EFFECTS OF GLACIAL DISCHARGE ON KELP BED ORGANISMS IN AN ALASKAN SUBARCTIC ESTUARY

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EFFECTS OF GLACIAL DISCHARGE ON KELP BED ORGANISMS IN AN ALASKAN SUBARCTIC ESTUARY

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Abstract

Global climate warming is having large-scale, pronounced effects on the physical environment of Arctic and subarctic nearshore marine ecosystems, such as the widespread melting of glaciers. The purpose of this study was to determine how changing environmental conditions due to glacial melting affect subarctic kelp bed community structure and organism fitness. This study compared kelp bed community structure under disparate environmental conditions on a glacially-influenced and an oceanic shore in the same subarctic Alaskan estuary. Laboratory tests assessed the effects of varying salinity and irradiance on growth and physiological competence (as maximum quantum yield (F_v/F_m)) of the dominant kelp, *Saccharina latissima*. Reciprocal *in situ* shore transplant studies examined seasonal growth, F_v/F_m, morphology and storage product levels (mannitol) in *S. latissima*. This study showed that kelp communities were distinctly different in these two nearshore regions within the same subarctic estuary. In addition, the kelp *S. latissima* from these two environments, exhibited phenotypic plasticity in terms of growth to varying levels of salinity and light availability, while both populations maintained high physiological competence year-round. However, this phenotypic plasticity was constrained within different seasonal growth patterns in the populations from the two shores, which likely are genetically fixed. This is the first time that phenotypic plasticity within a genetically fixed seasonal growth cycle has been described for macroalgae and especially for two populations in such close proximity. However, the ability to elicit plastic responses and seasonal adaptations in *S. latissima* may be limited

and concerns remain about the long-term persistence of this and other important foundation species and nearshore habitats with continued climate change.

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List of Abbreviations

α	photosynthetic efficiency
CMJ	motile jawed carnivore
CMX	motile other carnivore
COI-5P	5' end of cytochrome c oxidase I gene
E_k	minimum saturating irradiance
FDT	semi-motile tentaculate feeder
FST	sessile tentaculate filter feeder
FSX	sessile other feeder
F_v	variable fluorescence
F_v/F_m	maximum quantum yield
F_m	maximum fluorescence
F_o	minimum fluorescence
HMR	motile rasping herbivore
JAK-O	Jakolof Bay – Oceanic
Light I	Light I experiment
McN-E	McNeil Canyon - Estuarine
MLLW	mean lower low water
N1	Miller's Landing
N2	Fritz Creek
N3	McNeil Canyon
NaGISA	Natural Geography In Shore Areas

POM	particulate organic matter
PVC	polyvinyl chloride
RDPI	relative distance plasticity index
$rETR_{max}$	maximum relative electron transport rate
RGR	relative growth rate
RLC	rapid light curve
Sal I	Salinity I experiment
Sal II	Salinity II experiment
SCUBA	self-contained underwater breathing apparatus
S1	Kasitsna Bay
S2	Jakolof Bay
S3	Little Tutka Bay
WRS	Wilcoxon Rank Sum Test

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General Introduction

Global climate warming is having large-scale, pronounced effects on the physical environment of Arctic and subarctic nearshore marine ecosystems (Morrison et al. 2002, Clarke & Harris 2003, Hinzman et al. 2005, Fellman et al. 2010). Widespread melting of glaciers, decreased sea ice extent, rising sea level, escalating permafrost temperatures, higher ultraviolet radiation levels, and increased precipitation are only some of the long-term changes occurring in the Arctic (Weller et al. 2010). The substantial thinning of glaciers has increased glacial discharge in Alaska (e.g., Rabus & Echelmeyer 2002, Motyka et al. 2003, Berthier et al. 2010), at a rate that has doubled over the last 50 years (Arendt et al. 2002). Loss of glacial area, elevation decreases in ice caps and glaciers (Krabill et al. 2004, Barry 2006, Larsen et al. 2007) and ice mass flux into the ocean (Rignot et al. 2008) all represent the dramatic melting of glaciers and ice sheets currently occurring around the globe. Glaciers discharge cold oligotrophic water laden with silt (Pickard 1971, Silva & Prego 2002), which affects the salt budget, sediment load and turbidity of nearshore marine ecosystems (Wiencke et al. 2007). These changes in the physical and chemical environment can be expected to have severe impacts on nearshore marine habitats and communities.

Kelp beds are abundant and essential nearshore habitats in Alaska, which are being affected by the melting of glaciers. They are among the most productive ecosystems in the world and support tightly linked food webs (Mann 1973, Dayton 1985, Fredriksen 2003). Kelps are the foundation organisms of these complex, three-dimensional habitats that serve as nursery, refuge, forage and spawning sites for a variety

of organisms (Foster & Schiel 1985, Steneck et al. 2002). Kelp beds depend highly on the prevailing environmental conditions (Dayton et al.1999), and changes in these conditions can result in the loss of habitat structure and biodiversity (Steneck et al. 2002). Loss of marine biodiversity is a paramount concern worldwide (Gray 1997, Cheung et al. 2009), especially in the Arctic and subarctic where climate change is most pronounced and accelerated (e.g., IPCC 2007, Comiso et al. 2008, Manabe et al. 2011). Changes in benthic species distributions are already evident in areas of coastal glaciers in Antarctica (e.g., Dawber & Powell 1997, Sahade et al. 1998, Tatían et al. 1998), Svalbard (e.g., Włodarska-Kowalczuk et al. 2005, Ronowicz et al. 2011, Wesławski et al. 2011), southwestern Greenland fjords (e.g., Sejr et al. 2010), southern Chile fjords (e.g., Ríos et al. 2005), and southeastern Alaska fjords (e.g., Carney et al. 1999). Given the ecological importance of functional nearshore ecosystems, there is a strong need to understand and monitor how coastal ecosystems, and particularly foundation organisms, react to changing environmental conditions (Wernberg et al. 2010). The kelp *Saccharina latissima* is such a foundation organism that is particularly important in the Arctic and subarctic nearshore environments (Sharp et al. 2008, Wulff et al. 2010).

Kelp bed communities thrive best under low temperature, full salinity, high nutrients, high irradiance and low sedimentation (e.g., Kirst 1990, Schiel & Foster 2006). All of these environmental variables are prone to change under the influence of increased glacial melt in coastal environments. Temperature can have fundamental physiological effects on chemical reaction rates and therefore metabolic pathways (Lobban & Harrison 1997), and temperature rises can lead to physiological exclusion and thus changes in the

distribution of organisms. Low salinity due to increased freshwater input from glacial melt can negatively affect invertebrate osmoregulation and kelp photosynthesis and growth by causing osmotic stress (e.g. Kirst 1990, Cowart et al. 2009). Nutrients, with nitrogen being most important (Pedersen & Borum 1996), are necessary for growth and recruitment of primary producers (Hernández-Carmona et al. 2001). Low nutrient concentrations as are typical for melt-influenced and warmer waters can lead to the deterioration of kelp beds. Adequate light is necessary for algal recruitment and photosynthesis, and therefore growth and storage product synthesis (Foster & Schiel 1985). Light availability can be significantly reduced with increasing amounts of suspended sediments being discharged from melting glaciers. Suspended sediments not only lead to reduced light for primary producers, but also have abrasive effects on benthic organisms (Airoldi 2003, Bučas et al. 2007), and can cause smothering of epifauna (Smale & Barnes 2008). Extended time periods of high sedimentation can also change overall substrate characteristics such as grain size and available hard bottom, which are important habitat requirements for many invertebrate and macroalgal members of nearshore kelp bed communities (Foster & Schiel 1985, de Juan & Hewitt 2011). There is a pressing need to evaluate how these changing environmental parameters are affecting organism fitness and ecosystem health (Roleda et al. 2008).

Organism fitness and ecosystem health are not clearly defined parameters, and are often limited to pervasive presence/absence assessments. Aerial surveys provide large-scale distribution patterns of kelp beds, but they do not assess actual ecosystem health or functioning. The biodiversity of an ecosystem or community is sometimes used as an

indicator of its health and resilience, as diversity tends to decrease under environmentally stressful conditions (Allison 2004). On the individual organism level, appropriate response variables need to be selected that will give insight into organism fitness. In kelps, growth has often been used to gauge responses to environmental conditions (e.g., Pybus 1973, Boden 1979, Lüning 1979, Lyngby & Mortensen 1996). Growth integrates many physiological processes, and is thus a powerful tool for assessing the overall effect of a stressor on an organism's performance. A stressor is generally regarded as any environmental condition that reduces the optimal physiological performance of an organism (Cronin 2001). However, at the same time growth also is a rather coarse measurement where small performance changes due to environmental stressors might go unnoticed. The evaluation of photosynthetic yield of photosystem II (PSII) by pulse-amplitude modulated (PAM) fluorometry can be an indicator of the potential ability of an alga to perform photosynthesis (e. g., Bruhn & Gerard 1996, Machalek et al. 1996, Hanelt et al. 1997, Baker 2008). The combination of such fine-scale photosynthetic yield measures of the condition of the PSII apparatus with overall growth measurements allows us to assess adaptation strategies: Is the organism physiologically compromised, or can organisms respond to stress by stopping growth and thus conserving energy while they remain physiologically healthy? How long and at which levels of environmental stress can organisms maintain physiological health? What is the range of stress they can tolerate, and can they adapt long-term to adverse or sub-optimal conditions?

Species may acclimate to variable environmental conditions through phenotypic plasticity (without genetic change), or they may adapt to a continually changing

environment through the development of genetically different ecotypes (Lobban & Harrison 1997, Pigliucci et al. 2006). Phenotypic plasticity expands the ecological and physiological range of a species, allowing it to tolerate a certain range of changing environmental conditions. For example, many macroalgae exhibit a wide range of morphological variations, which allow them to flourish in both wave sheltered and exposed environments (Fowler-Walker et al. 2006). Such phenotypically tolerant species are typical for naturally highly variable environments such as intertidal or estuarine regions. Continuous exposure to extreme environmental conditions can expose a population of a species to selective pressures that it would not usually encounter, hence allowing for genetic assimilation (Waddington 1953, 1961, Bradshaw 1965, Schlichting & Smith 2002, Pigliucci et al. 2006). Genetic assimilation is the process whereby environmentally-induced phenotypic variation becomes fixed by secondary genetic control, and expression no longer requires the environmental cue. In the face of the impacts that climatic change such as increased glacial melt have on nearshore subarctic communities such as kelp beds, there is a need to understand both the community composition under various environmental conditions as well as the tolerance of key organisms to variability and change through phenotypic plasticity or the development of ecotypes.

The overarching goal of this study was to determine how resilient kelp bed communities and individual species are to changing environmental conditions caused by glacial melting. Specifically, I examined subarctic nearshore kelp bed community structure and organism fitness using growth rate and maximum quantum yield as fitness

measures. Kachemak Bay, Alaska was used as a model system to study potential effects that glacial melt may have on kelp beds as the bay presents a natural, strong environmental gradient from oceanic to glacially-influenced conditions on a spatial scale of just a few kilometers. The system is a natural laboratory where the effects of different environmental conditions on kelp bed communities and the responses of key species such as the important foundation kelp species, *S. latissima,* can be investigated under an overall similar geographic setting.

The first chapter of this study aimed to quantify the key environmental conditions on the oceanic and the glacially-influenced shores of Kachemak Bay, with specific attention to those variables influenced by glacial discharge (salinity, light intensity, nutrients, sedimentation, abrasion, and substrate cover). I then compared the kelp bed community structure (diversity) in the two hydrographically distinct regions of Kachemak Bay. The relationships between the community patterns and environmental variables were determined, and the most likely drivers of differences in nearshore kelp beds between the two shore regions were identified.

The aim of Chapter 2 was to investigate the tolerance of juvenile *S. latissima* from the two hydrographically distinct regions of Kachemak Bay to the dynamic glacial discharge effects of reduced salinity and irradiance. These two parameters were chosen because salinity is reduced by glacial meltwater input and irradiance is reduced by inorganic sediment input. My overarching question was if there is evidence for phenotypic plasticity and/or genetic differentiation in response to varying salinity and irradiance levels in *S. latissima.* I specifically compared growth and photosynthetic yield

of individuals collected from the glacially-influenced area that has reduced salinity and light intensity with those from the oceanic regime that has high salinity and light intensity. I determined if thalli from the disparate environments responded differently to the same salinity and irradiance conditions and if threshold levels at which *S. latissima* from each population stopped growing, but were still able to survive (i.e., maintain photosynthetic yield), could be determined.

In Chapter 3, I examined the *in situ* seasonal growth patterns of *S. latissima* populations of the glacially-influenced and oceanic shores of Kachemak Bay. While Chapter 2 focused on short-term responses to environmental conditions, here I looked for evidence of phenotypic plasticity and/or genetic differentiation in their seasonal growth patterns under *in situ* conditions including reciprocal transplant experiments between the two environments. Photosynthetic yield, storage product levels (mannitol), and morphological variation in *S. latissima* from the two environments were examined in correlation with their seasonal growth patterns. DNA barcoding of the 5'end of the cytochrome c oxidase I mitochondrial gene was conducted on individuals from both environments to confirm that they are indeed the same species.

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Chapter 1: Kelp bed dynamics in estuarine environments in subarctic Alaska[1]

1.1 Abstract

Glaciers have pronounced long- and short-term effects on nearshore marine ecosystems. Concerns exist about possible changes that may occur to nearshore habitats with the pronounced climatic alterations in subarctic and high-latitude environments. The present research studied the effects of glacial discharge on kelp bed community structure by comparing environmental conditions on one more exposed and one less exposed shore in a subarctic Alaskan estuary. Inorganic sedimentation, abrasion, and percent sand/silt substrate were significantly higher on the more exposed shore than the less exposed shore. Light intensity, salinity, nitrate concentrations and hard substrate cover were significantly lower on the more exposed shore. Kelp bed communities on the more exposed shore contained only one kelp species, *Saccharina latissima*, versus five kelp species on the less exposed shore. Taxonomic richness and overall organism abundance were significantly lower on the more exposed shore. Salinity, nitrate, inorganic sedimentation and abrasion were identified as important drivers of kelp communities that are dynamically influenced by glacial discharge. In contrast, other drivers, such as hard substrate and rugosity, reflect existing differences between the two shore environments that are not influenced on short time scales by glacial discharge. While it is currently difficult to separate the relative roles of these two types of drivers on kelp bed

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communities, increased rates of glacial discharge due to climate change may exacerbate specifically the effects of the dynamic drivers and further decrease species richness in kelp bed communities in high-latitude estuaries.

1.2 Introduction

Kelp beds are an example of an abundant and essential nearshore habitat type in coastal Alaska. Kelps are the foundation organisms of these complex, three-dimensional habitats that support tightly-linked food webs (Dayton, 1985; Fredriksen, 2003; Mann, 1973). They serve as nursery, refuge, forage and spawning sites for many associated invertebrates, fishes, birds and marine mammals (Foster and Schiel, 1985; Steneck *et al.*, 2002). As with other coastal habitats, kelp beds are highly dependent on the prevailing environmental conditions (Dayton *et al.*, 1999). Changes in these conditions can result in the loss of habitat structure, and thus the associated biota, as evidenced in several other high-latitude nearshore systems (e.g., Carney, Oliver, and Armstrong, 1999; Sejr *et al.*, 2009; Włodarska-Kowalczuk, Pearson and Kendall, 2005). Loss of marine biodiversity (e.g., Gray, 1997) is a paramount concern worldwide, especially in the Arctic and subarctic where climate-change effects are especially pronounced and accelerated (e.g., Comiso *et al.*, 2008; Hunt *et al.*, 2002).

In many subarctic and high-latitude estuaries, glaciers discharge cold, oligotrophic, and silt-laden water, influencing the salt and nutrient budgets, sediment load, and turbidity in the coastal environment (Pickard, 1971; Silva and Prego, 2002; reviewed by Wiencke *et al.*, 2007). The effects of such changing environmental

conditions on high-latitude kelp bed communities are not well understood. Overall algal abundance is typically decreased in glacially influenced estuarine environments (Klöser *et al.*, 1996; Schoch and Chenelot, 2004). Impacts of glacial discharge on nearshore communities in the Arctic and subarctic are of particular concern because climate change is causing accelerated rates of glacial melting at these latitudes (Motyka *et al.*, 2003; Rabus and Echelmeyer, 2002), resulting in unknown effects on nearshore habitats. Discharge rates have doubled at many locations in Alaska during the past 50 y (Arendt *et al.*, 2002), and glacial erosion rates 3.5 times higher than long-term (10^6 y) exhumation rates (Koppes and Hallet, 2002, 2006).

The goal of this study was to quantify environmental conditions in a glacially influenced estuary in subarctic Alaska and to examine the environmental variables that most influence kelp bed communities. We compared kelp bed communities on a more glacially exposed and a less glacially exposed shore in Kachemak Bay, south-central Alaska, in relation to environmental conditions. Stark environmental differences exist despite the close proximity of the two shores (~10 km apart); the less exposed shore receives cold, nutrient-rich seawater from the Gulf of Alaska, while this water is modified with significant input from a glacier system at the more exposed shore. We propose that the two shores of Kachemak Bay may be used as a model to identify specific drivers affecting nearshore kelp communities in such subarctic and high-latitude, glacially influenced estuaries. Comparison between these shores may give an indication of the direction in which nearshore systems will change if glaciers continue to melt as a result of future climate alterations. Therefore, we first quantified key environmental

variables in the two shore environments, and then we compared benthic community structure in the two hydrographically distinct regions of Kachemak Bay. We investigated the relationships between the community patterns and environmental variables and identified the most likely drivers of changes in nearshore kelp beds in this region.

1.3 Materials and methods

1.3.1 Study site

Kachemak Bay is a glacially formed, fjord-like estuary located on the eastern side of lower Cook Inlet, close to the Gulf of Alaska (Figures 1.1 and 1.2). It is the largest National Estuarine Research Reserve (4,000 km^2) in the United States, and it also is one of the most productive watersheds in south-central Alaska (Feely *et al.*, 1982; Larrance *et al.*, 1977). It is divided by a 6-km-long end moraine (Homer Spit) into an inner and an outer bay. Along the southern, less glacially exposed shore, well-mixed, oceanic water from the Gulf of Alaska flows towards the inner bay (Burbank, 1977) (Figures 1.1 and 1.2). This water is modified by discharge from nine glaciers of the 2380 km^2 Harding Ice Field and Grewingk–Yalik Complex. The freshwater input results in stratification of the water column and little deep-water mixing in the inner bay (Speckman *et al.*, 2005). The circulation patterns of the bay maintain predominantly oceanic conditions on the less exposed southern shore and estuarine conditions on the more exposed northern shore (Burbank, 1977; Schoch and Chenelot, 2004). The less exposed shore consists of bedded volcanic, sedimentary, and tertiary rocks of Triassic and Jurassic origin while the more

exposed shore is made up of surficial sediment deposits over bedded volcanic or metamorphic rock (Hayes, Brown and Michael, 1977).

Six study sites were selected, three on the more exposed and three on the less exposed shores of Kachemak Bay; each site was >1 km apart on each shore (Figure 1.1). The two shore areas were about 10 km apart. The more exposed north shore sites under the glacially influenced regime were located off of Miller's Landing (referred to as N1 at 59°38.26'N; 151°25.12'W), Fritz Creek (referred to as N2 at 59°39.82'N; 151°20.79'W), and McNeil Canyon (referred to as N3 at 59°41.19'N; 151°14.87'W). Less exposed south shore sites under oceanic conditions were at Kasitsna Bay (referred to as S1 at 59°28.24'N; 151°33.05'W), Jakolof Bay (referred to as S2 at 59°28.03'N; 151°32.13'W), and Little Tutka Bay (referred to as S3 at 59°28.48'N; 151°29.55'W). All sites were at depths of 5 m below mean lower low water (MLLW). To minimize the influence of naturally occurring differences in substratum between the two shore environments, the less exposed shore sites were chosen in flat areas dominated by sand, shell, and gravel.

1.3.2 Environmental conditions

Environmental conditions at each site were monitored during July and August 2006. Bottom temperature and light intensity were measured hourly, using HOBO data loggers (Onset Computers, Bourne, Massachusetts), fixed to a 30 m permanent transect line at each site. Water samples were collected twice a month, at the surface and just above the bottom. Salinity of each water sample (five replicate measurements) was determined with a handheld refractometer. A second set of bottom-water samples was filtered with Nalgene® syringe filters (0.45 μm) within 2.5 h of collection and frozen until

nutrient analysis. Nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), and silicate (SiO_4^{2-}) were determined using a Technicon AutoAnalyzer II (SEAL Analytical Inc., Mequon, Wisconsin). An additional replicate sample was taken from one site per shore during each sampling effort.

Sedimentation at each site was measured with two replicate sets of sediment traps, located 10 m apart along the permanent transect, 1 m above the bottom. Each trap set had three polyvinyl chloride (PVC) tubes, with a height : diameter ratio of 5 to prevent resuspension (Hargrave and Burns, 1979). The contents of each trap were collected twice a month, filtered onto pre-weighed Whatman® GF/F glass microfiber filters (0.7 μm), dried for 24 h at 60 °C, weighed, oxidized for 6 h at 500 °C, and reweighed. Organic content was estimated as the ash-free dry weight.

Abrasion due to suspended particles and water motion was estimated monthly from the weight loss of clod cards submerged for four weeks at each site (Konar, 2000). The clod cards were cured in seawater for 24 h, dried to constant weight, and attached to 4 x 8 cm Plexiglass cards. Pairs of clod cards were placed on five concrete blocks at each site (n = 10 clod cards), randomly located along the permanent transect. Control clod cards for each site were handled the same as *in situ* cards and then returned to a 20 L bucket of still seawater at ambient air temperature during each measurement period. At the end of a measurement period, all clod cards were dried to constant weight.

Rugosity of the substratum at each site was measured in June 2006 along three randomly located 30 m transects. A 1-m-long PVC bar was placed perpendicular to the transect line at five random points per transect. A chain attached to the bar was draped

along the substratum parallel to the bar. The ratio of chain length to the 1 m bar length was used to estimate rugosity (Hamilton and Konar, 2007).

1.3.3 Benthic community composition

The benthic community composition was examined at each site during late July through August 2006. Five 1 m^2 quadrats were placed at random locations along each of three random 30 m transects at each site. Individuals of each kelp species were counted within each quadrat, and percent cover of the kelp overstory was estimated. Solitary epifauna >2 cm length were identified and counted, and percent cover of the understory (sessile invertebrates and macrophytes other than kelps), as well as percent open substrate by category (sand/silt, gravel, cobble, boulder and shell) were estimated (Konar and Iken, 2003). Vouchers of macroalgal and invertebrate species were collected to confirm *in situ* identifications.

1.3.4 Statistical analyses

Univariate statistical analyses were performed to determine differences in environmental variables between shores. Means were determined for each site for the measurement period of July–August 2006 for the following variables: surface and bottom salinity, abrasion, inorganic sedimentation, particulate organic matter (POM), nitrate, ammonium, phosphate and silicate. Average rugosity and substrate type were determined for each transect at each site, and then site means across all three transects were determined. Means for light intensity and temperature were computed for a 30 d period during July–August when data were available for all six sites. Means for north and south shores were determined from averages of all sites per shore (n = 3). Data were tested for

normality and homogeneity of variances and nonhomogeneous data were log transformed. Student's t-tests (R 2.8.1 software; R Foundation for Statistical Computing, Vienna, Austria) were used to test for significant differences ($\alpha = 0.05$) between shores. Univariate measures of taxon abundance and taxon numbers were tested for normality and homogeneity of variances, and were fourth-root transformed. Student's t-tests were used to test for differences between shores ($\alpha = 0.05$).

Multivariate statistical analyses were performed using the software package Primer (v6, Plymouth Marine Laboratories, Plymouth, United Kingdom; Clarke and Warwick, 2001). Differences among sites and between shores based on environmental conditions were evaluated with hierarchical clustering based on Euclidean distances. Significant differences within the clusters were evaluated using the SIMPROF test ($\alpha = 0.05$) within Primer. All environmental variables were normalized (standardized) to a common scale using the appropriate Primer function. The following environmental variables were log transformed: abrasion, rugosity, hard substrate and sand/silt. Benthic data (percent cover and abundance) were analyzed both for taxa and for morphological functional groups. Macroalgal functional groups included: nonbranching filament, finely branching filament, coarsely branching filament, monostromatic or distromatic sheet, medium thick sheet, branched blade, peltate blade, leathery blade, and crustose form (after Littler and Littler, 1980). Epifaunal functional groups included: motile rasping herbivore (HMR), motile jawed carnivore (CMJ), motile other carnivore (CMX), semimotile tentaculate filter feeder (FDT), sessile tentaculate filter feeder (FST), and sessile other filter feeder (FSX) (after Bremner, Rogers, and Frid, 2006; Maurer and

Leathem, 1981). Biological data were fourth-root transformed and hierarchical clustering using group-average linkages was used to group communities based on the Bray-Curtis similarity metric. The individual taxa contributing to the dissimilarity between shores and the similarity of sites within shores were determined (SIMPER procedure; Clarke and Warwick, 2001).

The ordination of sites based on biological data (taxon abundance) in multidimensional space (nMDS plot) was overlaid with vectors of environmental variables to assess the influence and direction of these variables. The relationships between patterns in multivariate community structure and environmental variables were also examined using the BIO-ENV procedure (Clarke and Ainsworth, 1993). All variables that had mutual correlations >0.95 were reduced to a single representative (after Clarke and Warwick, 2001). Surface salinity, inorganic sediments, abrasion, and hard substrate were highly collinear with bottom salinity and were removed from the analysis. Phosphate and sand/silt were highly collinear with rugosity and were hence excluded from the analysis. The following remaining variables: light intensity, temperature, nitrate, ammonium, silicate, particulate organic matter (POM), bottom salinity, and rugosity were used in the BIO-ENV procedure. The effects of existing long-term differences in substrate between the shores and the effects of more dynamic variables fluctuating on shorter terms are difficult to separate, and substrate effects may confound the identification of other drivers of kelp communities. We repeated the BIO-ENV procedure and substituted bottom salinity with its collinear variable hard substrate to assess

differences in correlation strength when substrate characteristics were used in the analyses.

1.4 Results

1.4.1 Environmental conditions

Study sites at the more glacially exposed and less exposed shores of Kachemak Bay differed with respect to several of the environmental parameters (Table 1.1). Light intensity and surface and bottom salinity were significantly lower at the more exposed shore ($p < 0.05$, $p = 0.01$, $p < 0.01$, respectively). Nitrate and phosphate concentrations were significantly higher on the less exposed shore ($p = 0.05$, $p = 0.01$, respectively). Bottom-water temperature did not significantly differ between the two shores ($p = 0.93$). There were no significant differences in ammonium and silicate between shores ($p = 0.35$, $p = 0.32$, respectively). Mean ammonium levels were highly variable and ranged from ~1.3 to ~23 μM on both shores. The N:P molar ratios (N includes nitrate and ammonium; based on overall means in Table 1.1) of the more exposed and less exposed shores were 31 : 1 and 16 : 1, respectively. Sedimentation of inorganic matter was significantly greater at the more exposed shore than at the less exposed shore ($p = 0.04$); however, sedimentation of POM occurred at much lower rates overall, and did not differ significantly between the two shores ($p = 0.09$). Mean abrasion as weight loss of clod cards was significantly higher at the more exposed shore than at the less exposed shore sites ($p < 0.01$). Mean rugosity was significantly lower at the more exposed shore than at the less exposed shore ($p < 0.05$). The dominant substratum at the more exposed shore

was sand/silt, while the less exposed shore had a greater variety of substrata, from sand/silt to boulders (Table 1.2). The more glacially exposed shore sites grouped distinctly separate from the less exposed sites in hierarchical clustering (SIMPROF test, $p < 0.001$) while sites within a shore were not different (Figure 1.3).

1.4.2 Kelp bed community

Forty taxa were recorded at all six study sites (Table 1.3), representing three macroalgal divisions and six invertebrate phyla. Of these taxa, 22 were found exclusively on the less exposed southern shore, and eight were found exclusively on the more exposed northern shore. Taxon richness was significantly higher ($p < 0.05$) on the less exposed shore (5.44 ± 0.61 m^{-2}) than on the more exposed shore (2.98 ± 0.35 m^{-2}). Percent cover of total benthic organisms (all algae and invertebrates, overstory and understory) was significantly higher ($p < 0.01$) on the less exposed shore ($77.9 \pm 14.7\%$) than on the more exposed shore ($25.6 \pm 1.0\%$). This difference was mostly due to significantly greater ($p < 0.05$) kelp overstory at the less exposed shore ($66.2 \pm 19.2\%$) than on the more exposed shore ($23.11 \pm 1.6\%$). Five kelp species were present at the less exposed sites, compared to only one kelp species at the more exposed sites (Table 1.3). The identity of the dominant macroalgal functional groups did not differ significantly between the two shores (Table 1.4), likely due to high variability within sites. Of the epifaunal functional groups, motile non-jawed carnivores were significantly more abundant ($p = 0.05$) at the more exposed shore sites, and sessile non-tentaculate suspension feeders were significantly more abundant ($p < 0.05$) at the less exposed shore sites (Table 1.4).

Hierarchical clustering of all benthic taxa clearly separated the more exposed and less exposed shores of Kachemak Bay into two distinct groups (SIMPROF test, $p < 0.001$), similar to the separation observed for the site and shore clusters based on environmental variables (Figure 1.3). Communities were separated by an average of Bray-Curtis dissimilarities of 71.5% between the two shores. Twenty species contributed 80% to the dissimilarity between shores. The top contributors were the macroalgae *Cymathere triplicata*, crustose coralline algae, *Desmarestia aculeata*, *Neodelisea borealis*, and *Mastocarpus* sp, and the invertebrate taxa Balanoidea, Hydroida, and *Asterias amurensis*. Within each shore, sites were not significantly different and the more exposed sites were at least 64.5% similar, and the less exposed sites at least 68% similar. Five taxa (*Saccharina latissima*, *Mastocarpus* sp., *N. borealis*, Hydroida, and *A. amurensis*) contributed 78% to total similarity among the more exposed shore sites. Eight taxa (*S. latissima*, *C. triplicata*, crustose coralline algae, Balanoidea, *D. aculeata*, *Pterosiphonia* sp., *Agarum clathratum*, and *Pycnopodia helianthoides*) contributed 78% to total similarity among the less exposed shore sites.

1.4.3 Relationships between community structure and environmental variables

The more glacially exposed shore sites grouped distinctly separate from the less exposed shore sites in the nMDS ordination based on taxa abundance (Figure 1.3). Environmental factor vectors indicate that this separation was driven by higher POM, inorganic sedimentation, abrasion, and sand/silt levels and possibly higher ammonium levels on the more exposed shore and higher bottom and surface salinity, light intensity, rugosity, hard substrate, and nitrate, phosphate and silicate levels on the less exposed

shore. Bottom temperature added little to the separation of the two shore sites in multidimensional space (Figure 1.4).

The single environmental variable that best explained community patterns was bottom salinity for community structure based on both functional groups ($\rho_s = 0.780$) and on taxa ($\rho_s = 0.775$) (Table 1.5). The best two-variable combination was bottom salinity and nitrate for both functional groups and taxa ($\rho_s = 0.925$ each; Table 1.5). The addition of rugosity improved the correlation for taxa only slightly ($\rho_s = 0.946$) and the combination of nitrate, POM and rugosity for functional groups ($\rho_s = 0.929$) was only marginally higher than the best two-variable combination (Table 1.5). In addition, since surface salinity, inorganic sedimentation, abrasion and hard substrate were all collinear with bottom salinity, they also are important variables determining community structure. When hard substrate was substituted for bottom salinity, it became the environmental variable that best explained community patterns for both functional groups and taxa at similar correlation strengths as with bottom salinity (Table 1.6).

1.5 Discussion

Kelp bed communities on the more glacially exposed and less glacially exposed shores of Kachemak Bay, less than 10 km apart, were used to study the effects of subarctic and high-latitude estuarine environments on nearshore communities. The more glacially exposed shore sites had lower percent cover of kelps, other macroalgae, and epifauna. Only about half as many taxa were found at this shore compared to the less exposed shore. Thus, both abundance and taxonomic richness were relatively low in the

areas exposed to glacial and estuarine conditions. Environmental conditions at the more exposed shore sites were characterized by high inorganic sedimentation rates, low light levels, low-salinity waters, and depleted nutrient regimes. Many of these dynamic environmental variables identified as drivers of kelp bed community structure (salinity, sedimentation, nitrate) presumably are a result of the current levels of glacial discharge into the bay, likely eliciting biological responses over the generational time frames of the affected biota. In contrast, soft and homogeneous substrates dominating the more glacially influenced areas on the north shore result from long-term exposure to glacial silt sedimentation over the past 15,000 y (Field and Walker, 2003). They therefore occur over much longer time scales than biotic community responses and need to be recognized as inherent differences between the two shores. The strong correlation between some of the dynamic variables and sediment characteristics complicate the interpretation of responsible drivers of kelp community structure. In the following paragraphs, we will discuss the potential effects of both variable types on the benthic communities. Bottom salinity and nitrate were most strongly correlated with differences in functional groups and taxon composition between the two shore environments. However, many other dynamic variables (inorganic sedimentation, abrasion, and surface salinity) were highly collinear with bottom salinity and the importance of these variables has to be emphasized. Among the existing substrate differences, rugosity and hard substrate were important drivers.

Even though differences in bottom salinities between shores were less pronounced than in surface salinities, bottom salinity is likely more influential for benthic organisms.

In addition, at extreme low tides bottom salinity can decrease nearly to surface levels. The most important effect of changes in salinity is osmotic stress, which can exert physiological stress on macroalgae, especially subtidal kelps, which are less tolerant to salinity stress than many intertidal algae (Biebl, 1962; Fralick and Mathieson, 1973). However, some subtidal algal species, including the kelp *Saccharina latissima*, can withstand salinities as low as 16 (Gerard, DuBois, and Greene, 1987; Lüning, 1990), which may be a reason for its presence at the north shore. In addition, *S. latissima* is the only kelp that is able to grow on soft substrates, enabling it to inhabit the more exposed shore. Salinity also is a particularly important environmental factor determining development and survival of many marine invertebrates (Bressan, Marin, and Brunetti, 1995; Kashenko, 2007; O'Conner and Lawler, 2004). Some of the invertebrate taxa found at the more exposed shore seem to be able to withstand low salinities. For example, while echinoderms are usually rare in low-salinity environments because of osmoregulatory challenges, the sea star *Asterias amurensis* was common on the glacially influenced shore of Kachemak Bay and is known to survive at salinity levels of 22 (Kashenko, 2003). This may provide it with a competitive advantage over other sea stars that are common at the less exposed shore (e.g., Chenelot *et al.*, 2007) but are absent from the more exposed shore. *Asterias amurensis* was not recorded in Kachemak Bay until 1998 and may be considered a non-indigenous invasive species (Foster and Hines, 2000), which typically have wide ecological tolerances. The anemone, *Metridium senile*, also is able to tolerate variable salinities by retracting tentacles, contracting the body

wall, and increasing mucus production during periods of decreasing salinities (Shumway, 1978).

Nitrate concentration as a community driver may specifically influence differences in algal composition between the two shore environments in Kachemak Bay. Macronutrients can be depleted during summer at northern high latitudes due to high seasonal production (Chapman and Lindley, 1980; Dunton and Schell, 1986; Lee, 1973). Seasonal upwelling at the mouth of Kachemak Bay (Burbank, 1977; Muench, Mofjeld, and Charnel, 1973) may be responsible for maintaining nitrate concentrations >3 μM along the less exposed shore of Kachemak Bay, while the input of oligotrophic glacial waters probably contributes to the significantly lower concentrations (1-2 μM) along the north shore (Table 1.1). Some high-latitude kelps such as *Saccharina latissima* can maintain growth for months on internal nitrogen reserves (Korb and Gerard, 2000), while others become nitrogen-limited when ambient nitrate concentrations remain in the 1-2 μM range for more than a few weeks (Gerard, 1982; Zimmerman and Kremer, 1986). This may contribute to the reduced number of kelp species observed at the more exposed shore. Other nutrient variables were not identified as community drivers, but in part this may be due to their high variability. Ammonium can be an important source of nitrogen for kelps (e. g. Ahn, Petrell, and Harrison, 1998), but we cannot determine from our data whether ammonium levels are constant enough to keep nitrogen above limiting levels, especially on the north shore where nitrate levels were lower. The mean ratios of N : P ranged from 10 : 1 to 30 : 1 among all sites irrespective of shore, the latter ratio reflecting typical macroalgal N : P ratios (Lobban and Harrison, 1997). Low N : P ratios suggest

some nitrogen limitation of algal growth some of the time on each shore, but no phosphate limitation. Temperate macroalgae typically are not phosphate limited (Lobban and Harrison, 1997).

The average inorganic sedimentation rate at the more exposed shore in Kachemak Bay was almost 5 mg cm^{-2} day^{-1}. In laboratory experiments, 10 mg cm^{-2} of sediments prevented attachment of kelp spores and reduced survival of kelp recruits by 90% (Devinny and Volse, 1978). This suggests that sedimentation rates at the more exposed sites could limit kelp recruitment, possibly accounting for reduced kelp cover and explaining why only one kelp species, *Saccharina latissima*, was found. Although *S. latissima* was abundant at the more exposed shore, it showed reduced growth during the period of high glacial discharge, while variable growth continued on the less exposed shore during the same time frame (T. Spurkland and K. Iken, unpublished data). Settlement of fine-grained sediments on kelp thalli can reduce growth by limiting nutrient uptake (Lyngby and Mortensen, 1996). However, effects of sedimentation on macroalgae are not always negative; sediment deposits on High Arctic *S. latissima* can reduce detrimental effects of UV radiation (Roleda, Dethleff, and Wiencke, 2008). Other macroalgae abundant at the more exposed shore, such as the red alga *Mastocarpus* sp., seasonally produce meristematic upright portions from crustose bases, and these upright portions are more tolerant of burial and abrasion (Airoldi, 2003; Dethier, 1987). In contrast, crustose coralline algae, which are highly sensitive to sedimentation (Airoldi, 2003; Maughan, 2001) were only common on the less exposed shore of Kachemak Bay.

Invertebrates are also directly impacted by sedimentation. High loads of inorganic sediments clog the feeding apparatuses of suspension feeders and compromise the ability of suspension feeders to obtain food (Irving and Connell, 2002; Kowalke, 1999, 2000; Lovell and Trego, 2003; Slattery and Bockus, 1997). Other sedimentation effects include burial, smothering, abrasion/scour and decrease in the success of larval settlement (reviewed by Airoldi, 2003; Grigg, 1975; Ostarello, 1973). For example, intolerance of barnacles to heavy sedimentation (Seapy and Littler, 1982) may explain why they were much smaller and sparser on the more exposed than the less exposed shore in Kachemak Bay. However, such effects can be taxon-specific. Even though suspension feeders were generally more abundant on the less exposed shore of Kachemak Bay, sessile tentaculate suspension feeders made up a significant proportion of invertebrates at the more exposed shore sites (Table 1.4). The occurrence of suspension feeders at the more exposed shore sites may be attributable to the abundance of food in the form of suspended organic matter, which was similar for the two shores. Similarly, high sedimentation rates in an estuary in Spain resulted in an increased abundance of opportunistic suspension feeders (Saiz-Salinas and Urkiaga-Alberdi, 1999). With increasing sedimentation there appears to be a shift from encrusting to erect morphologies (Lissner *et al.*, 1991). An erect morphology reduces the settlement of sediments. Large, erect species such as the anemone *Metridium senile* and the polychaete *Eudistylia vancouveri,* which has a tough, wiry body, are able to extend above sediments. In addition, *Metridium senile* has anaerobic pathways involved in energy production during low oxygen exposure, which may occur during burial (Sassman and Mangum, 1973).

Inorganic sedimentation was strongly correlated with light intensity, which is a strong determinant of the depth range of macroalgae, especially at high latitudes (e.g., Gómez *et al.*, 2009). Light limitation may exclude some algal species from the kelp beds along the more glacially exposed, turbid shore. *Saccharina latissima*, the only kelp species found at both shore sites, is particularly well adapted to low light levels (e.g., Borum *et al.*, 2002). Continued glacial melting is likely to have severe effects on the vertical zonation of macroalgae due to the light attenuation effects of increased sediment input.

These considerations provide good evidence that reduced taxonomic richness and abundance in kelp bed communities may be linked to some of the dynamic environmental variables influenced by glacial discharge. However, until controlled experiments manipulating specific environmental variables are conducted we cannot exclude other drivers of the observed differences in kelp bed communities on the two shores. Specifically, the existing substrate differences between the two shores were identified as important drivers of kelp community composition. Rugosity, as a variable driving the kelp bed communities at the two shore systems in Kachemak Bay is closely related to the other identified drivers of inorganic sedimentation and hard substratum. High sedimentation over time smoothes the substratum, leaving little exposed hard structure for attachment (Airoldi, 2003). The kelp bed communities on the north shore of Kachemak Bay were dominated by macroalgal species such as the kelp *Saccharina latissima* and the red alga *Neodilsea borealis* that are able to recruit and survive attached to small structures such as shells and small pebbles (O'Clair and Lindstrom, 2000). In

contrast, most of the macroalgal species common at the south shore require a rocky substrate for attachment. Similarly, many sessile epibenthic organisms require hard structures for attachment (Liddell and Ohlhorst, 1988; Logan, 1988). Hence, substrate differences alone could drive several of the observed kelp community differences between the two shore environments.

An important consideration is that the effects of glacial discharge are likely to spread and/or intensify in the near future. Global average air temperatures are projected to rise 0.4°C over the next two decades, with the largest increases at high latitudes (IPCC, 2007). These changes will further increase the rate of glacial melting and discharge, and necessitate our understanding of the effects on nearshore benthic communities, which are vital components of productive, coastal ecosystems. Climate change is also thought to be responsible for recent increases in forest fires in Alaska (Berg and Anderson, 2006). Burned coastal regions are subject to increased erosion, enhancing sediment input into nearshore waters. Ongoing urbanization and industrial development along the Alaskan coast also increase sediment influx into nearshore systems. Increasing intensity and scale of these impacts are among the possible outcomes of enhanced glacial discharge. These potentially could result in the complete loss of kelps from the more glacially exposed north shore, and the expansion of the impacts noted on the north shore to the currently less exposed south shore.

Our study identified the most important dynamic and static environmental drivers affecting community composition that currently exist on small spatial scales in a subarctic estuary. While we currently cannot separate the effects of some of these drivers,

continued studies of these coastal dynamics are important to better predict the underlying mechanisms, and to better predict the impact of future environmental changes. Based on our results of important dynamic drivers, we would expect nearshore kelp bed communities to experience further decreases in richness and abundance, and these once diverse ecosystems may ultimately be reduced to a few resilient opportunistic species. Such systems may not be able to provide the ecosystem goods and services that kelp beds typically offer.

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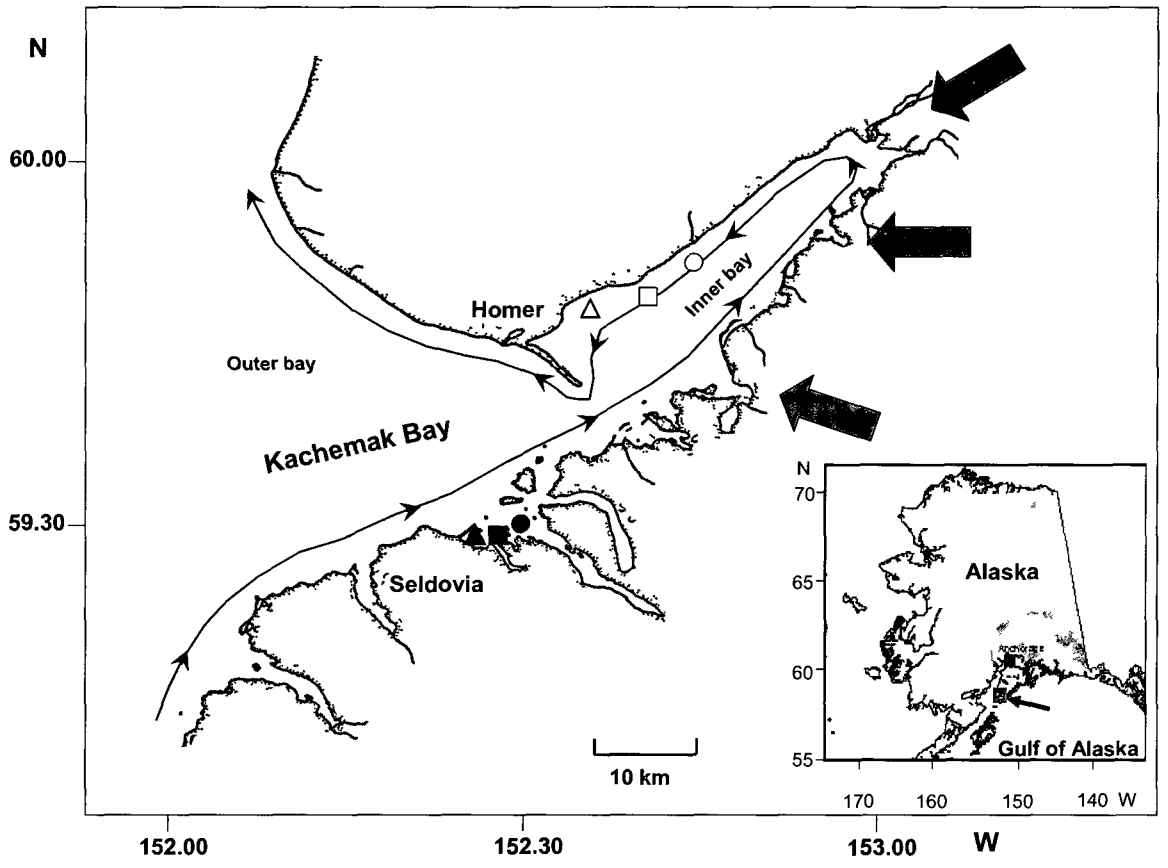

Figure 1.1. The study sites of kelp bed communities in Kachemak Bay. Study sites under more glacially exposed conditions on the north shore are marked with unfilled shapes: triangle (N1), square (N2), circle (N3); those under less glacially exposed conditions on the south shore are marked with filled shapes: triangle (S1), square (S2), circle (S3). Thin arrows indicate overall water circulation patterns. Thick arrows indicate regions of glacial freshwater and sediment discharge.

Figure 1.2. Landsat view of Kachemak Bay, Alaska, August 9, 2000. Sites more exposed to glacial discharge (yellow triangles) and sites less exposed to glacial discharge (red circles) are indicated. Glacial discharge is visible as light blue to white water color. Image is courtesy of U.S. Geological Survey, National Oceanic and Atmospheric Administration (NOAA), and the Kachemak Bay National Estuarine Reserve.

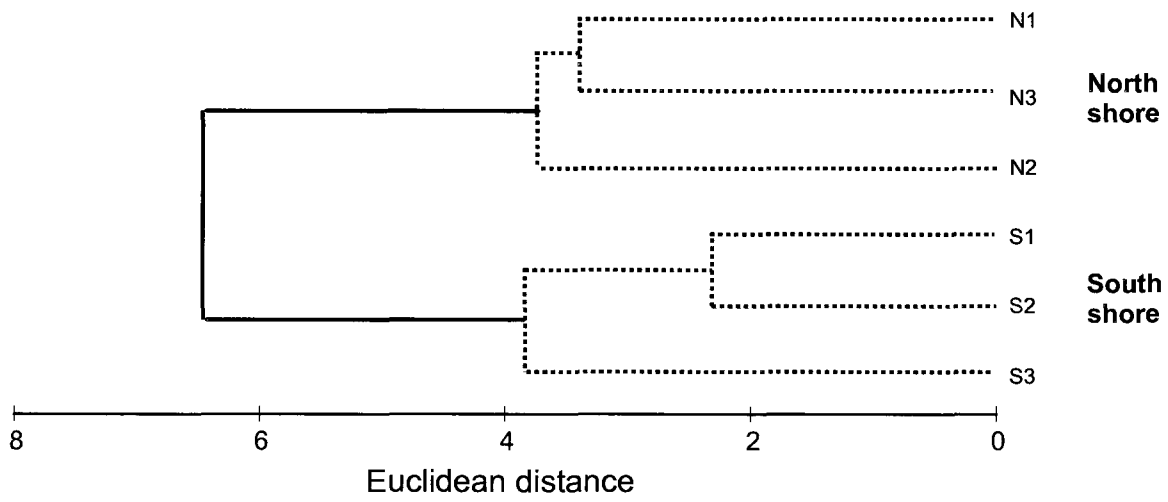

Figure 1.3. Hierarchical clustering of study sites of the more glacially exposed north (N1-N3) and less glacially exposed south (S1-S3) shores of Kachemak Bay based on environmental variables.

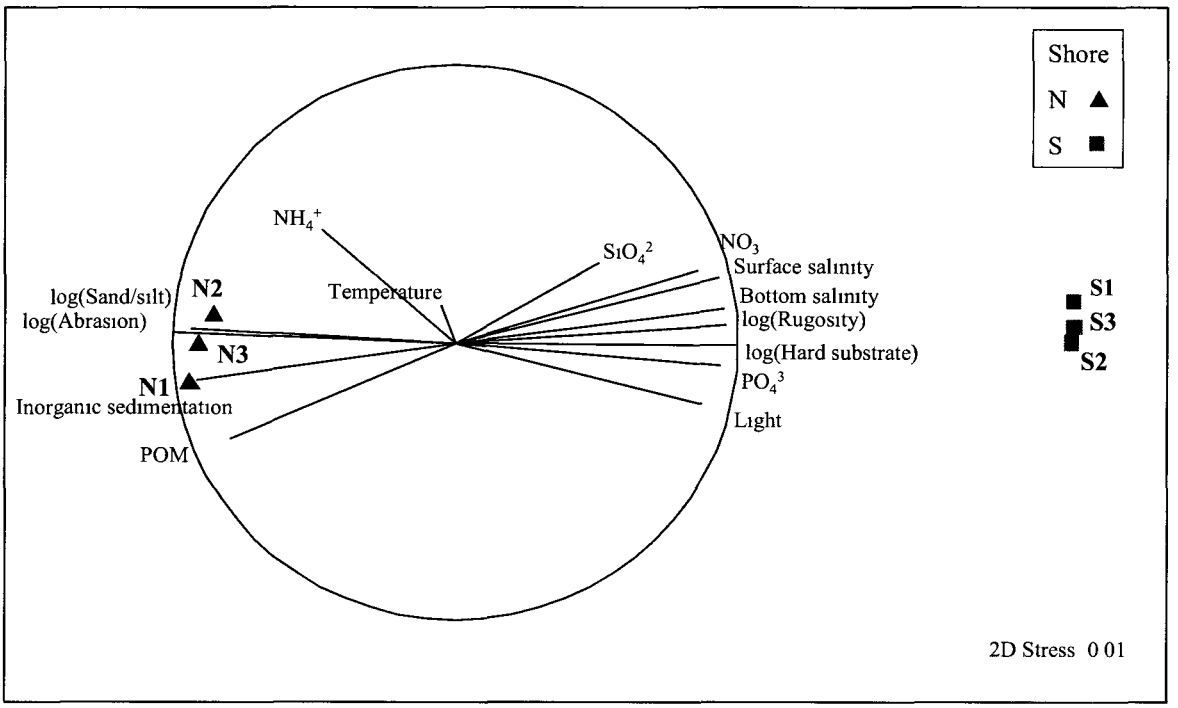

Figure 1.4. Nonmetric multidimensional scaling (nMDS) ordination calculated from Bray-Curtis similarities of epibenthic taxa abundances. Correlation vectors show directionality and strength (length of vector) of environmental variables on kelp bed communities. The circle indicates the possible maximum length of environmental vectors. North shore sites are indicated with black triangles, south shore sites are indicated with gray squares.

Table 1.1. Environmental data from the more glacially exposed north (N1-N3) and less glacially exposed south (S1-S3) shores of Kachemak Bay during July-August 2006 (mean ± SD for sites). n/a = data are not available. Bold type gives shore averages (mean ± SE shores).

Site	Temp (°C)	Light intensity (log lum m^{-2})	Surface salinity	Bottom salinity	NO_3^- (µM)	NH_4^+ (µM)	PO_4^{3-} (µM)	SiO_4^{2-} (µM)	Inorg sediment (mg cm^{-2} d^{-1})	POM (mg cm^{-2} d^{-1})	Abrasion (mg d^{-1})
N1	9.9±0.9	1.9±0.1	22.3±6.7	28.8±1.8	1.0±0.5	9.9±12.2	0.4±0.1	7.8±1.1	4.8±0.1	0.3±0.0	211.8±10.7
N2	10.0±0.9	1.6±0.4	26.5±0.7	30.0±0.0	2.1±1.3	13.9±10.2	0.5±0.1	9.7±3.4	3.4±1.1	0.2±0.1	209.0±11.2
N3	9.8±1.0	1.5±0.5	22.0±2.8	27.9±1.6	2.3±1.3	9.7±0.2	0.4±0.1	10.5±1.9	6.5±0.5	0.3±0.0	211.6±20.8
Avg	**9.9±0.1**	**1.7±0.1**	**23.6±1.5**	**28.9±0.6**	**1.8±0.4**	**11.2±1.4**	**0.4±0.0**	**9.3±0.8**	**4.9±0.9**	**0.3±0.0**	**210.8±0.9**
S1	n/a	2.2±0.2	33.6±0.9	34.3±1.1	3.0±1.2	7.8±7.0	0.6±0.0	9.7±1.9	0.9±0.2	0.2±0.0	159.9±7.7
S2	10.3±0.7	2.2±0.1	33.5±1.4	34.4±0.5	3.3±1.2	5.4±4.8	0.8±0.1	11.1±1.4	0.8±0.2	0.2±0.0	146.4±6.3
S3	9.4±0.9	n/a	30.9±0.2	32.8±0.4	3.5±0.1	12.4±2.5	0.8±0.1	10.3±0.9	1.0±0.4	0.2±0.1	152.0±4.1
Avg	**9.8±0.5**	**2.2±0.1**	**32.7±0.9**	**33.8±0.5**	**3.3±0.2**	**8.5±2.0**	**0.7±0.1**	**10.4±0.4**	**0.9±0.1**	**0.2±0.0**	**152.8±3.9**

Table 1.2. Rugosity data and substrate percent cover for the more glacially exposed north (N1-N3) and less glacially exposed south (S1-S3) shores of Kachemak Bay during July-August 2006 (mean ± SD for sites). Bold type gives shore averages (mean ± SE for shores).

Site	Rugosity ratio	Sand/silt	Gravel	Cobble	Boulder	Shell	Total hard substrate
N1	1.00±0.00	94.3±3.7	3.0±2.6	0.7±1.4	0.0±0.0	0.9±0.5	4.7±3.7
N2	1.00±0.00	92.8±5.3	1.9±1.2	0.3±0.6	1.3±3.9	0.8±0.3	4.3±4.1
N3	1.00±0.00	96.1±2.4	0.7±0.3	0.2±0.6	0.2±0.8	0.9±0.4	2.0±1.2
Avg	**1.00±0.00**	**94.4±1.0**	**1.9±0.7**	**0.4±0.2**	**0.5±0.4**	**0.9±0.0**	**3.7±0.8**
S1	1.13±0.10	40.1±12.0	4.5±4.1	3.1±3.2	7.3±16.1	41.8±11.1	56.7±9.8
S2	1.10±0.10	33.3±16.0	17.8±15.5	13.7±19.9	4.7±15.2	21.1±12.4	57.3±13.8
S3	1.17±0.12	18.7±9.6	22.9±23.2	8.3±9.5	18.7±24.8	16.8±13.4	66.7±8.9
Avg	**1.13±0.02**	**30.7±6.3**	**15.1±5.5**	**8.4±3.1**	**10.2±4.3**	**26.6±7.7**	**60.2±3.2**

Table 1.3. Presence (+) and absence (-) of macroalgae and epifauna on the more glacially exposed north (N1-N3) and less glacially exposed south (S1-S3) shores of Kachemak Bay during summer 2006. Invertebrate phyla include: Porifera (P), Cnidaria (C), Mollusca (M), Echinodermata (E), Arthropoda (A) and Annelida (AN).

	Sites					
	N1	N2	N3	S1	S2	S3
Mobile epibenthos (>2cm)						
Metridium senile (C)	+	-	+	-	+	-
Tonicella lineata (M)	-	-	-	+	+	+
Tonicella undocaerulea (M)	-	-	-	-	-	+
Asterias amurensis (E)	+	+	+	-	-	-
Dermasterias imbricata (E)	-	-	-	-	+	-
Evasterias troschelii (E)	-	-	-	+	+	-
Pycnopodia helianthoides (E)	-	-	-	+	+	+
Pagurus ochotensis (A)	-	-	-	-	-	+
Telemesus cheiragonus (A)	-	-	-	-	+	-
Hippolytidae (A)	-	-	-	+	+	-
Sessile epibenthos						
Ophlitaspongia pennata (P)	-	-	-	-	-	+
Hydroida (C)	+	+	+	-	-	-
Balanoidea (A)	-	+	+	+	+	+
Eudistylia vancouveri (AN)	+	+	-	-	-	-
Serpula vermicularis (AN)	+	+	+	+	+	+
Macroalgae						
Chlorophyta						
Ulva lactuca	+	+	+	-	+	+
Ulva linza	+	-	-	-	-	-
Arcosiphonia spp	-	-	-	+	-	+
Ochrophyta						
Agarum clathratum	-	-	-	-	+	+
Desmarestia aculeata	-	-	+	+	+	+
Costaria costata	-	-	-	-	+	-
Cymathere triplicata	-	-	-	+	+	+
Saccharina latissima	+	+	+	+	+	+
Saccharina subsimplex	-	-	-	+	+	-
Scytosiphon simplicissimus	-	-	-	-	-	-
Ochrophyta Sp 1	-	-	-	+	-	-
Rhodophyta						
Constantinea subulifera	-	-	-	-	-	+
Crustose corralline	+	-	-	+	+	+
Cryptopleura sp	-	-	-	+	+	+
Epiphyte on *Desmarestia aculeata*	-	-	-	-	+	-
Mastocarpus sp	+	+	+	-	-	-
Neodilsea borealis	+	+	+	-	-	-
Epiphyte on *Neodelisea borealis*	-	+	-	-	-	-
Pterosiphonia bipinnata	-	+	-	+	+	+
Sparlingia pertusa	+	-	-	-	-	-
Turnerella mertensiana	-	+	-	-	-	+
Branched blade Rhodophyta 1	-	-	-	-	+	+
Branched blade Rhodophyta 2	-	-	-	-	-	+
Filamentous Rhodophyta 1	-	-	-	-	+	-
Filamentous Rhodophyta 2	-	-	-	-	-	+

Table 1.4. Relative percent cover of macroalgal and epifaunal functional groups at sampling sites on the more glacially exposed north (N1-N3) and less glacially exposed south (S1-S3) shores of Kachemak Bay during summer 2006. Invertebrate functional groups: motile rasping herbivore (HMR), motile jawed carnivore (CMJ), motile other carnivore (CMX), semi-motile tentaculate filter feeder (FDT), sessile tentaculate filter feeder (FST), and sessile other filter feeder (FSX).

	Sites					
	N1	**N2**	**N3**	**S1**	**S2**	**S3**
Macroalgal functional groups						
Branched blade	24.1	19.7	53.3	0.3	2.6	4.3
Medium-thick sheet	30.1	76.0	39.6	6.8	0.0	3.5
Mono/distromatic sheet	42.2	0.4	2.2	0.0	4.3	10.0
Crustose algae	1.2	0.0	0.0	64.2	35.8	32.1
Coarse branched filament	0.0	0.0	4.8	21.3	50.3	46.8
Fine branched filament	0.0	3.9	0.0	7.4	7.0	3.3
Nonbranched filament	2.4	0.0	0.0	0.0	0.0	0.0
Peltate blade	0.0	0.0	0.0	0.0	0.0	0.1
Epifaunal functional groups						
Motile fauna - CMX	73.0	29.4	14.5	50.8	51.3	54.7
Sessile fauna - FSX	0.0	34.3	3.6	44.3	40.3	44.7
Sessile fauna - FST	9.6	36.3	45.7	4.6	2.7	0.3
Semi-motile fauna - FDT	16.9	0.0	36.2	0.0	0.0	0.0
Motile fauna - CMJ	0.6	0.0	0.0	0.2	5.5	0.1
Motile fauna - HMR	0.0	0.0	0.0	0.2	0.2	0.2

Table 1.5. Combinations of environmental variables providing the 'best matches' of biotic and abiotic similarity matrices, as measured by standard Spearman coefficient (ρ_s). Bold type indicates the combinations with maximum ρ_s for biotic analyses based on functional group abundance (A) and taxon abundance (B). Note that inorganic sedimentation, abrasion, surface salinity, and hard substrate) are highly collinear with bottom salinity and were hence excluded from the analysis.

A:	**Spearman rank correlation (functional groups)**
No. variables	Best variable combinations (ρ_s)
1	Salinity
	0.782
2	Salinity, NO_3^-
	0.925
3	**NO_3^-, POM, Rugosity**
	0.929
3	Salinity, NO_3^-, POM
	0.925

B:	**Spearman rank correlation (taxa)**
No. variables	Best variable combinations (ρ_s)
1	Salinity
	0.775
2	Salinity, NO_3^-
	0.925
3	**Salinity, NO_3^-, Rugosity**
	0.946

Table 1.6. Combinations of environmental variables providing the 'best matches' of biotic and abiotic similarity matrices, as measured by standard Spearman coefficient (ρ_s) when hard substrate is substituted with the collinear variable bottom salinity. Other collinear variables (see Table 1.5) are excluded from the analysis. Bold type indicates the combinations with maximum ρ_s for biotic analyses based on functional group abundance (A) and taxon abundance (B).

A:	**Spearman rank correlation (functional groups)**
No. variables	Best variable combinations (ρ_s)
1	Hard substrate
	0.754
2	Hard substrate, NO_3^-
	0.896
3	**Hard substrate, NO_3^-, POM**
	0.939
3	NO_3^-, POM, rugosity
	0.929

B:	**Spearman rank correlation (taxa)**
No. variables	Best variable combinations (ρ_s)
1	Rugosity
	0.775
2	Hard substrate, NO_3^-
	0.904
3	**Rugosity, NO_3^-, POM**
	0.914

Chapter 2: Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae)[1]

2.1 Abstract

In subarctic regions, melting of glaciers creates stressful environmental conditions, such as reduced salinity and irradiance, in coastal benthic habitats such as kelp beds. Our goal was to determine whether these stressors differently affect kelp juveniles of *Saccharina latissima* originating from two environmentally distinct shores, one under oceanic and one under estuarine, glacial influence. Laboratory tests assessed the effects of varying salinities and irradiances on growth and maximum quantum yield (F_v/F_m) of photosystem II of *S. latissima*. Overall, growth rates decreased with decreased salinity and irradiance. Growth rates of juveniles from the glacially-influenced shore were significantly lower than those of the oceanic shore in most salinity and irradiance treatments. Juveniles from both shores grew negligibly at salinities below 13 and an irradiance of 5 μmol photons m^{-2} s^{-1}. At salinity 10, F_v/F_m was significantly reduced, but F_v/F_m was not affected by decreased irradiance. *S. latissima* proved to be relatively tolerant to reduced salinities and irradiances but we detected limits to its resilience. Our results suggest that *S. latissima* populations exhibit phenotypic plasticity in their growth responses. This plasticity seems to be constrained within specific seasonal growth patterns in accordance with their environment of origin.

[1] Spurkland, T. and K. Iken. 2011. Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae). *Bot. Mar. 54*: 355-365.

2.2 **Introduction**

Kelp beds are abundant and essential nearshore habitats in Alaska with tightly linked food webs (Dayton 1985, Fredriksen 2003). As with other coastal habitats, kelp beds are highly dependent on prevailing environmental conditions (Dayton et al. 1999). Changes in these conditions due to anthropogenic climate change, other human activities, and natural climate oscillations can result in changes to or loss of habitat structure, and thus the associated biota. Given the importance of functional nearshore ecosystems, there is a strong need to understand and monitor how coastal ecosystems, and particularly foundation organisms such as the kelp *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Dreuhl *et* G.W. Saunders (previously *Laminaria saccharina* Lamour), react to changing environmental conditions.

The main environmental variables affecting kelps are salinity, light, temperature, nutrient supply and sedimentation (Dayton 1985, Steneck et al. 2002). The accelerated melt of glaciers in Alaska (Arendt et al. 2002, Motyka et al. 2003, Hinzman et al. 2005) increases the freshwater and sediment discharge into coastal regions, reducing salinity and attenuating light. Benthic communities in areas of glacial discharge are exposed to significantly higher turbidity and higher inorganic sedimentation (Wlodarska-Kowalczuk et al. 2005, Sejr et al. 2010) and lower salinity and irradiance than in areas under oceanic influence (reviewed by Smale and Barnes 2008, Spurkland and Iken 2011). Low salinity can exert physiological stress on marine macroalgae, especially subtidal kelps. The most important effects of salinity changes are osmotic and ionic stress (Kirst 1990). In

addition, the functionality and efficiency of the photosynthetic apparatus can be negatively affected by low salinities (<20-25) (Kirst and Wiencke 1995).

Laminaria and *Saccharina* species are classified as "shade thalli" (Lüning 1979), and depending on the species, temperature and photoperiod, growth can be saturated at irradiances of 20–100 μmol photons m^{-2} s^{-1} (Bartsch et al. 2008). Arctic *S. latissima* is well adapted to low light conditions, caused by dark, long winters and turbid waters. It has high pigment concentrations and photosynthetic and morphological adaptations (Borum et al. 2002, Bartsch et al. 2008). Consequently, *S. latissima* can be the dominant or only habitat-forming kelp in subarctic regions of high environmental variability (Spurkland and Iken 2011). It is important to assess the responses of *S. latissima* to low light and salinity conditions that are expected with increased glacial melt because changes in its growth and abundance will have severe impacts on overall community structure.

Growth has been used as a response variable for measuring how kelp species react to environmental conditions (Boden 1979, Lüning 1979, Lyngby and Mortensen 1996). Overall growth integrates the interactions and trade offs among many physiological processes and might be a relatively coarse response variable. More recently, pulse-amplitude modulated (PAM) fluorometry, a rapid, non-invasive technique that provides semi-quantitative information about maximum quantum yield (F_v/F_m) of PSII photochemistry (van Kooten and Snel 1990, Beer et al. 1998, Baker 2008) has been used as a refined indicator of physiological performance and thus of organism health in kelps (Bruhn and Gerard 1996, Machalek et al. 1996, Hanelt 1998). Among other indices,

F_v/F_m has been applied as an indicator of algal health under salinity stress (Wilson et al. 2004, Eggert et al. 2007, Kim and Garbary 2007). We suggest that both response variables combined, growth and F_v/F_m, will give us a more detailed insight into whether or not reduced growth rates in *S. latissima* coincide with reduced algal health (i.e., a compromise in the photosynthetic apparatus), and/or if these responses are used in adaptive strategies to adverse conditions.

Tolerances to environmental conditions in macroalgae may be manifested in several ways. Individuals of the same species under different environmental conditions may develop into different ecotypes through genetic differentiation (Lüning 1990) or they may exhibit phenotypic plasticity (Price et al. 2003). Macroalgal ecotypes are adapted to and grow better under environmental conditions from which they originate (Lüning 1990). Phenotypic plasticity is adaptive in that individuals are more fit in variable environments (Price et al. 2003) due to their ability to acclimate. Knowledge of ecotypic differentiation and phenotypic plasticity can assist us in evaluating foundation species resilience to environmental change.

The aim of this study was to investigate the effects of the key environmental variables, salinity and irradiance, on growth and F_v/F_m of PS II of juvenile *S. latissima* from two environmentally distinct shores in a subarctic Alaskan estuary. Although the shores are in close proximity (10 km apart), one experiences low salinity and light intensity (estuarine glacial influence) whereas the other shore experiences high salinity and light intensity (oceanic influence) during summer. This environmental setting was used to assess responses and possible adaptations of the foundation species *S. latissima* to

the predicted increases in glacial melt in estuaries. The main questions to be answered were: (1) Are growth rates and F_v/F_m different for estuarine and oceanic *S. latissima* at the same salinity or irradiance levels? (2) If so, which of these abiotic factors contributes the most to the differences in growth and F_v/F_m? (3) Is low growth in *S. latissima* an indicator of physiological stress? (4) Do populations from two distinct environments, one under oceanic and one under estuarine glacial influence, represent different ecotypes or exhibit phenotypic plasticity?

2.3 Materials and methods

2.3.1 Sample sites

Macroalgal samples were collected in Kachemak Bay, an inlet on the eastern side of lower Cook Inlet, close to the Gulf of Alaska (Figure 2.1). Cold, nutrient-rich seawater from the Gulf of Alaska flows along the southern shore of the bay. The estuary's upper southern shore and the head of the bay are influenced by glacial input, which then flows along the northern shore back to Cook Inlet (Burbank 1977). Hence, overall circulation patterns in Kachemak Bay create predominantly oceanic conditions on the southern shore and estuarine conditions on the northern shore (Burbank 1977). Only one kelp species, *Saccharina latissima* provides understory habitat structure in the glacially-influenced areas of the north shore compared to a diverse kelp community in the oceanic region on the south shore (Konar et al. 2009, Spurkland and Iken 2011). DNA barcoding, using the 5'end of the cytochrome c oxidase I gene from the mitochondrial genome of *S. latissima*

used in this study, confirmed that the individuals of both shores were the same species (T. Spurkland and G. Smith, unpublished data).

Monitoring during summer 2006 established that both shores experience very different environmental conditions, even though they are only about 10 km apart (Table 2.1, for details see Spurkland and Iken 2011). Among the environmental factors monitored, the estuarine northern shore had markedly lower salinity and light intensity than the oceanic southern shore (Table 2.1). For the present study, juvenile *S. latissima* from estuarine conditions were collected at McNeil Canyon (McN-E) (59°41.19' N, 151°14.87' W) on the northern shore, whereas juveniles from oceanic conditions were collected at Jakolof Bay (JAK-O) (59°28.03' N, 151°32.13' W) on the southern shore (Figure 2.1).

2.3.2 Salinity experiments

Juvenile *S. latissima* thalli (20–30 cm in length) were randomly collected at both sites from approximately 5 m below mean lower low water (MLLW) using self-contained underwater breathing apparatus (SCUBA) or by dredging. Thalli from both shores were held separately for three to five days for acclimation prior to experimentation in outdoor flow-through tanks (150 l) at the Kasitsna Bay Laboratory, located on the southern shore of Kachemak Bay. Screens made of layers of neutral grey plastic window screen mesh were placed over the tanks to simulate the natural subtidal light conditions based on June 2007 measurements (Li-193SA; Li-Cor, Lincoln, NE, USA) taken at solar noon *in situ* at JAK-O.

The first salinity experiment (Sal I) treatments were set at 31, 20 and 10. A salinity of 31 represents natural bottom-water salinity conditions under oceanic conditions at the Kachemak Bay southern shore (e.g., JAK-O; Spurkland and Iken 2011, Table 2.1). In contrast, a salinity of 20 is a typical bottom-water value recorded for the estuarine northern shore during periods of high glacial discharge in late summer (e.g., McN-E; Spurkland and Iken 2011, Table 2.1). A salinity of 10 was chosen as a low level that has been reported for other subarctic glacially influenced fjords (Munda 1978) and that could occur along the northern shore of Kachemak Bay if glacial melt discharge were to increase. For each treatment six *S. latissima* thalli from each shore were kept individually in 24 l randomly placed seawater tanks in a constant temperature room at 8 ± 2 °C. Kelps were exposed to a photoperiod of 16:8 h light:dark, at a photon flux density of ca. 50 μmol m^{-2} s^{-1}, using cool-white fluorescent lamps. The holdfast of each individual was attached to a weight to keep the thallus submerged. Water motion was maintained by aeration, and seawater from the Kasitsna Bay Laboratory outdoor flow-through seawater system was changed every three to four days. Reduced salinity conditions were adjusted by adding freshwater from a clear creek adjacent to the Kasitsna Bay Laboratory. Salinity within the tanks was measured using a hand-held refractometer (1 unit accuracy). Nutrient levels were maintained above limiting levels throughout experimentation by the addition of $NaNO_3$ (30 μM) and NaH_2PO_4 (2 μM) (Gerard et al. 1987), with the saturation level of nitrate for growth of *S. latissima* being 10 μM NO_3^- (Chapman et al. 1978). Ambient summer nitrate and phosphate levels at the Kasitsna Bay Lab are near limiting levels (3.3 ± 0.2 and 1.8 ± 0.4 μM, respectively) (Table 2.1, also see

Spurkland and Iken 2011). We chose to keep nutrient levels above limiting levels in order to rule out nutrients as a source of variation in growth or F_v/F_m so that we could isolate salinity effects. Salinity effects on growth (see below) were monitored for three weeks at midday every three to four days prior to the water changes. In this Sal I experiment, F_v/F_m could only be evaluated once at the conclusion of the experiment (see below). At the termination of the experiment the thalli were frozen for other measurements and destructive analyses reported elsewhere. The experiment was conducted late June to mid-July 2007.

A second salinity experiment (Sal II) was conducted to determine more precisely the salinity threshold between 10 and 20 (based on Sal I results) at which the individuals stopped growing, but were still able to survive. Collection sites, treatment and number of replicate thalli per shore and treatment were those described for Sal I. The salinity levels tested were 31 (control to compare to Sal I), 17 and 13. In this Sal II experiment, salinity effects on growth and maximum quantum yield (see below) were monitored for three weeks at midday every three to four days prior to the water changes. The experiment was conducted during September 2007.

2.3.3 Irradiance experiment

We examined the effect of three irradiance treatments on growth and maximum quantum yield of *S. latissima* from the two distinct shores (Light I experiment). Collection sites, treatments and number of replicate thalli per site and treatment were as described for both salinity experiments. The irradiance treatments were chosen based on mean *in-situ* irradiance measurements (Li-193SA; Li-Cor, Lincoln, USA) taken at solar

noon in June 2007 at both shores and were set at photon flux densities of approximately 50, 20 and 5 μmol m^{-2} s^{-1}, using cool white fluorescent lamps. Because Kachemak Bay experiences almost 19 hours of daylight during summer, measurements at solar noon were considered a good representation of the light climate during daylight hours. The highest level (50 μmol photons m^{-2} s^{-1}) represented the mean natural light level at approximately 5 m MLLW around solar noon at the oceanic site and the intermediate treatment (20 μmol photons m^{-2} s^{-1}) was typical for the estuarine site. The lowest treatment (5 μmol photons m^{-2} s^{-1}) was chosen as a low level found in areas of high sediment load in subarctic fjords (Svendsen et al. 2002) and could be observed in Kachemak Bay if sediment discharge from glaciers into the bay were to increase. Individual tanks were exposed to 50 μmol photons m^{-2} s^{-1} and reduced light treatments were adjusted with screens made of layers of neutral gray plastic window screen mesh. Salinity was set at 31 and all other environmental parameters were maintained as described for the salinity experiments. Growth and F_v/F_m measurements (see below) were made at approximately midday every three to four days prior to the water change for three weeks. The experiment was conducted during July and August 2007.

2.3.4 Growth measurements

Linear growth, hereafter referred to as growth unless otherwise stated, of juvenile *S. latissima* thalli was monitored using the hole punch technique (Parke 1948). *S. latissima* undergoes intercalary growth with maximum growth occurring between the stipe/lamina junction and ca.10 cm up the lamina (Mann 1973). Two 0.5 cm diameter holes were punched in the meristematic region of each lamina at 5 and 10 cm above the

stipe/lamina junction. The distance from each hole to the stipe/lamina junction was monitored every three to four days and growth (cm d^{-1}) was determined based on the location of the 10 cm hole. Every time an individual grew 10 cm or more a new hole was punched 5 cm above the stipe/lamina junction.

2.3.5 Maximum quantum yield of PSII

PAM fluorometry was used to determine F_v/F_m of PSII of each experimental thallus. F_v/F_m was determined as the ratio of variable to maximal fluorescence for dark-acclimated tissue:

$$F_v/F_m \equiv (F_m-F_o)/F_m$$

where, F_v is the difference between F_m and F_o; F_m is the fluorescence intensity with all the PSII reaction centers closed and primary electron acceptors reduced (thus active); F_o is the initial fluorescence with all reaction centers open and primary electron acceptors oxidized (thus inactive) (van Kooten and Snel 1990).

For the Sal I experiment, fluorescence measurements were made only once at midday prior to the conclusion of the experiment using a Diving PAM fluorometer (Walz GmbH, Effeltrich, Germany). One measurement was made on each thallus 10 cm above the stipe/lamina junction. Tissue was dark-adapted for 15 minutes (after Dring et al. 1996) prior to the measurement by placing a clip with a closed shutter on the lamina. Each measurement was made after opening the clip shutter. In contrast to Sal I, maximum quantum yield measurements during Sal II and Light I were made on dark-adapted tissues 10 cm above the stipe/lamina junction using an OS-30p PAM fluorometer (OptiScience Corp., Tyngsboro, NH, USA). F_v/F_m values during Sal II and Light I were determined

every two hours for the first 12 h of the study and thereafter every three to four days at midday for three weeks. The order in which individual kelps were measured was randomly determined each time.

2.3.6 Phenotypic plasticity

Phenotypic plasticity for two traits [growth rate (cm d^{-1}) and F_v/F_m] was quantified using the relative distance plasticity index (RDPI, devised for terrestrial plants; Valladares et al. 2006). RDPI, ranging from 0 (no plasticity) to 1 (maximal plasticity) was calculated as

$$\text{RDPI} = \sum(|x_{ij} - x_{i'j'}|/(x_{ij} + x_{i'j'})/n$$

where, x_{ij} , is a value of the trait for thallus i in treatment j, $|x_{ij} - x_{i'j'}|$, is the absolute difference in trait values computed for all possible pairings of thalli from the three different treatments within an experiment and n, the total number of pairs. Relative distances are defined as $|x_{ij} - x_{i'j'}|/(x_{ij} + x_{i'j'})$ for all pairs of individuals from a given shore exposed to different treatments within an experiment.

2.3.7 Statistical analysis

All data were tested for normality using the Shapiro-Wilk normality test and for homogeneity of variances using the Bartlett test and Fligner-Killeen test. Two-way ANOVA along with Tukey HSD paired multiple comparisons were performed to identify significant differences in overall growth rate and final F_v/F_m among treatments and between shores. Log transformed overall growth rate for each individual was determined for the number of days the thalli survived in each experiment. Simple linear regression was used to examine cumulative growth over time for all treatment/shore groups (n = 6)

for each experiment. Simple linear regression was also used to determine the growth rate (slope) of each individual, and the mean ± SE of each treatment group was determined. Individuals that died during a treatment were treated as missing values for cumulative growth and final F_v/F_m in the above analyses. Repeated measures analysis was conducted to examine between group effects (treatment, shore) in addition to within subject effect (time) on F_v/F_m values during Sal II and Light I. Salinity (Sal II) was rank transformed. Interval two and eight were removed from the Light I analysis due to missing values. Relative distances for each trait [growth rate (cm d^{-1}) and F_v/F_m] for each experiment (Sal I, Sal II, Light I) were compared with the non-parametric Wilcoxon rank sum test for differences in phenotypic plasticity (RDPI) between shores. All data analyses were conducted using R 2.12.2 software (R Foundation for Statistical Computing, Vienna, Austria). Significance for all analyses was set at $\alpha = 0.05$.

2.4 Results

2.4.1 Salinity and irradiance effects on growth rate

Overall growth rates of *S. latissima* decreased with decreasing salinity during the Sal I treatments for thalli from both shores (Figure 2.2A). Salinity treatment and shore were significant factors overall (two-way ANOVA: $F_{2,26}=31.533$, $p<0.0001$ and $F_{1,26}=14.255$, $p=0.0008$, respectively). The highest mean growth rate was 1.42±0.11 cm d^{-1} for the oceanic southern shore thalli growing under the salinity 31 treatment (Figure 2.2A). There was negligible growth in the salinity 10 treatment for thalli from both shores. Within each shore group, the mean growth rates of thalli differed significantly

between salinities 10 and 31, but not between salinities 20 and 31 (Figure 2.2A). The mean growth rates of the estuarine northern shore thalli were less than half those of the oceanic southern shore thalli at the upper two salinity levels, although differences between shores were only significant for the salinity 31 treatment. Over time, the thalli from both shores at salinity 10 became bleached; some blistered and the distal tissues gradually sloughed away until most individuals died. Cumulative growth was linear and significant at the upper two salinity levels whereas no significant growth occurred in juveniles from either shore at a salinity of 10 from either shore (Table 2.2).

As in Sal I, overall growth rates of *S. latissima* also decreased with decreasing salinity during the Sal II treatments for thalli from both shores (Figure 2.2B). The salinity x shore interaction (Sal II) was significant (two-way ANOVA, $F_{2,28}=3.345$, $p=0.05$) in contrast to Sal I, with the response to salinity differing between the two shores. The overall growth responses of oceanic southern shore thalli during Sal II were similar to those of Sal I, whereas growth of estuarine shore thalli at salinity 31 was much reduced compared to the same salinity during Sal I. This is likely due to seasonal timing of the experiments; Sal I was conducted in late June and July, while Sal II occurred during September and early October, and the estuarine thalli may exhibit a different seasonal growth pattern. Mean growth rates of thalli from the estuarine northern shore were significantly lower than those from the oceanic southern shore in all salinity treatments (Figure 2.2B). For thalli within both shore groups, growth did not differ between salinities of 31 and 17 but growth was significantly lower at a salinity of 13. All individuals irrespective of shore origin survived the salinity 13 treatment, even though

some individuals from both shores had bleaching at their tips after one week. The salinity threshold at which thalli remain alive, but do not grow is between 13 and 10. Cumulative growth was linear over time at all treatments for thalli from both shores (Table 2.2).

During the irradiance experiment (Light I), growth rates of *S. latissima* were generally highly variable but decreased overall with decreasing light treatments for thalli from both shores (Figure 2.2C). In Light I, irradiance treatment and shore were significant factors overall (two-way ANOVA: $F_{2,29}=58.006$, $p<0.0001$ and $F_{1,29}=47.567$, $p<0.0001$, respectively). Growth rates in the 50 and 20 μmol photons m^{-2} s^{-1} treatments were similar but differed significantly from those in the 5 μmol photons m^{-2} s^{-1} treatment in thalli from both shores (Figure 2.2C). The oceanic southern shore thalli had significantly higher growth rates than the estuarine northern shore thalli in both the 50 and 20 μmol photons m^{-2} s^{-1} treatments, but responses (almost no growth) were the same at the 5 μmol photons m^{-2} s^{-1} treatment (Figure 2.2C). Cumulative growth was linear and significant over time at all light treatments in juveniles from both shores (Table 2.2).

2.4.2 Salinity and irradiance effects on maximum quantum yield

Salinity treatment had a significant effect on F_v/F_m (two-way ANOVA: $F_{2,29}=53.380$, $p<0.0001$) of juvenile *S. latissima* at the end of the Sal I experiment but shore of origin was not a significant factor (two-way ANOVA: $F_{1,22}=1.259$, $p=0.2740$) across varying salinity levels (Figure 2.3A). The F_v/F_m values of juveniles at salinity 20 and 31 treatments were not significantly different in thalli from either shore. The F_v/F_m values of estuarine northern shore thalli in the salinity 10 treatment ranged from 0.260 to 0.471, and were significantly lower (almost half) than in the two higher salinity

treatments (Figure 2.3A). No oceanic southern shore thalli survived the entire experiment at a salinity of 10.

Tests of hypotheses for between-subject effects on F_v/F_m during Sal II revealed that the salinity x shore interaction was significant (p=0.0285) (repeated measures ANOVA, Table 2.3, Figure 2.4A). The salinity x shore interaction also was significant at the end of Sal II (two-way ANOVA: $F_{2,30}$=6.163, p=0.0057). Maximum quantum yield of the estuarine northern shore thalli in the salinity 13 treatment was significantly lower than all other treatment/shore groups (Figure 2.3B).

Similar F_v/F_m values were measured for juvenile S. *latissima* from both shores and among irradiance treatments over the course of Light I (Figure 2.4B). The light x shore interaction (between-subject effect on F_v/F_m) was significant (p=0.0115) (repeated measures ANOVA, Table 2.3). Neither light treatment nor shore origin had a significant effect on F_v/F_m (two-way ANOVA: $F_{2,27}$=2.767, p=0.0807, $F_{1,27}$=2.461, p=0.1283, respectively) at the end of Light I (Figure 2.3C).

2.4.3 Phenotypic plasticity (RDPI)

The phenotypic plasticity index (RDPI) values for growth rate under Sal I treatments of the estuarine and the oceanic thalli were 0.659 (n =108) and 0.678 (n = 85), respectively, and under Sal II RDPI were 0.545 (n = 96) and 0.587 (n = 96) for the two respective shores. RDPI values for growth rate under the Light I treatments for the estuarine and oceanic thalli were 0.576 (n = 96) and 0.621 (n = 108), respectively. Hence, thalli from both shores exhibited growth plasticity with changing salinity and irradiance. Plasticity in growth was not significantly different for thalli from the two shores under

salinity treatments (Wilcox rank sum test: p=0.73 for Sal I, p=0.37 for Sal II), but was significantly higher for oceanic thalli for light treatments (Wilcox rank sum test: p=0.04). RPDI values for F_v/F_m were much lower (= little plasticity overall) than for growth for thalli from both shore environments. RDPI for F_v/F_m under Sal I treatments of the estuarine and the oceanic thalli were 0.190 (n = 75) and 0.045 (n = 36), respectively, and under Sal II were 0.081 (n = 108) and 0.022 (n = 108), respectively. RPDI for F_v/F_m in the estuarine thalli was significantly higher than that of oceanic thalli for Sal I and Sal II (Wilcox rank sum test: $p<0.0001$, both experiments) but the overall very low plasticity values make this statistical significance ecologically questionable. RDPI values for F_v/F_m under the Light I treatments for the estuarine and oceanic thalli were also low with 0.011 (n=108) and 0.013 (n=108), respectively; shore responses were significantly different (Wilcox rank sum test: p=0.0432) but also likely ecologically irrelevant.

2.5 Discussion

Growth of juvenile *S. latissima* in subarctic Alaska was negatively affected by both reduced salinity and irradiance, whereas the functional state of the photosynthetic machinery of PSII was affected only at salinities at or below 13. This indicates that overall growth may be compromised by the conditions tested here but that physiological stress levels (based on F_v/F_m) in *S. latissima* were only low to moderate during the exposure times tested. These results present an important contribution to our understanding how foundation species, such as *S. latissima*, may react to changing environmental conditions brought about by climate change, human activities and natural

climate oscillations. Here, we will first discuss individually the effects of salinity and light conditions on *S. latissima* and then discuss its adaptive potential in terms of ecotypic differentiation or phenotypic plasticity in response to these variables.

Subtidal marine macroalgae live in a relatively constant osmotic environment with salinities ranging from 30 to 35 (Lüning 1990). Arctic kelps tolerate rapid changes in hypersalinity much better than hyposalinity during laboratory tests (Karsten 2007). For example, *S. latissima* is able to tolerate some degree of hyposalinity, with gametophytes and sporophytes tolerant to salinities of 17 to 32 (Druehl 1967). In our study juvenile *S. latissima* tolerated a salinity of 13 for three weeks, while juveniles at a salinity of 10 became severely stressed and mostly died. Therefore, a salinity level between 10 and 13 may be the threshold subarctic Alaskan *S. latissima* is able to tolerate, at least for these relatively short exposure periods. The waters of inner Kachemak Bay are stratified during summer with salinities as low as 5 in the top 5 m of the water column (Speckman et al. 2005). Therefore, at times, salinity conditions in the shallow areas of Kachemak Bay may already reach the tolerance limits of *S. latissima*. These conditions would be exacerbated if salinities continue to be reduced with increased glacial melting.

Hyposalinity can negatively affect photosynthesis in kelp (Karsten 2007), for example, by reduced F_v/F_m of PSII of dark-adapted tissue (Krause and Weis 1988). It must be noted, however, that F_v/F_m does not necessarily represent the entire potential of the thallus for photosynthesis as limitations may occur elsewhere in the photosynthetic process not measured by F_v/F_m, particularly in the dark reactions, without affecting PSII efficiency (reviewed by Kromkamp and Forster 2003). Maximum F_v/F_m rates of healthy

adult brown macroalgae (including *S. latissima*) are typically approximately 0.75 (Büchel and Wilhelm 1993, Dring et al. 1996, Hanelt 1998), indicating a constant and high potential efficiency of the PSII primary reaction (Krause and Weis 1988). Young sporophytes and gametophytes of *S. latissima* and *Laminaria hyperborea* (Gunnerus) Foslie may have lower maximum values than adults, with yields ranging from 0.50 to 0.65 considered healthy (Dring et al. 1996). Reduced yields are used to evaluate stress of the thallus. Mean F_v/F_m values of *S. latissima* juveniles from both shores in our study at salinity treatments of 31 to 13 were >0.6, indicating that maximum quantum yield was not compromised at these salinities. Rapid light curves (RLC, data not reported here) confirmed that there were no differences in photosynthetic activity between thalli from the two shores at salinities of 31 and 20. At a salinity of 10, however, F_v/F_m (0.37) decreased by nearly half for estuarine thalli and oceanic thalli did not survive. In our study, the sustained F_v/F_m values down to salinity 17, and yields >0.6 at a salinity of 13, indicate that the individuals from both shores experienced little stress at these salinity levels. Algae can have energy-demanding regulatory mechanisms to prevent PSII inhibition from hyposaline stress (Eggert et al. 2007). If PSII regulation indeed occurred in our study, metabolic energy required for this PSII regulation may have been derived from the energy savings of reduced growth of *S. latissima*, although this hypothesis will need further testing.

Many high-latitude kelps are low-light adapted, with high photosynthetic efficiencies and low light compensation and saturation points (Hanelt et al. 2003). Values for the photosynthetic parameters (α, $rETR_{max}$, E_k) derived from RLCs in this study (data

not reported here) indicate that subarctic *S. latissima* from both shores, is also low-light adapted. Based on our experiments, the irradiance threshold at which *S. latissima* survive for at least several weeks, but do not grow, may be around 5 μmol photons m^{-2} s^{-1}, which is comparable to other high-latitude studies. For example, respiration of Arctic *S. latissima* is usually compensated by photosynthesis at <7 μmol photons m^{-2} s^{-1} (Borum et al. 2002). *S. latissima* appears resilient to at least short-term irradiance reductions, which might be expected to occur with increases in seasonal glacial discharge.

Despite growth and F_v/F_m having the same overall patterns, *S. latissima* thalli from the two different environments responded to different extents to the salinity and irradiance treatments. Individuals from the oceanic shore generally out performed the individuals from the glacially exposed estuarine shore in terms of growth. These results were contrary to what was expected for different ecotypes in response to varying environmental conditions. The idea of ecotypes predicts better growth at conditions from which the thallus originates (Lüning 1990). If the *S. latissima* in our study were different ecotypes, we would expect estuarine thalli to grow better and have higher F_v/F_m at intermediate salinity (17-20) and light levels (20 μmol photons m^{-2} s^{-1}), whereas oceanic thalli should have highest performances at the highest treatment levels. *S. latissima* ecotypes based on salinity (Gerard et al. 1987) and light (Gerard 1988, 1990) have been previously suggested. Separate salinity ecotypes for *S. latissima* were determined for thalli from two salinity environments (25-29 vs. 28-32) (Gerard et al. 1987). Similarly, salinity ecotypes are known for the rockweed *Fucus vesiculosus* L., with one ecotype at its northern limit in the Baltic Sea (salinity 5) and another in the Atlantic (salinity 34)

(Raven and Samuelsson 1988, Nygård and Dring 2008). *F. vesiculosus* ecotypes from the Baltic also had higher ETR_{max} and relative growth rates (RGR) at low salinities (5-10) than ecotypes from the Irish Sea, where ETR_{max} and RGR decreased sharply at salinities below 20 (Nygård and Dring 2008). Distinct light-related ecotypes were proposed for *S. latissima* populations from turbid (approx. 2.5% of surface light) to non-turbid (15-20% surface light) environments (Gerard 1988, 1990). Estuarine *S. latissima* in our study did not exhibit enhanced growth at intermediate salinity and irradiance levels but instead, thalli grew equally little or less at the intermediate treatments typical of their natural environment than at the higher treatments. This suggests that the *S. latissima* of the two distinct environments in Kachemak Bay do not represent different ecotypes. It is likely that the environmental conditions at the two shores only vary seasonally, during summer glacial melt. Seasonal exposure differences may not be a sufficient selective pressure to drive manifestation of ecotypes. It may also be that the circulation pattern in Kachemak Bay ensures distribution of genotypes from the southern shore to the northern shore every reproductive season.

Thalli exhibiting phenotypic plasticity are able to adjust their physiological responses to varying environmental conditions (Agrawal 2001, Price et al. 2003). We detected plasticity in thallus growth from both shore environments as they all changed growth rates with changing salinity and light conditions. However, the results are probably most meaningful for the estuarine thalli as they were exposed in our experiments to improved conditions over their natural environment, whereas oceanic thalli were only exposed to worsened conditions. Estuarine thalli improved their growth

performance when conditions improved over those in their natural environment. Conversely, we detected little plasticity in maximum quantum yield as high F_v/F_m values were maintained irrespective of salinity or light treatment levels. However, although the two shore populations had similar values for the plasticity index for growth, absolute growth rates in estuarine northern shore thalli were never as high as those of oceanic southern shore thalli, despite their ability to respond to the improved conditions. The environmental differences between the two shores are most pronounced in the summer when our experiments were conducted. It is possible that *S. latissima* has seasonal growth patterns that differ in the populations on the two shores of Kachemak Bay. Seasonal growth constraints of the population on the estuarine northern shore may limit the maximum attainable growth during the summer and thus limit the range of plastic response to improved conditions.

Our study did not explicitly address seasonal growth patterns in *S. latissima*, but some inferences can be drawn from the different times at which laboratory experiments were conducted. For example, mean growth of estuarine northern shore thalli under the same "optimal" conditions (salinity 31, 50 μmol photons m^{-2} s^{-1}) declined from 0.6 cm d^{-1} in late June/July (Sal I) to 0.2 cm d^{-1} in September (Sal II). In contrast, oceanic southern shore thallus growth under the same conditions remained consistently high at 1.4 cm d^{-1} from late June/July through September. This confirms the notion of distinctly different seasonal growth patterns in *S. latissima* on the two shores. In systems of extreme seasonal environmental changes, maximum photosynthesis and maximum growth in kelps can be decoupled if optimal environmental conditions for both processes (light and nutrient

availability, respectively) do not temporally coincide (e.g., *Laminaria solidungula* J. Agardh) Dunton and Schell 1986). This decoupling is mainly driven by nitrogen limitations, and distinct nitrate ecotypes have been demonstrated for kelps at sites with high and low nitrate in summer in Nova Scotia (Espinoza and Chapman 1983). Complete decoupling of photosynthesis and growth may not occur in *S. latissima* in Kachemak Bay, but thalli from the estuarine shore may have adapted to early growth based on better light and nutrient availability and higher salinity in winter and spring (T. Spurkland and K. Iken, unpublished data). Growth in the estuarine thalli may then decrease during increased glacial discharge later in the summer. In contrast, higher light and salinity levels and somewhat higher nutrient levels at the oceanic shore may allow continued growth throughout summer. Overall, it appears that *S. latissima* populations from the estuarine environment in Kachemak Bay exhibit phenotypic plasticity in terms of growth, but their range of plastic response to optimal conditions may be seasonally constrained.

In summary, salinity and light reductions affected growth in both populations of *S. latissima*, whereas maximum quantum yield was largely unaffected. We found phenotypic plasticity in growth of *S. latissima*, in which the estuarine northern shore population appears to have developed a different seasonal growth strategy than that of the oceanic southern shore during the summer months of high glacial discharge in Kachemak Bay. *In situ* examination of *S. latissima* from both shores would provide further information regarding their growth strategies, and would be the first report of such distinct traits within a species on such small spatial scales. Seasonal modification of growth may yet be another way in which a species may adapt to a changing environment.

High F_v/F_m values in all manipulations but the lowest salinity conditions suggest that thalli are not physiologically stressed at these conditions despite reduced growth. Hence, growth alone may not be a sufficient measure of kelp physiological competence. Likewise, F_v/F_m or other photosynthetic indices alone may also not fully capture the possible functional consequences of changing environmental conditions. For example, altered growth strategies as suggested here may lead to less kelp productivity to provide habitat and food during the period of glacial melt. We therefore suggest that the combination of both response variables is useful to assess the effects of changing environmental conditions on nearshore kelps and habitats. Future scenarios of climate change could lead to even greater reductions in salinity and light, which could potentially result in the complete loss of kelps at the glacially influenced north shore. Plastic responses and seasonal adaptations may be limited, and we remain concerned about the persistence of this important foundation species during continued climate change.

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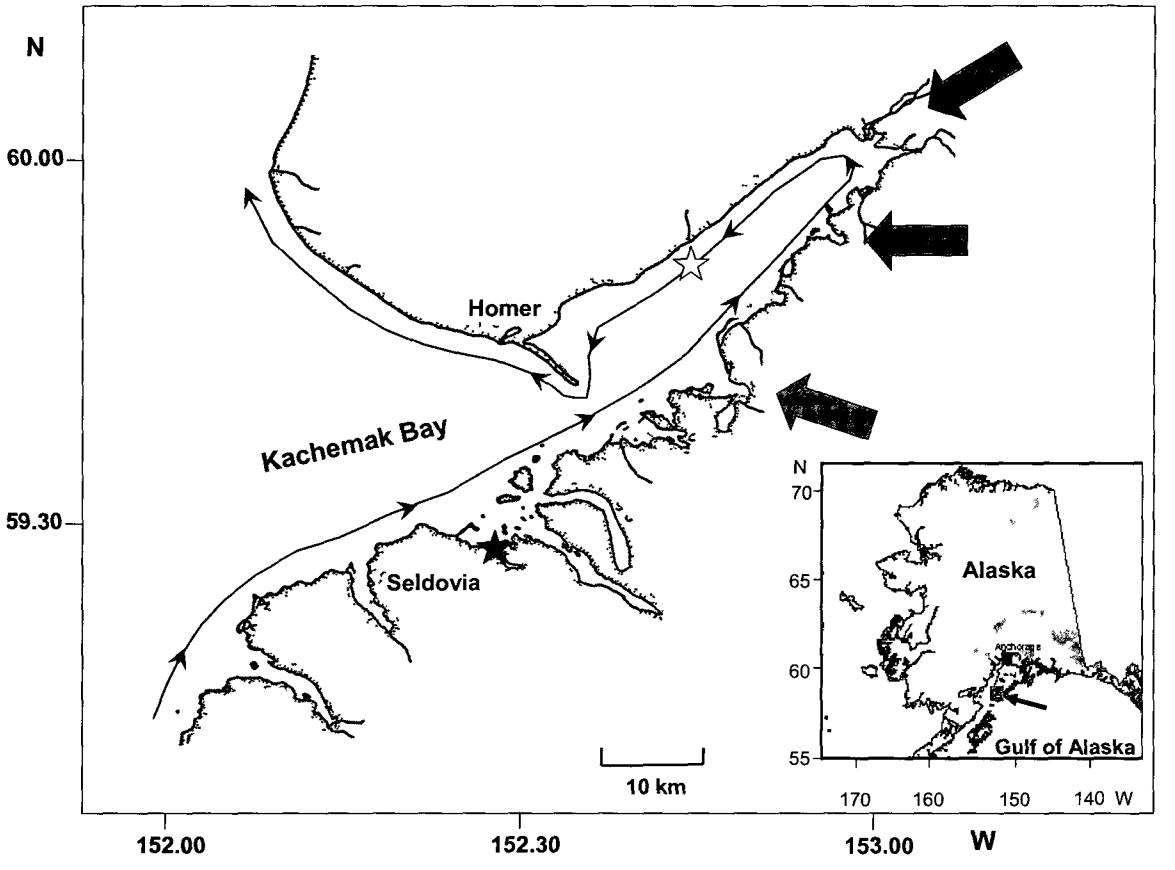
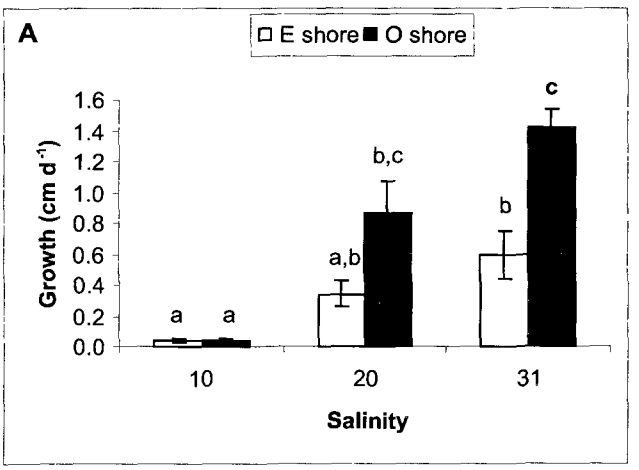
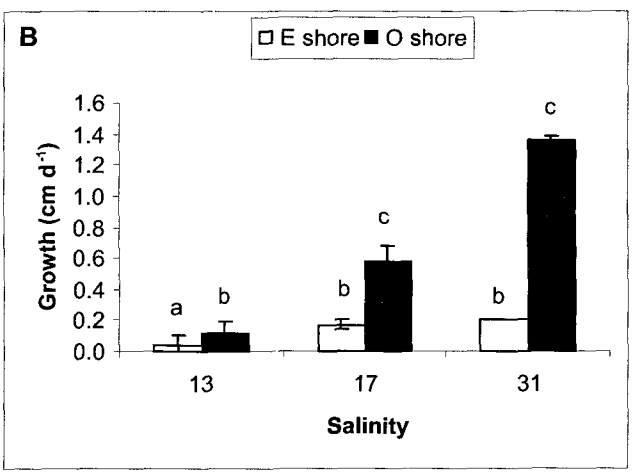
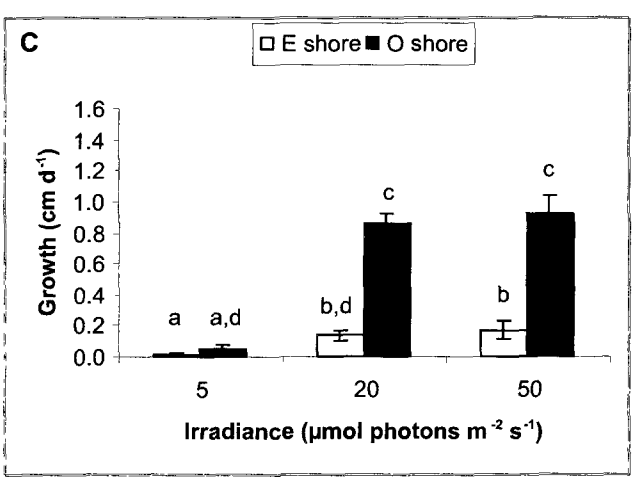
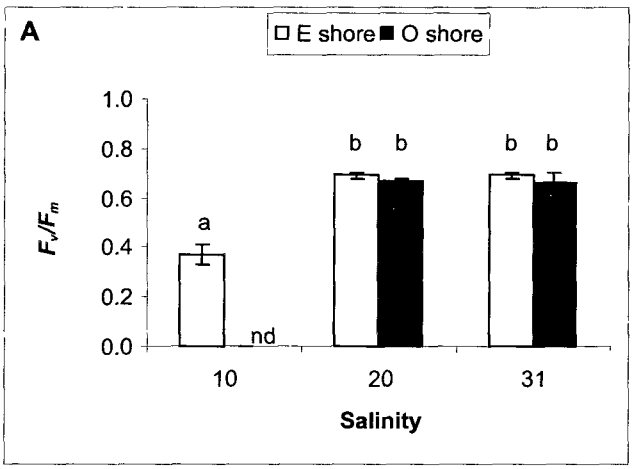


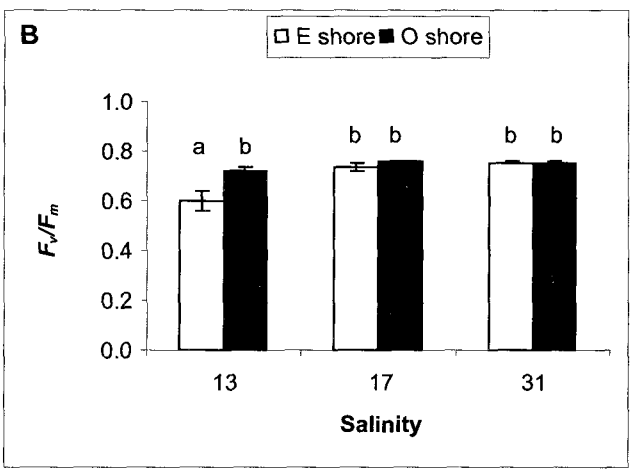
Figure 2.1. *Saccharina latissima*: collection sites at two environmentally distinct shores in Kachemak Bay, Alaska. The site under glacially influenced conditions on the northern shore is marked with a white star (McN-E), and the site under oceanic conditions on the southern shore is marked with a black star (JAK-O). Thin arrows indicate overall water circulation pattern. Thick arrows indicate regions of glacial freshwater and sediment discharge.

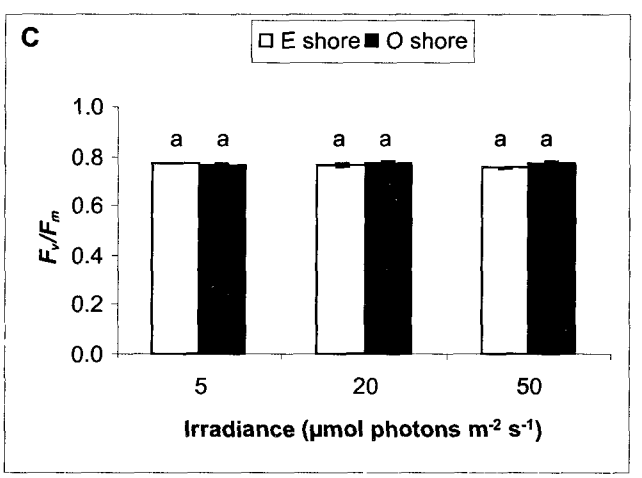

A
E shore
O shore
Growth (cm d-1)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
a
a,b
b,c
b
c
10
20
31
Salinity


B
E shore
O shore
Growth (cm d-1)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
b
b
c
b
c
13
17
31
Salinity


C
E shore
O shore
Growth (cm d-1)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
a,d
b,d
c
b
c
5
20
50
Irradiance (µmol photons m-2 s-1)


A
E shore
O shore
1.0
0.8
0.6
0.4
0.2
0.0
F_v/F_m
a
nd
b b
b b
10
20
31
Salinity


B
E shore
O shore
1.0
0.8
0.6
0.4
0.2
0.0
F_v/F_m
a b
b b
b b
13
17
31
Salinity


C
E shore
O shore
1.0
0.8
0.6
0.4
0.2
0.0
F_v/F_m
a a
a a
a a
5
20
50
Irradiance (µmol photons m^{-2} s^{-1})

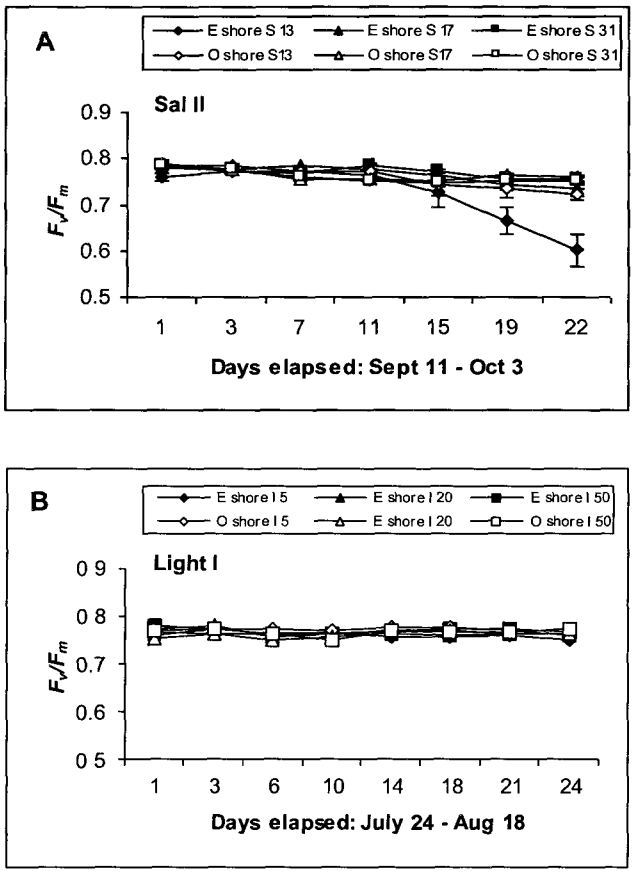


Figure 2.4. *Saccharina latissima*: mean (± SE) interval (3 to 4 days) maximum quantum yield (F_v/F_m) of juveniles at varying experimental salinity and light levels A. Interval F_v/F_m during Sal II treatments (S 13, S 17, S 31), n = 5 or 6 per treatment per shore, over 22 days (September and October 2008) at an irradiance of 50 µmol photons m^{-2} s^{-1}. B. Interval F_v/F_m during Light I treatments (I 5, I 20, I 50 µmol photons m^{-2} s^{-1}), n = 5 or 6 per treatment per shore, over first 21 days of experiment (July and August 2008) at a salinity of 31. E = estuarine northern shore thalli, O = oceanic southern shore thalli.

Table 2.1. Environmental data from the glacially exposed estuarine and the oceanic shores of Kachemak Bay during July/August 2006 (mean ± SE) (for details see Spurkland and Iken 2011).

Shore	Temp (°C)	Light intensity* (µmol photons m^{-2} s^{-1})	Surface salinity	Bottom salinity	NO_3^- (µM)	PO_4^{3-} (µM)	Inorg sedimentation (mg cm^{-2} d^{-1})
Estuarine	9.9±0.1	1.0±0.3	23.6±1.5	28.9±0.6	1.8±0.4	0.4±0.0	4.9±0.9
Oceanic	9.8±0.5	3.2±0.3	32.7±0.9	33.8±0.5	3.3±0.2	0.7±0.1	0.9±0.1

*Continuous light measurements were taken with HOBO light loggers (Onset Computer, Bourne, MA, USA), and light intensity (measured in log lumen m^{-2}) was converted to µmol photons m^{-2} s^{-1} (Thimijan and Heins 1983). In this case, the HOBO logger measurements underrepresent true light availability and can only be considered a comparative measure between shores.

Table 2.2. *Saccharina latissima*: Simple linear regression (including R^2 and significance values) of cumulative linear growth rate (cm d^{-1}) of juveniles under experimental salinity and light treatments (Sal I - over 21 days (late June and July 2008) at an irradiance of 50 µmol photons m^{-2} s^{-1}, Sal II - over 22 days (September and October 2008) at an irradiance of 50 µmol photons m^{-2} s^{-1}, Light I - over 24 days (July and August 2008) at a salinity of 31). Bold values indicate significant regressions. E = estuarine northern shore thalli, O = oceanic southern shore thalli.

Experiment / Shore/Treatment	n	Growth rate (β) (cm d)	Standard error	t	R^2	p
Sal I						
E10	5	0.0344	0.0169	2.03	0.15	0.0539
E20	6	0.3411	0.0695	4.91	0.41	**<0.0001**
E31	6	0.5947	0.1161	5.12	0.44	**<0.0001**
O10	6	0.0332	0.0314	1.05	0.05	0.3040
O20	6	0.9917	0.1391	7.13	0.61	**<0.0001**
O31	5	1.4229	0.0902	15.77	0.90	**<0.0001**
Sal II						
E13	6	0.0332	0.0040	8.21	0.66	**<0.0001**
E17	6	0.1576	0.0341	4.62	0.41	**<0.0001**
E31	6	0.1922	0.0561	3.43	0.28	**0.0018**
O13	5	0.1193	0.0193	6.17	0.58	**<0.0001**
O17	6	0.5718	0.0797	7.17	0.60	**<0.0001**
O31	5	1.3627	0.0626	21.77	0.94	**<0.0001**
Light I						
E 5	6	0.0173	0.0051	3.41	0.22	**0.0015**
E20	5	0.1375	0.0322	4.28	0.36	**0.0002**
E50	6	0.1700	0.0486	4.50	0.23	**0.0012**
O 5	6	0.0537	0.0208	2.59	0.14	**0.0135**
O20	6	0.8574	0.0438	19.58	0.91	**<0.0001**
O50	6	0.9275	0.0809	11.47	0.77	**<0.0001**

Table 2.3. *Saccharina latissima*: repeated measures ANOVA of maximum quantum yield of juveniles to test for effects of salinity or light, shore, time, and all possible interactions. Experiments are Sal II (13, 17, 31 treatments, n = 5 or 6 per treatment per shore, duration = 22 days in September and October 2008, irradiance = 50 µmol photons m^{-2} s^{-1}) and Light I (5, 20, 50 µmol photons m^{-2} s^{-1} treatments, n = 5 or 6 per treatment per shore, duration = 24 days in July and August 2008, salinity = 31). Bold values indicate significant effects.

Experiment	Source	*df*	MS	F	p
Sal II	Salinity	2	2.823	2.498	0.0992
	Shore	1	0.254	0.225	0.6389
	Salinity x Shore	2	4.526	4.014	**0.0285**
	Error:Sample	30	1.130		
	Time	6	15.539	44.560	**<0.0001**
	Salinity x Time	12	1.205	3.456	**<0.0001**
	Shore x Time	6	3.916	11.230	**<0.0001**
	Sal x Shore x Time	12	0.627	1.798	0.0512
	Error: Within	180	0.349		
Light I	Light	2	0.0005	1.316	0.2834
	Shore	1	0.0001	0.195	0.6618
	Light x Shore	2	0.0019	5.196	**0.0115**
	Error:Sample	30	0.0004		
	Time	5	0.0003	2.102	0.0682
	Light x Time	10	0.0003	1.864	0.0544
	Shore x Time	5	0.0005	3.333	**0.0070**
	Light x Shore x Time	10	0.0001	0.579	0.8290
	Error: Within	150	0.0002		

Chapter 3: Seasonal growth patterns of *Saccharina latissima* in a glacially-influenced subarctic estuary[1]

3.1 Abstract

Global climate warming is exacerbating the melting of glaciers in Arctic and subarctic nearshore regions. Glacial discharge causes increases in sedimentation, abrasion of organisms, and sand/silt cover along with lowered light intensity, salinity, nitrate and hard substrate cover. These effects can have deleterious consequences on foundation species, such as the kelps that provide important habitat structure and support tightly-linked food webs. The purpose of this study was to determine if the kelp, *Saccharina latissima*, from a glacially-influenced and an oceanic shore in a subarctic Alaskan estuary exhibits differing seasonal growth patterns in response to its environment. Reciprocal *in situ* shore transplant studies examined seasonal patterns in growth, physiological competence (as maximum quantum yield), morphology and storage product levels (mannitol) of *S. latissima*. *In situ* growth was seasonally different at the two shores, with a shorter growing season at the glacially-influenced shore. During glacial melt season, the thalli on the two shores were morphologically distinct. Mannitol levels were typically higher in thalli from the oceanic shore, with generally low mannitol levels at the end and the initial start of the growing season on both shores. Maximum quantum yield was consistently high ($\geq$0.7) on both shores and did not vary seasonally on the two shores. Growth rates of glacially-influenced transplants to the oceanic shore suggest that the glacially-influenced population has a different seasonal growth pattern from that of the

[1] Prepared for submission to *Phycological Research*

oceanic shore, which seems to be genetically fixed or based on differences in gene expression. It appears that *S. latissima* is a highly resilient species, partly due to high phenotypic plasticity, which may have led to genetic fixation under persistent glacial conditions.

3.2 Introduction

Global climate change has recently accelerated its effects on the physical environments of Arctic and subarctic marine ecosystems (Clarke & Harris 2003, Hinzman et al. 2005, Kerr 2006, Fellman et al. 2010) with further changes predicted for the first half of this century. For example, glaciers have increased their discharge due to substantial thinning in Alaska (e.g. Rabus & Echelmeyer 2002, Motyka et al. 2003, Berthier et al. 2010) at a rate that has doubled over the last 50 years (Arendt et al. 2002). Glacial discharge modifies coastal marine environmental conditions. In a subarctic estuary in Kachemak Bay, Alaska, we found higher inorganic sedimentation, abrasion and soft substrate cover, and lower light intensity, salinity, nitrate and hard substrate cover at a glacially-influenced shore than at an oceanic shore (Spurkland & Iken 2011a). Kelp bed community structure was distinct under these environmentally differing conditions with taxonomic richness and overall organism abundance significantly lower on the glacially-influenced shore. For example, only one kelp species, *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Dreuhl *et* G.W. Saunders, was found on the glacially-influenced shore while five kelp species were found on the oceanic-influenced shore (Spurkland & Iken 2011a). Since kelps are important nearshore foundation

organisms, it is of paramount importance to determine how species typically found in glacially-influenced areas, such as *S. latissima*, will respond to increased glacial melt. The survival of coastal ecosystems depends on the presence of foundation kelps as they are providers of ecosystem goods and services (e.g., Kremen 2005).

Climate change is affecting the distribution and phenology of many organisms, with some species altering their seasonal growth patterns in response to changes in their environment (e.g., Lyon et al. 2008, Rosenzweig et al. 2008). An important question in terms of species responses to environmental change is whether variation in life-history traits between populations is based on acclimation through phenotypic plasticity (no genetic change) and/or through physiological adaptation with the development of genetically distinct ecotypes (Lobban & Harrison 1997, Pigliucci et al. 2006). Phenotypic plasticity is the ability of an organism to express different phenotypes in response to varying environmental conditions (Agrawal 2001). This plasticity is adaptive, as individuals with plastic responses have higher fitness in variable environments than those without (Price et al. 2003). Presumably, under continued environmental pressure, this phenotypic plasticity eventually can lead to genetic fixation of traits (ecotypes) through a process called genetic assimilation (Waddington 1953, 1961, Bradshaw 1965, Schlichting & Smith 2002, Pigliucci et al. 2006). Genetically fixed ecotypes express a trait independent of the environmental stimulus. The adaptive significance of genetic assimilation is related to the decrease in costs of phenotypic plasticity associated with the maintenance or production of the sensory and regulatory machinery (DeWitt et al. 1998, Relyea 2002). Also, once genetic assimilation has occurred, traits can be plastically

expressed within the new genotype with higher accuracy and probability to the specific environmental conditions, thus adding adaptive value to genetic assimilation (Pigliucci et al. 2006). As such, genetic assimilation might be considered pre-adaptive for species to respond to increased environmental variability or extremes such as from climate change.

Both phenotypic plasticity and ecotypic differentiation have been suggested for various brown algal species. The lack of within-species genetic differences over varying temperature regimes in Atlantic *Saccharina* species indicates phenotypic plasticity of individuals rather than the selection of temperature ecotypes (Bolton & Lüning 1982). Similarly, *Macrocystis pyrifera* (L.) C. Agardh displays considerable plasticity in terms of both morphology and productivity in response to the local physical and chemical environment (Brown et al. 1997). Kelp variations in the morphology of *Ecklonia radiata* (C. Agardh) J. Agardh also were due to morphological plasticity rather than genetically fixed traits (Fowler-Walker et al. 2006). In contrast, the kelp *S. longicruris* (Bachelot de la Pylaie) Kuntze exhibits varying seasonal growth patterns in response to differing nitrogen environments in Nova Scotia (Gagné et al. 1982), which are genetically fixed (Espinoza & Chapman 1983). Marine and brackish ecotypes are also well documented for the fucoid, *Fucus vesiculosus* L. in the Atlantic and the Baltic Sea, respectively (Nygård & Dring 2008, Gylle et al. 2009). Various thallus morphologies of the kelp *Eisenia arborea* Areschoug are explained as genetically fixed traits that arose under different nutrient availability and drag force regimes (Roberson & Coyer 2004).

Several studies have reported variations in thallus morphology (e.g., Stuart et al. 1999, Fowler-Walker 2006, Nygård & Dring 2008) and storage product levels (reviewed

by Bartsch et al. 2008) as responses to the environment and to seasonal growth. Because the thallus is the site of photosynthesis, its form (shape, size, thickness) is crucial to growth and carbon balance (Nicotra et al. 2010). Thin sheet-like macroalgae often have higher photosynthetic rates per unit biomass and undergo faster growth than elongate, thick, leathery thalli, but may be less be less sensitive to UV radiation as a result of more protective tissue (Littler et al. 1983, Johansson & Snoeijs 2002). The sugar alcohol mannitol is one of the main primary photosynthetic products, and serves as a storage compound along with the polysaccharide laminaran in brown algae (Bartsch et al. 2008). Strong seasonal changes in mannitol and laminaran have been reported for kelps, with the arctic kelp *Laminaria solidungula* notable for its use of these storage products to jumpstart growth in winter in darkness under the ice (Henley & Dunton 1995, 1997). In order to better understand the physiology of growth and seasonal growth patterns it can hence be informative to examine morphology and storage products levels.

In controlled short-term laboratory experiments we showed that *S. latissima* from both glacially-influenced and oceanic shore environments in a subarctic estuary in Alaska exhibited phenotypic plasticity in their growth responses to some environmental variables (Spurkland & Iken 2011b). There we hypothesized that this growth plasticity may be constrained within different seasonal growth patterns for the populations at both shores. The development of distinct seasonal growth patterns under differing environmental conditions may be adaptive for species in response to increased environmental changes due to climate change. Therefore, the aim of this study was to determine *in situ* seasonal growth patterns and establish evidence whether or not these seasonal patterns are a plastic

response to a variable environment or a genetically fixed trait in the different populations. Specifically we asked (1) Does *S. latissima* exhibit different seasonal growth patterns when living in a glacially-influenced environment or in an oceanic environment? (2) Are reciprocal transplants constrained to their original seasonal growth patterns or can they plastically adjust to changed conditions? and, (3) Are there differences in physiological competence (as maximum quantum yield), morphology and storage product levels (mannitol) in *S. latissima* from these disparate environments in correlation with their seasonal growth patterns? DNA barcoding on individuals from both environments was used to confirm that both populations are indeed the same species.

3.3 Materials and methods

3.3.1 Study sites

This study was conducted in Kachemak Bay, Alaska, which is an inlet on the eastern side of lower Cook Inlet, close to the Gulf of Alaska (Figure 3.1). Cold, nutrient-rich seawater from the Gulf of Alaska flows along the southern shore of the bay making this side oceanic in conditions. Towards the head of the bay the water becomes influenced by glacial input, which then flows along the northern shore back to Cook Inlet making this side glacially-influenced (Burbank 1977). The southern and northern shores in Kachemak Bay experience very different environmental conditions, especially in salinity, light, nutrients and sedimentation, even though the shores are only ca. 10 km apart (Spurkland & Iken 2011a). For the present study, one site at the glacially-influenced shore (G) and one at the oceanic shore (O) were chosen for *in situ* kelp growth studies in

2007 and 2008-2009 (Figure 3.1). Additionally, *S. latissima* were randomly collected from each of the above sites to determine maximum quantum yield of PS II (F_v/F_m), morphology and mannitol content. Environmental variables were monitored at the G and O sites and some additional sites along these shores during summer of 2007, and only at sites G and O during 2008-2009.

3.3.2 Environmental variables

Temperature, light intensity, salinity and nutrients were monitored in conjunction with kelp growth on each shore according to methods described in detail in Spurkland & Iken (2011a). Hourly bottom temperature and light intensity measurements were taken using HOBO data loggers (Onset Computers, Bourne, MA, USA). Surface and bottom salinity (five replicate measurements each) were measured monthly during summer 2007 and 2008 and about bimonthly during fall, winter and spring (September 2008-July 2009). Single replicates of bottom water samples for nutrient analysis were collected at the same intervals as for salinity and filtered (0.45 μm Nalgene® syringe filters) samples were analyzed for nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), and silicate (SiO_4^{2-}) on a Technicon AutoAnalyzer II (SEAL Analytical Inc., Mequon, WI). These environmental variables were chosen because of their relevance to kelp bed and general nearshore ecosystem functioning.

3.3.3 Summer *in situ* growth

We determined summer *in situ* growth of adult *S. latissima* from July 14-August 31, 2007 at the G and O sites, to compare growth on the two shores during the period of maximum glacial melt. We further examined the relationships among summer growth,

maximum quantum yield, morphology, and mannitol content (see below) for thalli from the two shores. Thalli were randomly collected by scuba, brought to the surface, tagged with plastic labels, and marked 10 cm above the stipe/lamina junction for growth determinations with the hole punch method (Parke 1948). Thalli were then attached at their haptera 1 m apart to transect lines on the bottom at ca. 5 m mean lower low water (MLLW) to facilitate re-sampling at low visibility. The distance the hole moved up the lamina was measured *in situ* by scuba at 1-2 week intervals for 5 weeks, and growth was recorded as cm d^{-1}. Every time a plant grew 10 cm or more another hole was punched at 10 cm above the stipe/lamina junction to ensure that there was always a hole present on the thallus for measurement.

3.3.4 Seasonal *in situ* growth and reciprocal transplant experiments

Reciprocal transplant experiments between the two shores were conducted beginning late June 2008 continuing through early July 2009 to investigate possible differences in seasonal growth patterns between the *S. latissima* populations of the glacially-influenced and the oceanic shores. Juvenile thalli (approx. 75 cm length) were collected at 5 m MLLW at both shores by scuba and brought to the surface. Thalli were randomly selected to serve as natural controls, handling controls, and transplants (n = 15 each per shore). All thalli were tagged with plastic labels and a hole was punched 10 cm above the stipe/lamina junction. The natural controls for each shore were then attached 1 m apart along transect lines, which were placed on the bottom (5 m MLLW) at the shore of origin. Thalli that served as handling controls were treated as the natural controls, except that they were placed in a cooler filled with ambient seawater for ~ 4 h to simulate

transport conditions to the opposite shore before they were placed back on the bottom at their original shore. Transplant thalli were treated as above and were transported in coolers filled with ambient seawater to the other shore site, where they were placed on the bottom.

Growth was monitored monthly by scuba from June through September 2008 and about bimonthly during winter and spring (October 2008-July 2009) by bringing thalli to the surface, measuring growth, and returning thalli immediately to the bottom. Lost thalli (~ 3-4 thalli for controls and transplants per shore per monitoring event) were replaced to maintain approximately the same number of thalli for growth measurements each month. High thallus losses occurred in September 2008 at both shores due to gastropod grazing, inclement weather and other unknown factors, and a new experiment was set up. For this new experiment, 12 juvenile thalli were transplanted between shores, and 12 thalli were placed at their site of origin to serve as controls. The G site transects were lost between January and March 2009 due to ice movement and new transplants were placed there in late May.

Due to the loss of transects at the G site in winter, growth at this shore was instead determined from randomly collected thalli, which provided the only growth measure for this time period (November – March) at the glacially-influenced shore. For these randomly collected thalli, thin new growth tissue at the basal meristem was easily distinguished from the previous season's leathery growth that was still attached at the tip of the thallus. The distance from the stipe/lamina junction to the old, leathery tissue reflected new growth. This new growth was not observed in mid-November 2008; hence,

to be conservative, all growth was assumed to have started after the November monitoring, although it may have occurred later. A total of 30 *S. latissima* thalli were measured for this new growth in mid-March 2009 at the G site.

3.3.5 Maximum quantum yield

Pulse-amplitude modulated (PAM) fluorometry was conducted to determine maximum quantum yield (F_v/F_m) of the *S. latissima* thalli at the termination of the summer *in situ* growth monitoring (August 26-31, 2007). In addition, maximum quantum yield was determined on adult thalli (n = 6 per sampling event) that were randomly collected every 1 to 3 months during 2008-2009 from both shore sites (herein, referred to as "temporal samples") to complement the seasonal *in situ* growth experiment. Thalli were brought to the surface and were kept in ambient seawater for no longer than 1 h in coolers covered with neutral grey density screens to maintain *in situ* bottom light conditions until measurements were made. F_v/F_m was measured at midday on dark-adapted tissues (15 min, Dring et al. 1996) at 20 cm above the stipe/lamina junction using an OS-30p PAM fluorometer (OptiScience Corp., Tyngsboro, MA, USA). Three replicate measurements were taken across each lamina.

3.3.6 Thallus morphology

Morphological measurements were taken following PAM fluorometry on all thalli. Lamina width and thickness at 10 cm above the stipe/lamina junction, and stipe length and maximum diameter were measured. A 30 cm^2 sample was removed from the center of the lamina 10 cm above the stipe/lamina junction for the determination of

relative dry mass (DM) after 72 h at 60 °C. Total thallus length was only determined for the 2008/2009 temporal samples.

3.3.7 Mannitol content

Mannitol content of *S. latissima* was based on the rapid oxidation of sugar alcohols by periodic acid (Cameron et al. 1948, Larsen 1978). The amount of periodic acid used was determined by titration with 0.1 N sodium thiosulfate after the addition of potassium iodide and sulfuric acid and comparison with a blank. It is important for the amount of excess periodic acid in the reaction mixture to be similar for all mannitol determinations in order to arrive at comparable results. Therefore, the sample amount necessary to obtain a consumption of periodic acid corresponding to 6.5-8.5 ml of 0.1 N sodium thiosulfate was determined. Dried tissue samples from relative DM determinations (see above) were kept frozen until processing. Samples were milled and passed through a 250 μm mesh. Triplicate mannitol measurements per individual were done for samples where sufficient material was available, and are reported as mean percent mannitol.

Mannitol content was determined for the thalli at the end of the summer growth experiment in August 2007 on both shores and also for additional thalli collected mid-June 2007 (n = 22 for G, n = 33 for O). The 2008-2009 temporal thalli were used to analyze seasonal patterns of mannitol content. Where DM of samples was low (e.g., oceanic shore thalli in June 2007 and samples from both shores in winter and late spring 2009), equal aliquots of two individuals were pooled for each mannitol determination.

3.3.8 Statistical analysis

All data were tested for normality using the Shapiro-Wilk normality test and for homogeneity of variances using the Fligner-Killeen test; nitrate data were log-transformed to meet these requirements. Repeated measures analysis of variance was conducted to examine the between group effect (shore), as well as the within subject effect (time) on fourth-root transformed summer 2007 *in situ* growth rates. Multiple comparisons of growth at both shores for all summer 2007 monitoring intervals were made with Student's t-tests (parametric data) or Wilcoxon Rank Sum Tests (WRS; non-parametric data; Bonferroni corrected p-value for $\alpha = 0.05$ significance was $p<0.005$). Since there were no significant differences for either shore between the natural and the handling controls of the seasonal reciprocal transplant experiment, the two control types were combined by shore for all analyses and are henceforth referred to as indigenous thalli. Reciprocal transplant experimental data were analyzed with Student's t-tests or WRS (Bonferroni corrected p-value for $\alpha = 0.05$ significance was $p<0.0002$) to compare the growth rates between indigenous thalli of opposite shores, between indigenous thalli and their respective transplants, and between indigenous thalli and transplants from the opposite shore over time. Analysis of variance tests (two-way ANOVA) along with Tukey HSD paired multiple comparisons were used to test for significant differences between shores and among months in terms of *Fv/Fm*, morphology, and mannitol levels. Spearman's rank correlations were conducted to determine relationships between growth rate and each of the following: thallus width, DM, and mannitol. All data analyses were

conducted using R 2.12.2 software (R Foundation for Statistical Computing, Vienna, Austria). Significance for all analyses was set at $\alpha = 0.05$.

3.3.9 DNA barcoding of *Saccharina latissima* COI-5P

DNA barcoding, using the 5'end of the cytochrome c oxidase I gene (COI-5P) from the mitochondrial genome, was done with 20 *S. latissima* specimens (5 juveniles and 5 adults from each shore) to confirm that individuals were of the same species despite the observed morphological differences. Thalli were randomly collected from ~5 m MLLW at both shores, dried in silica gel and kept at room temperature until DNA extraction. Dried samples (~ 40 mg) were ground with a mortar and pestle under liquid nitrogen, and were stored at -20°C until further use. DNA extraction was carried out with slightly modified methods described in McDevit & Saunders (2009). A ~ 20 mg aliquot of each ground sample was suspended and stirred in 1 ml of 100% acetone at room temperature to remove PCR-inhibiting compounds. Samples were centrifuged at 13 000 *g* for one minute, and the supernatant discarded. The acetone wash was repeated four times and remaining samples were air-dried for 10 min. Samples were rinsed 4-5 times with a buffer wash (Saunders 1993, Saunders & Kraft 1995). Digestion was done at room temperature for 1 h with the addition of 600 µl DNA extraction buffer, 60 µl 10% Tween-20, and 6 µl Proteinase K (50 mg ml^{-1}) (Saunders 1993, Saunders & Kraft 1995) to each sample. The DNA extract of the aqueous layer was cleaned using the GenElute™ Plant Genome DNA Miniprep Kit (Sigma-Aldrich, Inc., Saint Louis, MI, USA) following the manufacturer's protocol with a final elution volume of 50 µl.

Polymerase Chain Reaction (PCR) amplification of COI-5P (700 bp) was done using previously published primer combinations GAZF2/GAZR2 (Lane et al. 2007) and T7GAZF2/T3GAZR2. All PCR reactions were conducted in a GeneAmp® System 2400 Thermal Cycler (Perkin-Elmer, Norwalk, CT, USA). The thermal profile was as follows: an initial denaturation at 94 °C for 4 min followed by 35 cycles at 94 °C for 30 sec, 50 °C for 30 sec, and 72 °C for 1 min, with a final extension at 72 °C for 8 min, and storage at 4 °C. Unused primers and nucleotides were removed by using an ExoSAP-IT Kit (USB, Cleveland, OK, USA).

Products were sequenced at Northwoods DNA, Inc. (Bemidji, MN, USA) and analyzed using an Applied Biosystems 330XL automated sequencer. Forward sequence reads were edited to produce contigs (continuous sequences) in Sequencher 4.5 (Gene Codes Corporation, Ann Arbor, MI, USA). Multiple sequence alignments were generated in MEGA version 5 (Tamura et al. 2011) using the Clustal W algorithm. Estimates of average evolutionary divergence between sequences for each shore and between shores were conducted using the Maximum Composite Likelihood Model (MEGA 5, Tamura et al. 2011).

3.4 Results

3.4.1 Environmental variables

Environmental variables on the two shores differed during the summer 2007 glacial melt period with the exception of temperature. Bottom temperatures were similar between the two shores (WRS, $p>0.1$, Figure 3.2A) from June through August 2007. In

2008-2009, temperature data were only available for the oceanic shore, and 2007 temperatures did not differ significantly from 2008 temperatures on the oceanic shore (WRS, $p>0.1$). Surface and bottom salinities in 2007 were also lower on the glacially-influenced than on the oceanic shore (Student's t-test, $p<0.005$ (surface), WRS, $p<0.01$ (bottom), Figure 3.2B). The trend was similar for the glacial melt period (June – August) of 2008 (WRS, $p<0.01$ (surface), $p<0.05$ (bottom)). In contrast, there were not significant differences in surface and bottom salinity from mid-November 2008 through mid-March 2009 between the two shores (Student's t-test, $p>0.6$ (surface), $p>0.9$ (bottom)). Light intensity was lower on the glacially-influenced shore than on the oceanic shore (WRS, $p<0.0001$, Figure 3.2C) during the glacial melt period of June through August 2007. Light intensity over 230 days in 2008-09 was also significantly lower at the glacially-influenced than the oceanic shore (WRS, $p<0.0001$).

The nutrient regimes on the two shores of Kachemak Bay were not significantly different from June 2008 through January 2009 for nitrate, ammonia, phosphate, and silicate (Student's t-tests, $p>0.5$, $p>0.3$, $p>0.8$, $p>0.9$, respectively, see Figure 3.2D for nitrate). For both shores, nitrate was lowest in June 2008 and followed by increased levels in November 2008 and January 2009. Overall environmental variable patterns between glacially-influenced and oceanic shores were confirmed to those detailed in Spurkland & Iken (2011a).

3.4.2 Summer *in situ* growth, 2007

In situ growth rate differed significantly between the two sites (Table 3.1, Figure 3.3) with low values on the glacially-influenced shore (mean = 0.04 ± 0.01, $n = 11$), and

significantly higher but also highly variable results on the oceanic shore (mean = 0.33 ± 0.04, n = 32). Shore had a significant effect (between-subjects) on growth rate, as did time (within-subjects effect), with growth rate decreasing over time on both shores (repeated measures ANOVA, Table 3.1). Growth slowed more abruptly on the glacially-influenced shore than on the oceanic one, and completely stopped at the glacially-influenced shore at the beginning of August.

3.4.3 Seasonal *in situ* growth and reciprocal transplant experiments, 2008-2009

Growth of indigenous thalli on the glacially-influenced shore was negligible from July 2008 through January 2009, while indigenous growth on the oceanic shore slowed from ~0.6 cm d^{-1} in July 2008 to nearly zero in November and then increased to about 2 cm d^{-1} in May 2009 (Figure 3.4A). Growth of oceanic indigenous thalli was significantly higher than of indigenous glacially-influenced thalli in late June and August 2008 (Table 3.3). Growth of indigenous and transplant glacially-influenced thalli were both negligible and did not differ significantly for July 2008 through January 2009 (Table 3.3, Figure 3.4B, C). Similarly, growth patterns in indigenous and transplant oceanic thalli were similar, with no significant differences (Table 3.3), although growth of oceanic transplants at the end of the experimental phase in July 2009 was only about half than in indigenous thalli (Table 3.3, Figure 3.4B,C). Hence, transplant thalli conserved the overall growth patterns found on their indigenous shores although some adjustment (reduced growth in oceanic transplants) to local conditions (glacial influence) may be discernable.

No data on indigenous growth at the glacially-influenced shore transects were available after January 2009 due to loss of transects. However, some inferences can be made from randomly collected *S. latissima* in March 2009, where thin basal meristem tissue indicated new growth since mid-November. New growth for November – March ranged from 65-184 cm (mean 1.03 ± 0.04 cm d^{-1}) on the glacially-influenced shore (see asterisk in Figure 3.4A, B).

3.4.4 Maximum quantum yield

Maximum quantum yield (F_v/F_m) values were high (≥0.7) in thalli on both shores throughout this study (Table 2). There was no difference in F_v/F_m (WRS, $p>0.08$) between the thalli from the two shores. The interaction between the factors shore and month was significant (two-way ANOVA, $p<0.005$), but F_v/F_m was only significantly different between the two shores in late July 2008 with higher yields on the oceanic than the glacially-influenced shore (Table 3.2).

3.4.5 Thallus morphology

Thallus width of *S. latissima* from *in situ* growth experiments in late August 2007 was significantly narrower (9.7 ± 0.5 cm; Student's t-test, $p<0.0001$) on the glacially-influenced shore than the oceanic shore (31.5 ± 2.0 cm) (Figure 3.5A, B). There was a positive correlation between growth rate (mid-July - August) and thallus width (both shores) determined in late August 2007 (Spearman's rank correlation, $\rho_s = 0.65$, $p<0.0001$). Thallus thickness did not vary between the two shores (Student's t-test, $p>0.7$, 1.3 ± 0.04 mm on both shores), but relative DM was higher in glacially-influenced thalli (0.47 ± 0.02 mg mm^{-2}) than in oceanic shore thalli (0.30 ± 0.01 mg mm^{-2}) (Student's t-

test, $p<0.0001$). Relative DM, determined in late August, was negatively correlated with growth rate (mid-July – August, both shores; Spearman's rank correlation, $\rho_s = -0.67$, $p<0.0001$). Stipe length of *S. latissima* from the glacially-influenced shore was significantly longer (7.1 ± 0.5 cm) than from the oceanic shore (4.2 ± 0.2 cm, Student's t-test, $p<0.0001$). The shorter stipes of the oceanic shore thalli had significantly greater mean diameters (5.4 ± 0.1 cm) than the longer stipes of the glacially-influenced shore thalli (4.9 ± 0.1 cm, Student's t-test, $p<0.006$). Overall, glacially-influenced thalli were narrower and more leathery (higher relative DM) with less distinctly frilled margins than thalli of the oceanic shore.

Thallus morphology of randomly collected temporal samples over the course of a year (June 2008 - July 2009) mostly followed the same trends as observed for the 2007 thalli (see above; Table 3.2). Both shore and month were significant factors affecting all morphometric measures (two-way ANOVA, $p<0.05$ for the shore x month interaction for all measurements). Oceanic thalli were generally nearly twice as wide as glacially-influenced thalli (Table 3.2). Glacially-influenced laminae were typically thicker and heavier (relative DM) compared to oceanic laminae although differences were only significant for some sampling periods. Relative DM on both shores was generally low from mid-January to mid May 2009, coinciding with the period of rapid growth. Stipe morphometrics were typically not significantly different for thalli of the two shores, although stipes of glacially-influenced thalli were significantly longer than the oceanic stipes on some sampling dates (Table 3.2). Total thallus length was typically longer in

glacially-influenced thalli, but this difference was mostly not significant because of high variability on both shores.

3.4.6 Mannitol content, 2007 and 2008-2009

Mannitol content in mid-June 2007 of glacially-influenced thalli (21.4 ± 2.74%, n = 10) was significantly higher (Tukey HSD, $p<0.0001$) than in oceanic thalli (10.1 ± 0.53%, n = 4 from pooled samples) (Figure 3.6A). In contrast, mannitol content in late August 2007 was significantly higher (Tukey HSD, $p<0.0001$, 12.9 ± 3.43%, n = 29) in oceanic compared to glacially-influenced thalli (5.0 ± 0.59%, n = 11). This reversal was mainly due to a significant decrease in mannitol in glacially-influenced thalli (Tukey HSD, $p<0.0001$), while mannitol in oceanic thalli did not change between the two sampling periods (Tukey HSD, $p>0.2$, Figure 3.6A). The shore x month interaction was also significant (two-way ANOVA, $p<0.0001$). Mannitol content determined in August 2007 was positively correlated with the mid-July through August growth (combined both shores; Spearman's rank correlation, $\rho_s = 0.78$, $p<0.0001$).

Mannitol levels from temporal samples during 2008-2009 were typically higher in oceanic thalli compared to glacially-influenced thalli, although differences were only significant in August and September (two-way ANOVA, Tukey HSD, $p<0.03$ and $p<0.0006$, respectively, Figure 3.6B). Mannitol levels were lowest during the winter (during low growth at both shores) in thalli from both shores (March, 3.18 ± 0.32% for glacially-influenced thalli, 4.00 ± 0.03% for oceanic thalli), and reached their peak on the glacially-influenced shore during late May (17.41 ± 1.03%) and on the oceanic shore in September (17.35 ± 0.03%). The interaction between shore and month was significant

(two-way ANOVA, $p<0.0001$). Mannitol content over the course of a year did not directly correlate with growth rate (Spearman's rank correlation, $\rho_s = 0.23$, $p>0.4$).

3.4.7 DNA barcoding of *Saccharina latissima* COI-5P

DNA barcoding of the 5'end of the COI of the *S. latissima* genome confirmed that the individuals of both shores belong to the same species. A 645 base-pair COI-5P sequence from glacially-influenced and oceanic thalli of Kachemak Bay was compared with 82 previously published *S. latissima* records (McDevit & Saunders 2010) from Europe and the Canadian Atlantic and Pacific; populations of Kachemak Bay were 99-99.9% similar to *S. latissima* from these published collections. The two Kachemak Bay populations (glacially-influenced and oceanic) were 99.97% similar to each other, with population-level variation at different base positions compared to previous *S. latissima* isolates in GenBank. Some ambiguities within both populations seem to be shared, likely contributing to the high similarity between the two populations. This suggests some genetic mixing occurs between the populations in our study area.

3.5 Discussion

In situ growth of *S. latissima* on the glacially-influenced and oceanic shores of Kachemak Bay differed over the course of a year, supporting the notion of differing seasonal growth patterns on the two shores. Further, reciprocal transplant thalli mostly maintained the seasonal growth patterns typical for their indigenous environment. Thus, while we confirmed that the *S. latissima* populations of the two shores are from the same species, individuals did not adjust their overall growth pattern to changed environmental

settings over the course of a year and they displayed distinct seasonal growth patterns that may be genetically fixed. Thallus width, relative DM and mannitol levels correlated with growth during some time periods. Seasonal modification of growth may be a way in which species may adapt to prevailing environmental conditions such as glacial discharge.

Kelp of the same species living under varying environmental conditions can exhibit different seasonal growth patterns, which are often attributed to ambient nitrogen availability (e.g. Lüning 1979, Gagné et al. 1982, Espinoza & Chapman 1983, Brown et al. 1997). For example, different seasonal growth patterns in *S. longicruris* occur in Nova Scotia, Canada, under contrasting nutrient regimes (Gagné et al. 1982). Under nitrogen-replete conditions, growth follows the seasonal light pattern, while under nitrogen-depleted conditions growth is limited to winter and early summer. The seasonal growth patterns of two populations of *S. longicruris* in Shag Bay, Nova Scotia differed locally, with a shorter growth season at an exposed site compared to a sheltered site (Mann 1972, Chapman & Craigie 1977, Gerard & Mann 1979). The differences at Shag Bay could not be clearly related to nitrogen availability, but it was suggested that morphological differences between the populations may be affecting differential nitrogen uptake. These results are comparable to what we observed at the glacially-influenced and oceanic sites in Kachemak Bay. While nitrogen availability did not differ between the two shores in Kachemak Bay, the significantly different morphologies of the two *S. latissima* populations might influence their ability to uptake nitrogen, thus supporting distinct seasonal growth patterns.

Algal thallus morphology is influenced by the rate of growth and environmental conditions. The shape of the bases of the laminae of *S. latissima* of both Canadian and British thalli appear to be a function of the rate of growth, with cuneate bases typical of slow growing thalli, and cordate ones typical of fast-growing thalli (Burrows 1964). Rates of transverse growth are less for narrow, strap-like thalli, than those of wide undulate thalli (Koehl et al. 2008). Thalli living in high flow environments develop a more streamlined shape than those in more sheltered environments (Gerard 1987, Fowler-Walker et al. 2006, Koehl et al. 2008). Both shores of Kachemak Bay are dynamic environments due to tidal currents, but there is higher abrasion of clod cards on the glacially-influenced shore (Spurkland and Iken 2011a). The often corrugated frill of fast-growing thalli can enhance surface turbulence and increase the rate of nutrient uptake (Neushul 1972, Hurd et al. 1996). In our study, the broad, thin (low DM), and distinctly frilled oceanic thalli may provide greater surface area to scavenge enough dissolved nitrogen to sustain longer seasonal growth (Figure 3.5B). In contrast, the narrower and more leathery (higher DM) thalli on the glacially-influenced shore in Kachemak Bay may be limited in their growth pattern by insufficient nutrient uptake (Figure 3.5A). Increased surface area likely also provides more photosynthetic area (King & Schramm 1976) and carbon reserves (Chapman & Craigie 1978), resulting in higher growth rates. Hence, the distinct seasonal growth rates of *S. latissima* on the two shores in Kachemak Bay may be related to different nitrogen acquisition due to their morphology at similar ambient nitrogen levels.

Based on laboratory manipulations of reduced salinity and irradiance on growth of juvenile *S. latissima* growth, we have previously suggested that the two populations in Kachemak Bay may represent two plastic phenotypes (Spurkland & Iken 2011b). In that study we proposed that the two populations are able to adjust their growth to changes in their physical environment, but that this ability may be seasonally constrained. The results of our reciprocal transplant experiment in the present study showed that at least the glacially-influenced thalli transplanted to the oceanic shore maintained the overall seasonal growth patterns typical for their original shore (for July through March as indigenous glacially-influenced patterns are not known after March, Figure 3.4B, C). These transplants did not change to patterns typical for the oceanic shore. Even though they were transplanted to a better growing environment (e.g., more light, higher salinity), they arrested their growth in late May, while the indigenous oceanic thalli continued to grow at a maximum rate. Oceanic thalli transplanted to the glacially-influenced shore also maintained their original pattern at least for July through January. Since experimental thalli on the glacially-influenced shore were lost in January, we cannot conclude for the remaining growing season. However, growth of oceanic transplants at the glacially-influenced shore in early July was lower than in indigenous thalli at the oceanic shore, indicating that some phenotypic adjustment to glacial conditions may have occurred. This lends support to our hypothesis that overall seasonal growth patterns are genetically fixed while plastic adjustments are possible within these seasonal patterns, but our results are insufficient to provide unequivocal evidence. Another possibility to take into consideration is that there may be differences in gene expression occurring in

relation to seasonal growth (Nicotra et al. 2010). Growth plasticity within fixed seasonal growth pattern may provide an advantage to *S. latissima* in environments that are prone to high variability, such as seasonal glacial discharge, which may be enhanced by climate change.

Seasonal growth patterns of the two *S. latissima* populations in Kachemak Bay correlated not strongly but somewhat with their respective storage product levels. Mannitol is a major product of photosynthesis, and changes in mannitol levels suggest variations in photosynthetic activities (Bidwell 1967). Mannitol levels decrease with decreasing photosynthetic activity due to water depth and lower light availability (Lüning 1979, Dominik & Zimmerman 2006), which may explain the lower mannitol levels in our glacially-influenced than oceanic thalli during turbid glacial melt conditions. Mannitol also is a storage carbon reserve that can be used by some kelps to jumpstart growth in late winter (Iwao et al. 2008). For example, the Arctic *Laminaria solidungula* J. Agardh depends on carbon stores produced during the summer to initiate growth in winter when nutrient conditions are good (Dunton & Schell 1986, Henley & Dunton 1995, 1997). In contrast, Arctic *S. latissima* with a short growing season between late April and late July does not depend on stored carbon reserves for winter and spring growth but meets growth demands through photosynthesis (Dunton 1985). Similarly, in our study, late fall and winter mannitol levels were low in thalli from both shores, indicating that few carbon reserves were available for new growth. Overall, mannitol levels in thalli from both shores were positively correlated with growth during the glacial melt period and our results indicate that they are synthesized and accumulated during growth in spring and

summer, and are utilized for maintenance but less for growth during the fall and early winter. The overall lower mannitol levels in glacially-influenced compared to oceanic thalli may mirror the overall lower growth and shorter seasonal growth patterns in the glacially-influenced population. Consistently high F_v/F_m values in thalli of both shores throughout the year indicate that they are physiologically healthy even under reduced growth, and photosynthesis may compensate for energy needs during growth onset. A direct correlation between mannitol concentrations and growth, however, may be skewed by the fact that mannitol can be translocated in kelps at velocities of <10 cm h^{-1} (Schmitz & Lobban 1976, Bartsch et al. 2008), which might not have been detected in our localized measurements. Mannitol also is an important organic osmolyte that serves as a compatible cytoplasmic solute with an enzyme protective function (Kirst 1990, Rousvoal et al. 2011). Under hypo-osmotic stress the mannitol pool may vary due to transformation into reserve products, reduction due to use in enzyme inhibition, degradation, or release into the medium (Kirst 1990). Particularly the glacially-influenced thalli in our study experience reduced salinities during glacial discharge, which may affect their mannitol levels independent of growth patterns, but which may contribute to the observed differences between the two *S. latissima* populations in Kachemak Bay.

Our results support the idea of phenotypic growth plasticity constrained within distinct and likely genetically fixed seasonal growth patterns in the two *S. latissima* populations at environmentally different shores of Kachemak Bay. Phenotypic plasticity expands the ecological range of a species, thereby exposing it to new selective pressures, allowing for genetic assimilation when exposed for sufficient time periods (Pigliucci et

al. 2006, Nicotra et al. 2010). Once genetic assimilation occurs, environmental cues are no longer required for the expression of the new trait. In Kachemak Bay, glacial influence has existed for about 15,000 y (Field & Walker 2003), suggesting that this may have presented a sufficiently long selective pressure for seasonal growth patterns in *S. latissima* to become genetically fixed. Some level of phenotypic plasticity can be maintained in this genetically fixed seasonal pattern and may provide *S. latissima* the opportunity to plastically respond to environmental changes on much shorter time frames. In the short-term, organisms' ability to incorporate phenotypic plasticity will be of utmost importance in determining their persistence under changed climatic conditions (Nicotra et al. 2010). The genetic fixation of growth patterns to the glacial conditions may allow the glacially-influenced *S. latissima* population to exhibit growth plasticity to a more specific subset of environmental variability such as from increased glacial melt due to climate warming. Although this plasticity and adaptability make *S. latissima* a particularly resilient species in the face of environmental change, it has recently been identified as a possible sentinel species (Merzouk & Johnson 2011). Already changes in local abundance of *S. latissima* along European coastlines are occurring, which may be associated with temperature changes (e.g. Pehlke & Bartsch 2008, Moy et al. 2008, Müller et al. 2010, Ottensen 2010).

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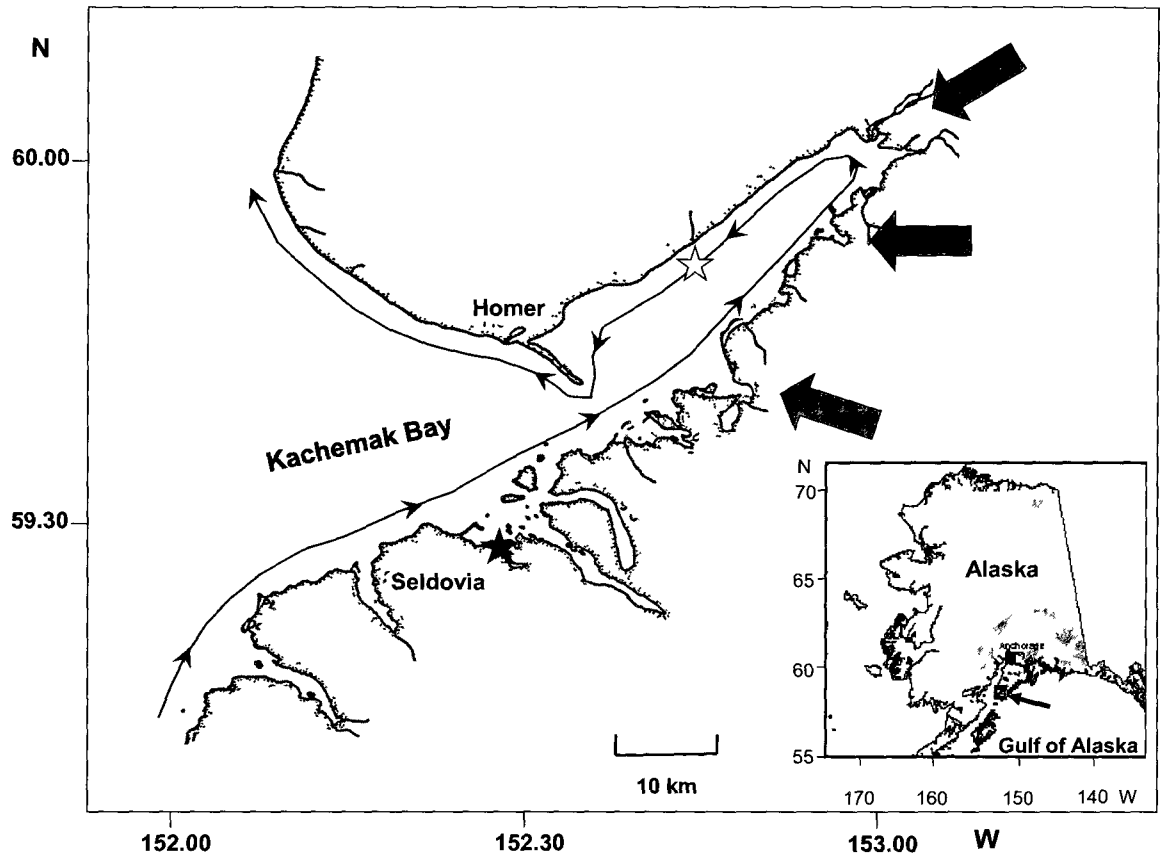
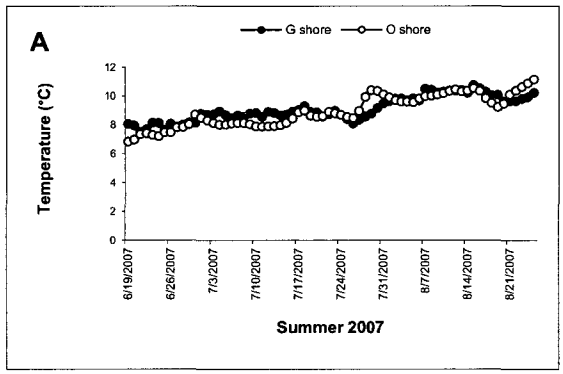
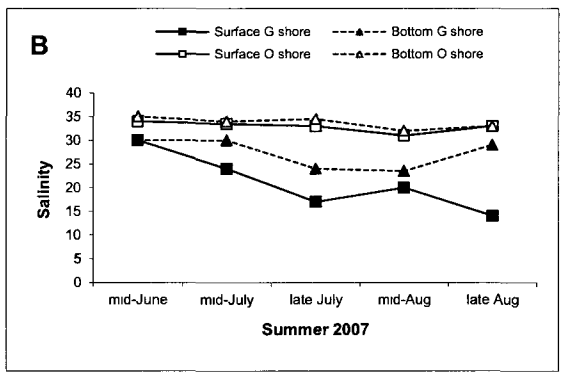
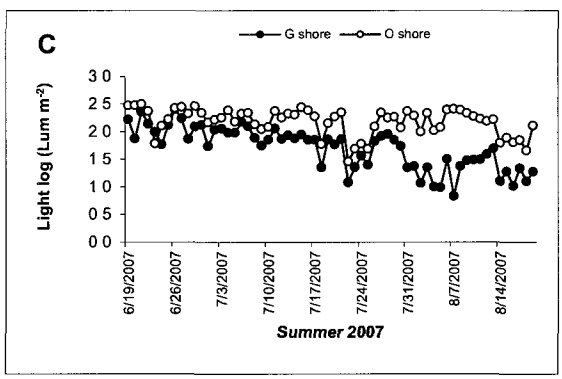
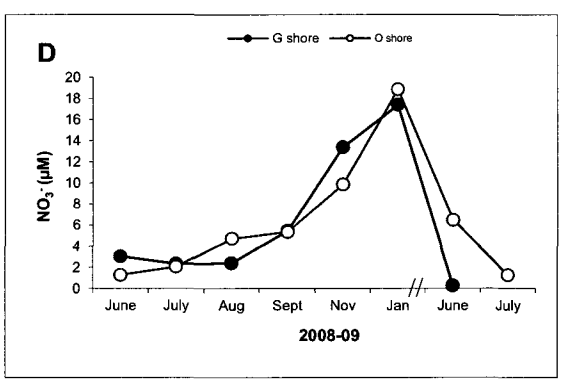


Figure 3.1. *Saccharina latissima*: collection and study sites at two environmentally distinct shores in Kachemak Bay, Alaska. The site under glacially-influenced conditions (G) on the northern shore is marked with a white star, and the site under oceanic conditions (O) on the southern shore is marked with a black star. Thin arrows indicate overall water circulation patterns. Thick arrows indicate regions of glacial freshwater and sediment discharge.


A
G shore
O shore
Temperature (°C)
12
10
8
6
4
2
0
6/19/2007
6/26/2007
7/3/2007
7/10/2007
7/17/2007
7/24/2007
7/31/2007
8/7/2007
8/14/2007
8/21/2007
Summer 2007


B
Surface G shore
Bottom G shore
Surface O shore
Bottom O shore
Salinity
40
35
30
25
20
15
10
5
0
mid-June
mid-July
late July
mid-Aug
late Aug
Summer 2007


C
G shore
O shore
Light log (Lum m-2)
30
25
20
15
10
05
00
6/19/2007
6/26/2007
7/3/2007
7/10/2007
7/17/2007
7/24/2007
7/31/2007
8/7/2007
8/14/2007
Summer 2007


D
G shore
O shore
NO3- (µM)
20
18
16
14
12
10
8
6
4
2
0
June
July
Aug
Sept
Nov
Jan
June
July
2008-09

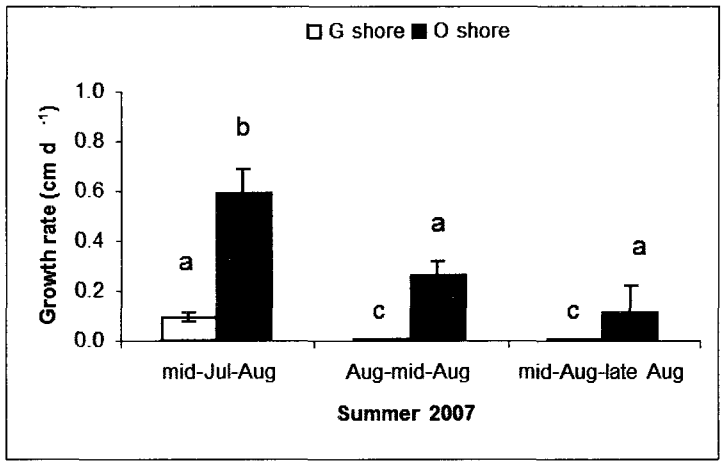
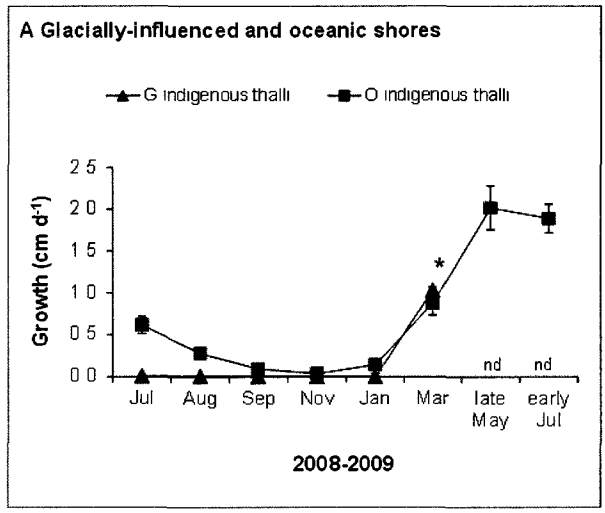
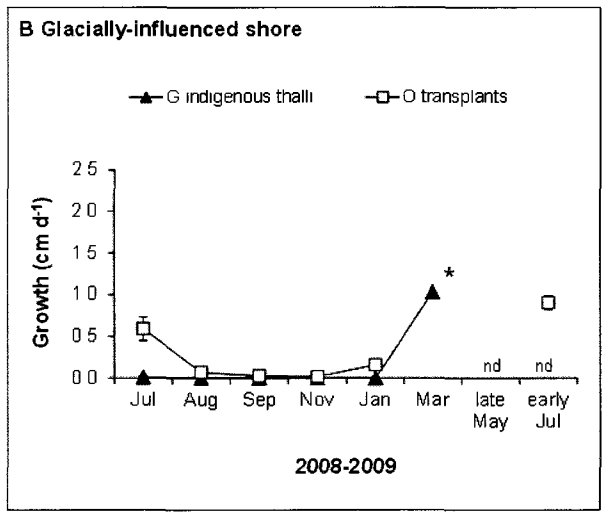
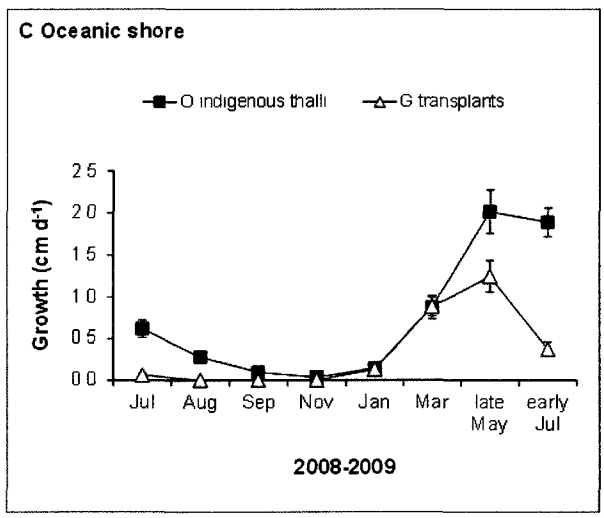


Figure 3.3. *Saccharina latissima*: mean (± SE) overall *in situ* growth rate (cm d^{-1}) of thalli on the glacially-influenced (G) and oceanic (O) shores of Kachemak Bay from mid-July through August 2007. Different letters above bars indicate significant differences (Student's t-test, Bonferroni adjusted p-value = 0.0033).


A Glacially-influenced and oceanic shores
G indigenous thalli
O indigenous thalli
Growth (cm d-1)
2.5
2.0
1.5
1.0
0.5
0.0
*
nd
nd
Jul
Aug
Sep
Nov
Jan
Mar
late May
early Jul
2008-2009


B Glacially-influenced shore
G indigenous thalli
O transplants
Growth (cm d-1)
2.5
2.0
1.5
1.0
0.5
0.0
*
nd
nd
Jul
Aug
Sep
Nov
Jan
Mar
late May
early Jul
2008-2009


C Oceanic shore
O indigenous thalli
G transplants
Growth (cm d-1)
2.5
2.0
1.5
1.0
0.5
0.0
Jul
Aug
Sep
Nov
Jan
Mar
late May
early Jul
2008-2009

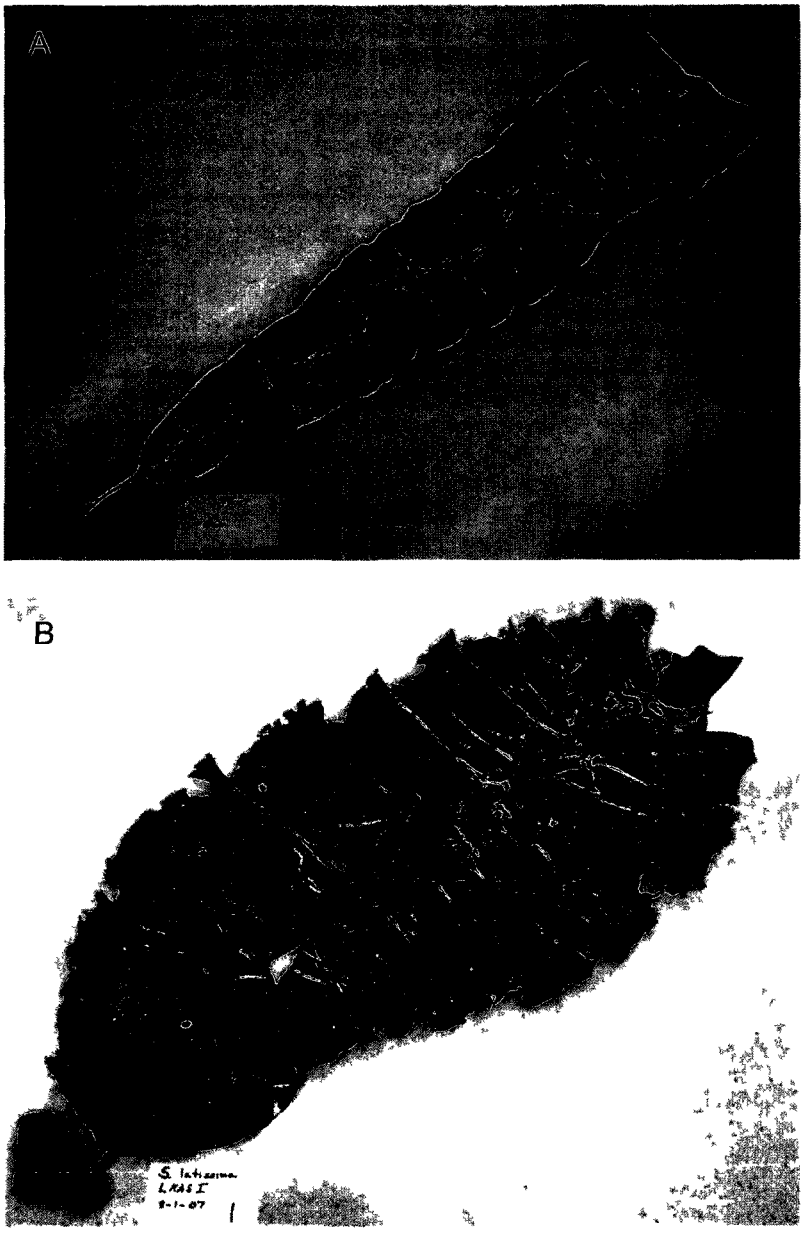


Figure 3.5. *Saccharina latissima*: thallus morphology. A. Thallus of *S. latissima* collected from the G site (7/15/07) showing the long, narrow strap-like morphology characterizing the glacially-influenced shore during the glacial melt period. B. Thallus of *S. latissima* from the O site (8/1/07) exhibiting the wider, thinner, frilled morphology typical for the oceanic shore during summer.

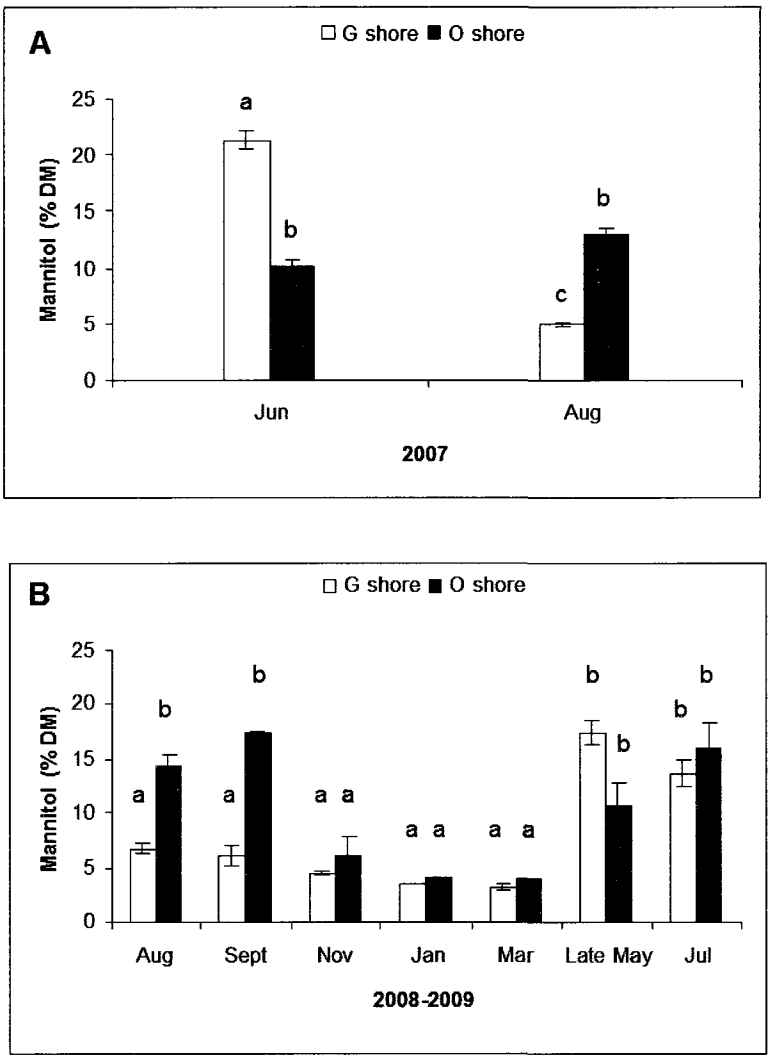


Figure 3.6. *Saccharina latissima*: mean (± SE) mannitol (% DM) on the glacially-influenced (G) and oceanic (O) shores of Kachemak Bay, Alaska in July-August 2007 (A) and from June 2007 to early July 2009 (B). Different letters above bars in each panel indicate significant differences (two-way ANOVA, Tukey HSD, $p<0.05$).

Table 3.1. *Saccharina latissima*: repeated measures ANOVA of *in situ* growth rate (cm d^{-1}) to test for effects of shore and time and their interaction during late July and August 2007 at the glacially-influenced and oceanic shores in Kachemak Bay, Alaska. Bold values indicate significant effects.

Experiment	Source	*df*	MS	F	p
Growth *in situ* 2007	Shore	1	3.51	38.96	**<0.0001**
	Error: Sample	36	0.09		
	Time	2	1.69	42.42	**<0.0001**
	Shore x Time	2	0.09	2.17	0.1216
	Error: Within	78	0.04		

Table 3.2 *Saccharina latissima*: mean (± SE) maximum quantum yield (*Fv/Fm*) and of morphometrics from late June 2008 through early July 2009 of randomly collected thalli from the glacially-influenced and oceanic shores of Kachemak Bay, Alaska. Significant differences are indicated with * (two-way ANOVA, Tukey HSD, $p<0.05$).

Parameter	late Jun 08	Jul 08	Aug 08	Sept 08	mid-Nov 08	mid-Jan 09	mid-Mar 09	late May 09	early Jul 09
F_v/F_m									
Glacially-influenced shore	0 76±0 01	0 70±0 01	0 74±0 01	0 73±0 01	0 75±0 01	nd	nd	0 73±0 03	0 75±0 01
Oceanic shore	0 77±0 01	0 77±0 01	0 78±0 01	0 77±0 01	0 74±0 02	nd	nd	0 72±0 02	0 73±0 02
p	1 0000	* 0 0074	0 0989	0 5386	1 0000	nd	nd	1 0000	0 9959
Lamina width (cm)									
Glacially-influenced shore	9 7±0 7	10 6±0 7	9 9±0 4	9 6±0 7	9 2±0 9	13 0±1 4	10 0±0 9	10 6±0 5	12 5±0 8
Oceanic shore	19 6±2 9	19 2±2 0	19 2±1 8	18 2±1 0	15 9±2 3	16 9±1 2	12 0±1 4	19 2±3 0	18 4±1 8
p	* 0 0003	*0 0004	*0 0015	*0 0014	*0 0421	0 7856	0 9987	*0 0215	0 4319
Lamina thickness (mm)									
Glacially-influenced shore	1 4±0 03	1 4±0 03	1 4±0 04	1 4±0 03	1 4±0 11	nd	0 8±0 03	1 1±0 11	1 3±0 04
Oceanic shore	1 3±0 07	1 0±0 05	0 9±0 07	0 9±0 02	1 1±0 08	nd	0 9±0 04	1 0±0 04	1 1±0 06
p	0 7789	*0 0010	*0 0010	*0 0053	*0 0011	nd	0 9994	1 0000	0 6000
Dry mass mg mm^2									
Glacially-influenced shore	0 26±0 04	0 50±0 03	0 55±0 01	0 56±0 05	0 58±0 04	0 09±0 01	0 06±0 00	0 17±0 04	0 39±0 01
Oceanic shore	0 11±0 06	0 11±0 01	0 13±0 03	0 20±0 00	0 34±0 04	0 07±0 01	0 08±0 00	0 17±0 02	0 15±0 03
p	0 1797	*<0 0001	*<0 0001	*<0 0001	*0 0010	0 5628	0 5219	1 0000	0 1012
Stipe length (cm)									
Glacially-influenced shore	6 6±1 4	6 1±0 7	5 4±0 4	6 4±0 5	6 9±0 8	5 9±0 7	6 1±0 4	5 6±0 7	8 1±0 9
Oceanic shore	5 2±0 4	4 0±0 6	3 2±0 5	2 3±0 2	3 6±0 4	4 2±0 4	5 0±0 6	4 2±0 6	4 8±0 8
p	0 9996	0 1911	0 2493	*0 0305	*<0 0001	0 8684	0 9966	0 9602	0 0977
Stipe diameter (mm)									
Glacially-influenced shore	3 6±0 2	4 9±0 2	4 9±0 2	4 7±0 2	4 7±0 3	4 9±0 2	4 0±0 2	4 1±0 4	5 5±0 2
Oceanic shore	4 5±0 3	4 6±0 2	3 5±0 2	3 4±0 1	4 4±0 2	3 6±0 2	3 8±0 2	4 9±0 3	4 5±0 4
p	0 5428	1 0000	*0 0257	0 1485	0 9998	0 0928	1 0000	0 5437	0 4059
Total length (cm)									
Glacially-influenced shore	212 9±24 9	216 8±15 3	126 0±18 5	115 3±13 3	71 7±9 2	89 9±8 7	133 0±14 1	209 0±33 9	339 0±16 9
Oceanic shore	145 8±20 8	197 3±20 7	100 0±12 1	87 8±8 0	38 3±3 6	42 5±4 0	140 0±11 9	162 8±14 1	266 7±18 9
p	0 5188	1 0000	0 9988	0 9913	*0 0005	*0 0249	1 0000	0 9946	0 9387

Table 3.3. *Saccharina latissima*: multiple comparisons of growth rates (cm d^{-1}) from June 2008 to July 2009 between indigenous thalli of opposite shores, indigenous thalli and their respective transplants, and indigenous thalli and transplants from the opposite shore in Kachemak Bay, Alaska (Student's t-test, Bonferroni corrected significant p-value = 0.0001). Bold values represent significant effects.

Parameter	Jul	Aug	Sept	mid-Nov	mid-Jan	mid-Mar	late May	early Jul
Indigenous G:Indigenous O	**<0.0001**	**<0.0001**	0.0007	0.0007	0.8690	nd	nd	nd
Indigenous G:Transplant G	0.0092	0.2912	0.3860	0.5890	0.6674	nd	nd	nd
Indigenous O:Transplant O	0.7850	0.2172	0.0566	0.1852	0.7467	nd	nd	0.0002
Indigenous G:Transplant O	**<0.0001**	0.0005	0.0657	0.0401	0.8930	nd	nd	nd
Indigenous O:Transplant G	**<0.0001**	0.0024	0.0297	0.0004	0.9710	0.9535	0.0393	**<0.0001**
Transplant G:Transplant O	**<0.0001**	0.0222	0.0735	0.0484	0.7463	nd	nd	0.0033

General Conclusions

The purpose of this study was to determine how environmental conditions due to glacial melting affect community structure and organism fitness in subarctic kelp beds. This study showed that two adjacent nearshore regions (one glacially-influenced and one under oceanic influence) within the same subarctic estuary vary in kelp bed community structure. In addition, the kelp foundation species, *Saccharina latissima* on both shores, exhibited phenotypic plasticity in terms of growth to varying levels of salinity and light availability. However, this plasticity was constrained within different seasonal growth patterns in the populations from the two shores, although both maintained high physiological competence (maximum quantum yield of PSII) year-round. This is the first time that phenotypic plasticity within a genetically fixed seasonal growth cycle has been described for macroalgae and especially for two populations in such close proximity.

Chapter 1 of the present research examined the effects of glacial discharge on kelp bed community structure by comparing environmental conditions on a glacially-influenced shore to those on an oceanic shore in Kachemak Bay, Alaska. The environmental variables differed on the two shores with the glacially-influenced shore exhibiting higher inorganic sedimentation, abrasion and sand/silt substrate cover. In contrast, higher salinity, light intensity, nitrate concentrations and hard substrate cover were observed on the oceanic shore. Taxonomic richness and overall species abundance were less on the glacially-influenced shore than on the oceanic shore. The glacially-influenced shore had lower cover of kelps, other macroalgae, and epifauna. Only one kelp species, *S. latissima,* was present on the glacially-influenced shore, while five kelp

species characterized the oceanic shore. Salinity, nitrate, inorganic sedimentation and abrasion were identified as the primary drivers of kelp communities, and are variables that are dynamically influenced by glacial discharge. In contrast, other drivers, such as hard substrate and rugosity, reflect existing differences between the two shores that are the result of long-term exposure to glacial silt sedimentation over the past 15,000 years (Field & Walker 2003). While it is difficult to separate the relative roles of these two types of drivers on kelp bed communities, increased rates of glacial discharge due to climate warming may exacerbate the effects of the dynamic drivers and further decrease species richness in Arctic and subarctic estuaries.

Further evaluation of the effects of the dynamic drivers influenced by glacial discharge on benthic community structure was conducted in Chapter 2 in controlled laboratory investigations. The experiments examined the separate effects of specific environmental variables (salinity and irradiance) on the growth and physiology of the important kelp foundation species, *S. latissima*. The goal was to determine whether these stressors differently affect juvenile kelp originating from the two disparate shores in Kachemak Bay. Laboratory tests assessed the effects of varying salinities and irradiances on growth and maximum quantum yield (F_v/F_m) of PSII over ~21 day experiments. Overall, laboratory growth rates were negatively affected by both reduced salinity and irradiance treatments for kelps from both shores; however, oceanic thalli out-performed glacially-influenced thalli in terms of growth at most salinity and irradiance treatments. Juveniles from both shores grew negligibly at salinities below 13 and at an irradiance of 5 μmol photons m^{-2} s^{-1}. Physiological competence (based on F_v/F_m) was significantly

reduced at salinity 10, but F_v/F_m was not affected by reduced irradiance in thalli from both shores. Hence, low growth rates did not equate to physiological stress in *S. latissima.* I showed that *S. latissima* was relatively tolerant to reduced salinities and irradiances but I also detected limits to its resilience to the tested variables. *Saccharina latissima* from both environments exhibited phenotypic plasticity in their growth responses under varying salinity and light conditions, but this plasticity appeared to be constrained within different seasonal growth patterns. In contrast, there was no evidence of ecotypic differentiation in the short-term response to glacial melt and discharge effects such as reduced salinity and light.

In situ examination of *S. latissima* from the two environmentally distinct environments of Kachemak Bay further investigated their respective seasonal growth patterns (Chapter 3). During summer, the period of highest glacial melting and discharge, *in situ* growth of *S. latissima* ceased earlier on the glacially-influenced shore than on the oceanic shore. In contrast, maximum quantum yield remained high and did not differ significantly on the two shores over the course of the year, indicating that thalli remained physiologically healthy during periods of reduced growth. During glacial melt in the summer, the thalli on the two shores were morphologically distinct; the glacially-influenced thalli were narrow, leathery and flat, while the oceanic thalli were wide, thin and undulate. The morphological form of the oceanic thalli may be important for their ability to uptake nitrogen from surrounding waters during their extended growth period. Mannitol levels as a main storage product in kelps differed between thalli from the two shores, with generally higher levels in the oceanic shore thalli. Mannitol levels dropped

when growth stopped on both shores, and did not seem to play a role in jumpstarting growth in late winter/early spring. When *S. latissima* from the glacially-influenced shore was transplanted to the oceanic shore, they did not grow in the same seasonal pattern as the indigenous oceanic thalli, even though they experienced the favorable environmental conditions of the oceanic shore. There are less data available to determine whether or not the oceanic shore transplants maintained their typical oceanic seasonal growth pattern or adjusted to the typical glacially-influenced pattern, as the experimental set was lost over winter due to ice movement. However, in fall, transplants from the oceanic to the glacially-influenced shore also maintained the seasonal growth pattern typical for the oceanic shore. This suggests that there may be genetic differentiation between the thalli from the two shores, or that there may be differences in gene expression relating to seasonal growth (Nicotra et al. 2010). Within these genetically fixed seasonal growth patterns, however, thalli from the two shores seem to maintain phenotypic plasticity as a response to varying environmental conditions (see Chapter 2). This is the first report of such distinct traits within a species on such a small spatial scale.

My thesis confirmed that the use of multiple measures of organism fitness in response to variable environmental conditions is more informative than one measure alone. While growth was affected by environmental stressors, physiological fitness (maximum quantum yield) was not, indicating that growth alone would likely overestimate the environmental effects while maximum quantum yield alone would underestimate them. The evaluation of additional physiological parameters of foundation organisms such as *S. latissima* would be useful to further our understanding of their

acclimation and/or adaptation to the ambient light field. Specifically, the measurement of additional photosynthetic characteristics such as maximum relative electron transport rates ($rETR_{max}$), minimum saturating irradiance (E_k), and photosynthetic efficiency (α) would provide additional information on the relative photosynthetic performance *in vivo* of *S. latissima* and the extent to which performance is limited by photochemical and nonphotochemical (heat dissipation) processes (Baker 2008). Also, an investigation into secondary metabolite levels would increase our knowledge on resource allocation in kelps. Assuming resource trade-off theories apply, and growth and secondary metabolite production draw from the same energy pool (DeWreede & Klinger 1988, Pavia & Toth 2008), then expression of one comes at the expense of the other. Particularly if environmental variability triggers seasonality in resource input (e.g. available light for photosynthesis and growth in kelp) it may regulate the potential investment in costly defensive traits (Poisot et al. 2011). Secondary metabolites in brown algae serve as defenses against grazers, pathogens, and epiphytes (reviewed by Amsler & Fairhead 2005), and are also important in photoprotection against UV radiation (Pavia et al. 1997). Hence, knowledge of seasonal levels of metabolites such as phlorotannins in kelp in comparison with growth rates would elucidate more details on resource allocation strategies in environmentally-stressed environments. Sequencing of the COI-5P gene in this study confirmed that the *S. latissima* populations on the two shores of Kachemak Bay are indeed the same species. Further investigations at the molecular level such as sequence evaluation of other genes and/or introns from more individuals and the use of genetic markers such as microsatellites to examine gene flow (Liu et al. 2010) should

provide further insight into possible genetic differentiation in *S. latissima*. The use of microarrays, once the *S. latissima* genome is determined, will allow elucidation of gene expression (O'Donnell et al. 2010) in *S. latissima* in response to varying environmental conditions.

On the community level, assessment of functioning and health was done through biodiversity assessments of the kelp bed communities in the glacially-influenced and the oceanic environments on Kachemak Bay. Recent work on the effects of climate change suggests that changing environmental conditions may lead to functional homogenization of ecosystems, where specialist species with their specific ecosystem functions are replaced with generalist species tolerant to a wide variety of environmental conditions (Clavel et al. 2011). This in turn will lead to changes in the goods and services an ecosystem can provide (de Groot et al. 2002). For example, the loss of multiple kelp species and the persistence of only one kelp foundation species may lead to changed structural and microclimatic conditions in the kelp beds with consequences for associated community biodiversity (Angelini et al. 2011). My results confirmed these patterns, and *S. latissima* can be considered such a generalist species. In addition, altered seasonal growth patterns, as suggested here, may lead to less kelp productivity to provide habitat and food to associated organisms in environmentally stressed environments. Such system-wide studies in the future would provide valuable information on community health, complementing studies on fitness of foundation organisms.

The effects of glacial discharge are likely to intensify in the near future (Hinzman et al. 2005, Berthier et al. 2010, Weller et al. 2010). Global average air temperatures are

projected to rise by 0.4 °C over the next two decades, with the largest increases at high latitudes (IPCC 2007). These changes will further accelerate the rate of glacial melting and discharge and necessitate our understanding of glacial effects on these essential nearshore benthic communities (Fellman et al. 2010). In addition, climate change is also responsible for increases in forest fires in Alaska (Berg & Anderson 2006), which leads to increased erosion and sediment input into nearshore waters. Industrial development and ongoing urbanization also increase sediment input into nearshore systems. Based on my study of important dynamic drivers such as sedimentation affecting nearshore kelp bed community structure, further decreases in taxonomic richness and abundance can be expected. Ecosystems that were once diverse may ultimately be reduced to a few resilient opportunistic species (Clavel et al. 2011). And even in these more resilient species such as *S. latissima*, the ability to elicit plastic responses and seasonal adaptations may be limited and concerns remain about the long-term persistence of important foundation species and nearshore habitats with continued climate change.

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