	0	0	0	0	149	0	0	6	0	13	1	1	0	0	27	0	4	0	0	0	**10.05**	**33**
Dumontia contorta	0	250	0	0	0	0	0	0	0	25	11633	0	0	0	0	0	0	0	0	0	**595.4**	**2599**
Ulothrix flacca	3	0	38	0	0	0	0	0	0	0	0	0	6	0	0	1	0	0	0	0	**2.4**	**9**

Destructive Sampling Damp/Dry Weight (g/m^2) May

Quadrat	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	Mean	SD
Porphyra spp. 'stamfordensis'	0	0	0	0	2	21	0	0	0	0	2	0	0	0	12	0	0	0	0	0	**1.85**	**5**
Porphyra yezoensis f narawaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	**0.1**	**0**
Fucus vesiculosis	1644	5833	4879	484	1899	1902	1581	0	1489	4838	8500	418	2274	6139	3224	1236	2844	2109	222	1197	**2636**	**2276**
Ulva lactuca	0	0	120	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	3	**9.55**	**28**
Ulva intestinalis	0	0	0	1	1	0	0	0	0	7	12	100	0	0	0	0	140	0	12	0	**13.65**	**37**
Bangia fuscopurpurea	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	31	0	0	0	0	**2.95**	**9**
Porlysiphonia stricta	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**0.05**	**0**
Cystoclonium purpureum	0	0	0		207	0	0	0	0	16	0	0	0	64	0	0	0	0	0	0	**14.35**	**49**