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Igor Krupnik, Michael A. Lang, and Scott E. Miller Editors

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# Interannual and Spatial Variability in Light Attenuation: Evidence from Three Decades of Growth in the Arctic Kelp, *Laminaria* solidungula

## Kenneth H. Dunton, Susan V. Schonberg, and Dale W. Funk

ABSTRACT. We examined long-term variations in kelp growth in coincidence with recent (2004-2006) measurements of underwater photosynthetically active radiation (PAR), light attenuation coefficients, chlorophyll concentrations, and total suspended solids (TSS) to determine the impact of sediment resuspension on the productivity of an isolated kelp bed community on the Alaskan Beaufort Sea coast. Attenuation coefficients exhibited distinct geographical patterns and interannual variations between 2004 and 2006 that were correlated with temporal and geographical patterns in TSS (range 3.5-23.8 mg  $L^{-1}$ ). The low chlorophyll levels (<3.0  $\mu$ g  $L^{-1}$ ) in all three years were unlikely to have contributed significantly to periods of low summer water transparency. Blade elongation rates in the arctic kelp, Laminaria solidungula, are excellent integrators of water transparency since their annual growth is completely dependent on PAR received during the summer open-water period. We noted that blade growth at all sites steadily increased between 2004 and 2006, reflective of increased underwater PAR in each successive year. Mean blade growth at all sites was clearly lowest in 2003 (<8 cm) compared to 2006 (18-47 cm). We attribute the low growth in 2003 to reported intense storm activity that likely produced extremely turbid water conditions that resulted in low levels of ambient light. Examination of a 30-year record of annual growth at two sites revealed other periods of low annual growth that were likely related to summers characterized by exceptional strong storm activity. Although kelp growth is expected to be higher at shallower sites, the reverse occurs, since sediment re-suspension is greatest at shallower water depths. The exceptionally low growth of kelp in 2003 indicates that these plants are living near their physiological light limits, but represent excellent indicators of interannual changes in water transparency that result from variations in local climatology.

#### INTRODUCTION

Research studies conducted over the past two decades have clearly documented that kelp biomass, growth, and productivity in the Alaskan Beaufort Sea are strongly regulated by light availability (photosynthetically active radiation, PAR). Results from a variety of experimental studies, including the linear growth response of kelp plants to natural changes in the underwater light field (Dunton, 1984; 1990; Dunton and Schell, 1986;), carbon radioisotope tracer experiments (Dunton and Jodwalis, 1988), and laboratory and field physiological work (Henley and Dunton, 1995; 1997) have been used successfully to develop models of kelp productivity in relation to PAR. Yet, until recently, the relationship

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between water turbidity—as measured by total suspended solids (TSS) or optical instruments—and benthic algal production was unknown. Aumack et al. (2007) were the first to establish the quantitative link between water column turbidity, PAR and kelp production through a model that uses TSS data to predict estimates of kelp productivity in an area known as the Stefansson Sound Boulder Patch on the central Alaskan Beaufort Sea coast. This information is essential for evaluating how changes in water transparency are related to higher suspended sediment concentrations from anthropogenic activities near the Boulder Patch, coastal erosion, and increased freshwater inflow (McClelland et al., 2006). The quantitative measurements of TSS collected by Aumack et al. (2007) in summers 2001 and 2002 were a critical first step in the establishment of an accurate basin-wide production model for the Stefansson Sound Boulder Patch.

The productivity of Laminaria solidungula in subtidal coastal ecosystems is an important factor that regulates benthic biodiversity and ultimately, the intensity of biological interactions such as competition, facilitation, predation, recruitment, and system productivity (Petraitis et al., 1989; Worm et al., 1999; Mittelbach et al., 2001; Paine 2002). On a larger scale, biodiversity measurements can serve as an indicator of the balance between speciation and extinction (McKinney, 1998a; 1998b; Rosenzweig, 2001). The interesting biogeographic affinities of organisms in the Boulder Patch led Dunton (1992) to refer to the area as an "arctic benthic paradox," based on the Atlantic origin of many of the benthic algae (e.g. the red algae Odonthalia dentata, Phycodrys rubens, Rhodomela confervoides) in contrast to the Pacific orientation of many of the invertebrates (most polychaetes and gastropods). This unique character of the biological assemblage, combined with the Boulder Patch's isolated location (Dunton et al., 1982), suggests the potential of the area as a biogeographic stepping-stone. Thus, the Boulder Patch likely has large biological and ecological roles outside Stefansson Sound.

The overarching objective of our study was to use synoptic and long-term measurements of PAR, light attenuation coefficients, total suspended solids (TSS; mg L<sup>-1</sup>), and indices of kelp biomass to determine the impact of sediment resuspension on kelp productivity and ecosystem status in the Stefansson Sound Boulder Patch. Between 2004 and 2006, we initiated studies to monitor water quality, light, kelp growth, and the associated invertebrate community in the Boulder Patch. This research program was designed to address ecosystem change as related to anthropogenic activities from oil and gas development. Our initial effort was

focused on establishing a quantitative relationship between total suspended solids (TSS) and benthic kelp productivity (see Aumack, 2003; Aumack et al., 2007). Our current objectives included (1) defining the spatial variability in annual productivity and biomass of kelp, (2) monitoring incident and in situ ambient light (as PAR) and TSS, and (3) using historical datasets of kelp growth to establish a long-term record of kelp productivity.

#### MATERIALS AND METHODS

Our overall sampling strategy during summers 2004, 2005, and 2006 incorporated: (1) semi-synoptic maps of TSS and light attenuation parameters generated through sampling at 30 randomly-selected points in a 300 km<sup>2</sup> area that included the Boulder Patch and the region south of Narwhal Island to Point Brower on the Sagavanirktok Delta (Figure 1; 70°23′N; 147°50′W); (2) long-term variations in underwater PAR at three fixed sites and incident PAR at one coastal site during the summer open-water period; and (3) kelp growth at several monitoring stations established during the 1984-1991 Boulder Patch Monitoring Program (LGL Ecological Research Associates and Dunton, 1992). A majority of our study sites were located within the Stefansson Sound Boulder Patch, which is characterized by noncontiguous patches of >10% rock cover. These patches are depicted by gray contour lines in Figures 1–5.

#### SYNOPTIC SAMPLING

In order to describe the spatial extent and patterns of TSS, light attenuation, chlorophyll, nutrients, and physiochemical properties across Stefansson Sound, we sampled 30 sites across the monitoring area (Figure 1), which ranges in depth from 3 to 7 m. The location for each site was chosen by laying a probability-based grid over the area and randomly choosing a location within each grid cell. This method allowed sampling locations to be spaced quasi-evenly across the landscape while still maintaining assumptions required for a random sample (i.e., all locations have an equal chance of being sampled). All 30 sites were visited on three separate occasions during summers 2004, 2005, and 2006 using a high-speed vessel (R/V Proteus). We measured TSS, incident PAR, inorganic nutrients (ammonia, phosphate, silicate, nitrogen), water column chlorophyll, and physiochemical parameters (temperature, salinity, dissolved oxygen, and pH) during each synoptic sampling effort.

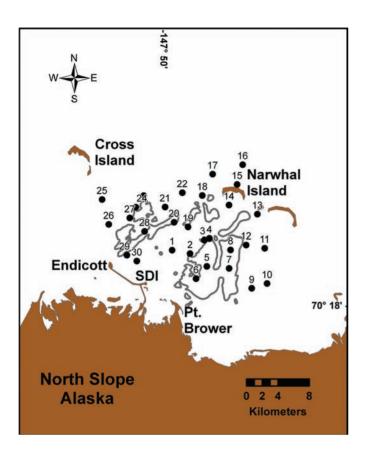


FIGURE 1. The project study area showing 30 synoptic collection sites used in summers 2004, 2005, and 2006. SDI: Satellite Drilling Island. Gray contour lines show >10% rock cover.

Replicate water samples were collected at 2 and 4 m depths using a van Dorn bottle. All samples were placed in pre-labeled plastic bottles, with sampling point geographic coordinates (Lat/Long) recorded using a handheld Garmin Global Positioning System, GPSMap 76S (Garmin International Inc., Olathe, Kansas, USA). In situ physiochemical measurements were made from the vessel. All other samples were stored in a dark cooler and transported to a laboratory on Endicott Island for processing.

#### Light Attenuation

Simultaneous surface and underwater measurements of PAR data were collected using LI-190SA and LI-192SA cosine sensors, respectively, connected to a LI-1000 datalogger (LI-COR Inc., Lincoln, Nebraska, USA). The LI-190SA sensor was placed at a 4 m height on the vessel mast. Coincident underwater measurements with the LI-192SA

sensor were made using a lowering frame deployed at 2 and 4 m depths. Care was taken to avoid interference from shading of the sensor by the vessel. The Brouger-Lambert Law describes light attenuation with water depth:

$$\frac{k = \ln(I_o/I_z)}{z} \tag{a}$$

where  $I_o$  is incident (surface) light intensity,  $I_z$  is light intensity at depth z, and k is the light attenuation coefficient (m<sup>-1</sup>).

#### TSS

A known volume of water from each sample was filtered through pre-weighed, pre-combusted glass fiber filters (Pall Corporation, Ann Arbor, Michigan, USA). Following a distilled water rinse filters were oven-dried to constant weight at 60°C. The net weight of particles collected in each sample was calculated by subtracting the filter's initial weight from the total weight following filtration.

#### Chlorophyll

For chlorophyll measurement, 100 ml of water from each replicate sample was filtered through a 0.45 µm cellulose nitrate membrane filter (Whatman, Maidstone, England) in darkness. After filtration, the filters and residue were placed in pre-labeled opaque vials and frozen. The frozen filters were transported to The University of Texas Marine Science Institute (UTMSI) in Port Aransas, Texas, for chlorophyll analysis. At UTMSI, filters were removed from the vials and placed in pre-labeled test tubes containing 5 ml of methanol for overnight extraction (Parsons et al., 1984:3–28). Chlorophyll *a* concentration, in µg L<sup>-1</sup>, was determined using a Turner Designs 10-AU fluorometer (Turner Design, Sunnyvale, California, USA). Non-acidification techniques are used to account for the presence of chlorophyll *b* and phaeopigments (Welschmeyer, 1994).

#### **Nutrients**

Water samples were frozen and transferred to UTMSI for nutrient analysis. Nutrient concentrations for  $\rm NH_4^+, PO_4^{3-}, SiO_4,$  and  $\rm NO_2^- + NO_3^-$  were determined by continuous flow injection analysis using colorimetric techniques on a Lachat QuikChem 8000 (Zellweger Analytics Inc., Milwaukee, Wisconsin, USA) with a minimum detection level of 0.03  $\mu M$ .

#### Physiochemical Parameters

Temperature (°C), salinity (‰), dissolved oxygen (% and mg  $L^{-1}$ ) pH, and water depth (m), were measured using a YSI Data Sonde (YSI Inc., Yellow Springs, Ohio, USA).

#### PERMANENT SITES

#### Underwater Irradiance

In addition to the synoptic sampling, we established eight permanent sites for collection of long-term data. Continuous underwater PAR measurements were collected at three sampling sites (DS-11, E-1, and W-1) in the Boulder Patch study area (Figure 2) and terrestrial PAR measurements at one coastal location (Endicott Island). These sites have been the focus of previous long-term monitoring efforts; measurements of PAR and kelp growth are reported in published literature (Dunton, 1990). Site DS-11, established as a reference site, has been a primary research site for the Boulder Patch since 1978. This site lies well outside the area most likely impacted by sediment plumes originating from the pro-

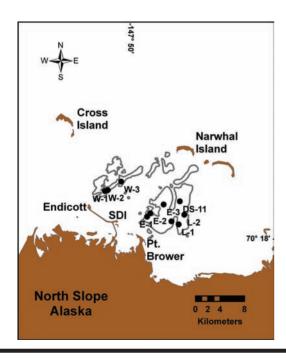


FIGURE 2. The project study area. The indicated sites are historical Boulder Patch stations that have been visited repeatedly since 1984. During summers 2004, 2005, and 2006, long-term light was measured at sites DS-11, E-1, and W-1; kelp blade length data were also collected at these sites.

posed Liberty Project, including construction of a buried pipeline and Stockpile Zone 1 (Ban et al., 1999). All three Boulder Patch sites are located on seabed characterized by >25% rock cover. Sites were chosen based on either their southern-most location in the Boulder Patch (W-1, E-1), existence of historical PAR data (W-1, E-1, and DS-11), and their likelihood of being impacted by oil and gas development through dredging activities associated with pipeline or island construction.

Underwater data were collected using LI-193SA spherical quantum sensor (for scalar measurements) connected to a LI-1000 datalogger (LI-COR Inc., Lincoln, Nebraska, USA) at each site. Sensors were mounted on PVC poles and positioned just above the kelp canopy to prevent fouling or shading by kelp fronds. Instantaneous PAR measurements were taken at 1 min intervals and integrated over 1 h periods. Coincident surface PAR measurements were taken with LI-190SA terrestrial cosine sensor connected to LI-1000 datalogger located on Endicott Island.

#### Kelp Elongation

At each of the nine dive sites (depth range 5–7 m) within the Boulder Patch (DS-11, Brower-1, E-1, E-2, E-3, L-1, L-2, W-1, and W-3), SCUBA divers collected 15-30 individual specimens of Laminaria solidungula attached to large cobbles and boulders in summers 2004, 2005, and 2006. Samples were placed in pre-labeled black bags, transported to Endicott, and processed. Blade segments from every specimen, which corresponded to one year's growth (Dunton, 1985), were measured and recorded to produce a recent (3–4 vr) growth record of linear blade expansion at each site. Blades measured in summer reflect growth during both the present and previous calendar year since more than 90% of a kelp's frond expansion occurs between November and June under nearly complete darkness (Dunton and Schell, 1986). Linear growth in L. solidungula from the Boulder Patch is heavily dependent on photosynthetic carbon reserves that accumulate during the previous summer in proportion to the underwater light environment. A growth year (GWYR) is dictated by the formation of a new blade segment, which begins in mid-November every year and is defined by the summer that precedes new blade formation (e.g., basal blade growth measured in summer 2007 depicts GWYR 2006).

#### Kelp Biomass

Frond lengths of *Laminaria solidungula* plants were measured at W-3, E-1, E-3, and DS-11 along four 25 m

transects. Transects radiated from a central point at random chosen directions at 280°, 80°, 260°, and 110°Magnetic.

#### Statistics and GIS

TSS concentrations, chlorophyll a concentrations, and the attenuation coefficient (k) were matched with their respective geographic coordinates and plotted using GIS software ArcMap 9.2 (ERSI, Redlands, California). Data were interpolated across a polygon of Stefansson Sound, including the Boulder Patch, using Geospatial Analyst extension and Kriging function in ArcMap following Aumack et al. (2007). Data were analyzed using standard parametric models. Spatial and interannual significance among k, TSS, and chlorophyll measurements were determined using a paired t-test to examine significant differences (p < 0.05) among treatment variables using Microsoft Excel. Significant differences in PAR among years and sites was tested using a two-way analysis of variance (ANOVA) using time as a block with a general linear models procedure (SAS Institute Inc, 1985) following Dunton (1990).

#### **RESULTS**

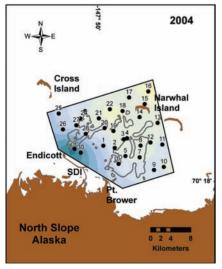
#### SYNOPTIC SAMPLING

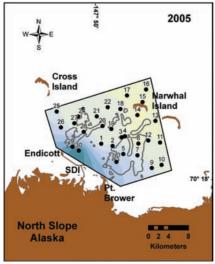
Light attenuation (k) was derived from coincident in situ measurements of surface and underwater PAR at 2 and 4 m depths collected at 30 stations on three differ-

ent occasions each summer. Attenuation was consistently elevated in coastal zones with highest k values observed near Endicott Island and SDI (Satellite Drilling Island) indicating more turbid water closer to shore (Figure 3). Lower k values were recorded offshore along the eastern and northeastern sides of Stefansson Sound. In summer 2004, k ranged from 0.43–1.34 m<sup>-1</sup> (mean 0.73  $\pm$  0.14) throughout Stefansson Sound. In 2005 k ranged from 0.47–1.32 m<sup>-1</sup> (mean 0.69  $\pm$  0.03) and in 2006, k was 0.54–1.08 m<sup>-1</sup> (mean 0.72  $\pm$  0.01). The majority of the Boulder Patch, including areas with dense kelp populations (>25% rock cover), were found predominantly in offshore waters where attenuation measurements were consistently less than 1.0 m<sup>-1</sup>.

The TSS concentrations were dramatically lower in summers 2004 and 2006 compared with 2005, yet the same general trends were observed (Figure 4). Since a paired t-test indicated that the TSS values measured at 2 and 4 m depths were not significantly different in either year (2004 p = 0.065; 2005 p = 0.156) the means of the two depths are displayed. In 2004, the highest concentrations (7.6–8.3 mg L<sup>-1</sup>) were found near Endicott Island and SDI and in a turbid area just north of Narwhal Island (5.7–6.1 mg L<sup>-1</sup>). The TSS ranged from 3.8–7.6 mg L<sup>-1</sup> outside the Boulder Patch with a mean of 5.0 mg L<sup>-1</sup>. Inside the Boulder Patch the data ranged from 4.0 to 8.3 mg L<sup>-1</sup> (mean 5.0 mg L<sup>-1</sup>); the overall site average was 5.0  $\pm$  1.8 mg L<sup>-1</sup>.

The TSS measurements were much higher and varied greatly throughout Stefansson Sound during summer





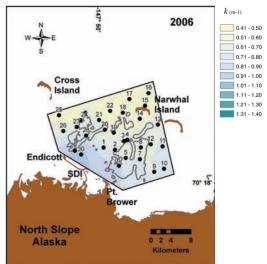


FIGURE 3. Combined mean attenuation coefficient (*k*) values calculated from measurements collected at 2 m and 4 m water depths in summers 2004, 2005, and 2006.

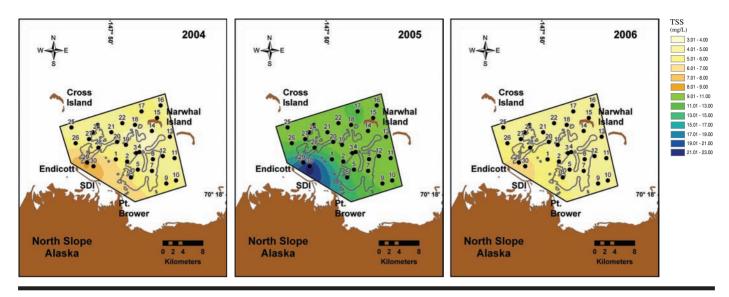


FIGURE 4. Combined mean total suspended solids (TSS) from samples collected at 2 m and 4 m water depths in 2004, 2005, and 2006.

2005 (7.5–23.8 mg  $L^{-1}$ ; mean 11.1  $\pm$  1.1 mg  $L^{-1}$ ). The highest values (17.6–23.8 mg  $L^{-1}$ ) were located nearshore, adjacent to Endicott Island, SDI, and Point Brower. Outside the Boulder Patch, TSS ranged from 7.5 to 23.8 mg  $L^{-1}$  (mean 11.2 mg  $L^{-1}$ ). Inside the Boulder Patch, values ranged from 9.0 to 17.6 mg  $L^{-1}$  (mean 11.0 mg  $L^{-1}$ ).

In 2006, TSS concentrations were similar to those measured in 2004 (range of 3.5–6.9 mg L $^{-1}$ ; mean of 4.7  $\pm$  0.2 mg L $^{-1}$ ). The highest values were again adjacent to Endicott Island, SDI and Point Brower. Outside the Boulder Patch, TSS ranged from 3.6 to 6.9 mg L $^{-1}$  (mean 4.6  $\pm$  0.2 mg L $^{-1}$ ). The TSS values ranged from 3.5 to 5.9 mg L $^{-1}$  inside the Boulder Patch with a mean of 4.6  $\pm$  0.2 mg L $^{-1}$ .

Chlorophyll *a* measurements from 2 and 4 m depths were relatively low but significantly different from each other in all years (p < 0.05). In all three years, 4 m chlorophyll values were higher than the 2 m measurements (Figure 5). The 2005 chlorophyll means were the highest followed by 2004 means, with the lowest values occurring in 2006. In 2004, chlorophyll measurements ranged from 0.11 to 2.63  $\mu$ g L<sup>-1</sup> (mean 0.39  $\pm$  0.2  $\mu$ g L<sup>-1</sup>). In summer 2005, values ranged from 0.11 to 3.54  $\mu$ g L<sup>-1</sup> (mean 0.76  $\pm$  0.08  $\mu$ g L<sup>-1</sup>) compared to 0.11–0.41  $\mu$ g L<sup>-1</sup> (mean 0.18  $\pm$  0.01  $\mu$ g L<sup>-1</sup>) in 2006.

Ammonium concentrations (Table 1) were significantly different among samples collected at 2 and 4 m in all years (p <0.05); all values were low (0.12  $\pm$  0.06  $\mu M$  at 2 m and 0.17  $\pm$  0.07  $\mu M$  at 4 m in 2004; 0.40  $\pm$  0.04  $\mu M$  at 2 m and 0.65  $\pm$  0.04  $\mu M$  at 4 m in 2005 and

 $0.25 \pm 0.05 \,\mu\text{M}$  at 2 m and  $0.12 \pm 0.02 \,\mu\text{M}$  at 4 m). Ammonium ranged from  $0.0\text{--}0.52 \,\mu\text{M}$  in 2006. Highest concentrations were noted at sites adjacent to barrier islands (Sites 13 and 15); lowest values were noted offshore  $(0.0\text{--}0.02 \,\mu\text{M})$ .

In general, phosphate concentrations were low. Mean values in 2004 were 0.24  $\pm$  0.03  $\mu M$  at 2 m and 0.19  $\pm$  0.05  $\mu M$  at 4 m. Phosphate values ranged from 0.11–0.39  $\mu M$  with the highest concentrations collected at sites adjacent to Endicott. Several other random sites displayed higher values at either 2 or 4 m. The lowest values were observed at sites seaward of Narwhal Island (0.0–0.02)  $\mu M$ . In 2005, phosphate measurements were lower in 2 m samples (mean 0.29  $\pm$  0.01  $\mu M$ ) versus the 4 m samples (mean 0.35  $\pm$  0.01  $\mu M$ ). The same pattern held for the 2006 (2 m mean 0.17  $\pm$  0.01  $\mu M$ ; 4 m mean 0.20  $\pm$  0.01  $\mu M$ ).

Silicate values collected from 2 and 4 m in 2004 were not significantly different (p = 0.51), ranging from 0.07–4.90  $\mu$ M; mean 1.84  $\pm$  0.26  $\mu$ M (Table 1). Silicate was quite low at 2 and 4 m in 2004 compared to 2005 (2 m mean 5.64  $\pm$  0.19  $\mu$ M; 4 m mean 5.19  $\pm$  0.16  $\mu$ M) and 2006 (2 m mean 7.05  $\pm$  0.14  $\mu$ M; 4 m mean 6.89  $\pm$  0.16  $\mu$ M).

 $NO_2^- + NO_3^-$  measurements throughout Stefansson Sound were also generally low, with 2004 station means ranging from 0.0–0.29  $\mu$ M at 2 m; 0.12  $\pm$  0.21  $\mu$ M at 4 m (Table 1). The 2005 station means ranged from 0.0–0.61  $\mu$ M at 2 m; 0.03–1.98  $\mu$ M at 4 m, and 2006 means were 0.03–0.33  $\mu$ M at 2 m; 0.02–0.44  $\mu$ M at 4 m. In all three

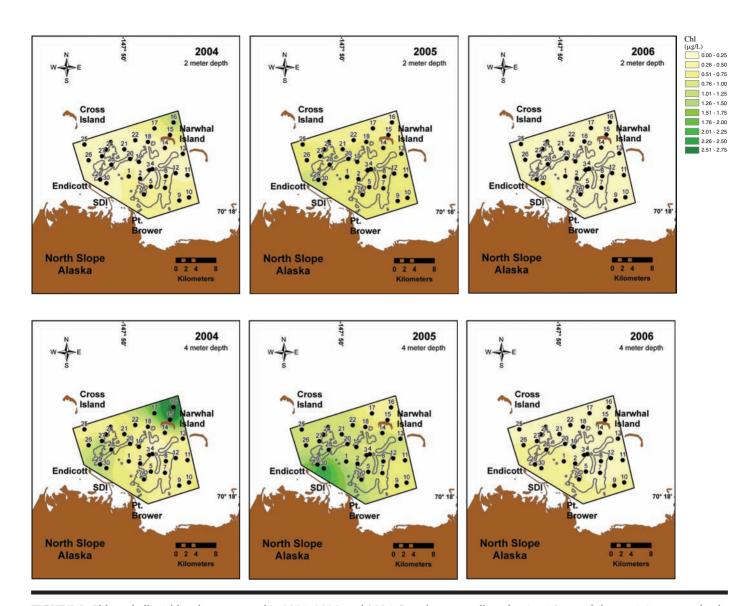


FIGURE 5. Chlorophyll a (chl) values measured in 2004, 2005, and 2006. Samples were collected at (top) 2 m and (bottom) 4 m water depth.

**TABLE 1.** Measurements of ammonium, phosphate, silicate, and nitrate + nitrite at 30 sites measured annually in July and August 2004, 2005, and 2006. Samples were collected at 2 and 4 m water column depths. Values are  $x \pm SE$ .

| YEAR<br>μΜ | Ammonium<br>(NH <sub>4</sub> <sup>+</sup> ) 2 m | Ammonium<br>(NH <sub>4</sub> <sup>+</sup> ) 4 m | Phosphate<br>(PO <sub>4</sub> <sup>3-</sup> )<br>2 m | Phosphate<br>(PO <sub>4</sub> <sup>3-</sup> )<br>4 m | Silicate<br>(SiO <sub>4</sub> )<br>2 m | Silicate<br>(SiO <sub>4</sub> )<br>4 m | Nitrate +<br>Nitrite<br>(NO <sup>2-</sup> +<br>NO <sup>3-</sup> ) 2 m | Nitrate +<br>Nitrite<br>(NO <sup>2+</sup> +<br>NO <sup>3-</sup> ) 4 m |
|------------|---|---|--|--|--|--|---|---|
| 2004       | $0.12 \pm 0.06$                                 | $0.17 \pm 0.07$                                 | $0.24 \pm 0.03$                                      | $0.19 \pm 0.05$                                      | $1.76 \pm 0.18$                        | $1.84 \pm 0.26$                        | $0.14 \pm 0.10$   | $0.15 \pm 0.01$   |
| 2005       | $0.40 \pm 0.04$                                 | $0.65 \pm 0.05$                                 | $0.29 \pm 0.01$                                      | $0.35 \pm 0.01$                                      | $5.64 \pm 0.19$                        | $5.19 \pm 0.16$                        | $0.21 \pm 0.04$   | $0.29 \pm 0.08$   |
| 2006       | $0.25 \pm 0.05$                                 | $0.12 \pm 0.02$                                 | $0.17 \pm 0.01$                                      | $0.20 \pm 0.01$                                      | $7.05 \pm 0.14$                        | $6.89 \pm 0.16$                        | $0.07 \pm 0.01$   | $0.10 \pm 0.02$   |

sampling years, the 4 m nitrate concentrations were slightly higher than the 2 m but were not significantly different.

Mean sea surface temperature (2 m and 4 m) increased throughout the Boulder Patch each year between 2004 and 2006 (Table 2). Summer 2004 was characterized by frequent storm activity, which was reflected in depressed surface water temperatures that were negative at some sites. The 2006 mean 2 m temperature (4.6  $\pm$  0.2 °C) was more than double the value measured in 2004 (2.1  $\pm$  0.6 °C). The 4 m mean temperature increased more than fourfold between 2004 and 2006 (0.9  $\pm$  0.7; 4.2  $\pm$  0.2).

Salinity measurements were homogeneous across the Boulder Patch and means were consistent between summers 2004 and 2005 at both 2 m (23.8  $\pm$  1.0%; 23.8  $\pm$  1.7%) and 4 m (26.8  $\pm$  1.2%; 26.6 $\pm$  1.4%) depths, but values dropped precipitously in 2006 (2 m 16.9  $\pm$  0.35%; 4 m 20.7 $\pm$  0.5%; Table 2). In 2004, the salinity range at 2 m was 20.4–27.4%; the 4 m 2004 range was 23.5 to 31.7%. In summer 2005, measurements at 2 m ranged from 17.7 to 26.21% and at 4 m salinity varied from 24.9 to 30.8%. During 2006, the 2 m salinity low was measured at 11.3 % and the high was 23.5%; the 4 m low was 12.3 % and high 30.0%. At 2 m, waters were slightly fresher than at 4 m during all three years.

We only report pH data from 2004 and 2006 since the probe malfunctioned during the 2005 field season (Table 2). In 2004, pH measurement means were remarkably constant at  $8.2 \pm 0.04$  at both 2 and 4 m. The measurements in 2006 were also very consistent (7.9  $\pm$  0.01 %) throughout the sampling area and between the 2 and 4 m depths, but were more acidic than the 2004 values. Measurements of dissolved oxygen revealed values at or near saturation in all years (Table 2). The range in values reflect differences in water temperature and wind induced turbulence of surface waters.

#### PERMANENT STATIONS

Blade elongation in *Laminaria solidungula* displayed large spatial and temporal variability as reflected in measurements from nine sites (Table 3). Mean site blade growth was lower at every site in GWYR 2003 compared to GWYRs 2004, 2005, and 2006, reflecting the exceptionally poor weather conditions in summer 2003 that produced extremely low levels of ambient PAR. Kelp collected in 2004 (GWYR 2003) had annual average growth rates ranging between 4.4 and 10.4 cm. In contrast, blade elongation ranged from 10 to 25.5 cm in GWYR 2004 and from 16.7 to 47.3 cm in GWYR in 2005 and 2006, comparable to previous studies (Dunton, 1990; Martin and Gallaway, 1994). Specimens from DS-11 showed the greatest annual growth of all sites in most years.

In conjunction with blade elongation rates, we collected PAR measurements during summers 2004, 2005, and 2006. Surface irradiance followed a typical cyclical pattern, peaking between 1200–1400 µmol photons m<sup>-2</sup> s<sup>-1</sup> in the afternoon before declining to nearly undetectable levels after midnight (Figure 6). Highest levels of underwater PAR were normally recorded by scalar sensors in the early afternoon (1400 hrs), which also corresponded to the period of maximum incident PAR. In 2004, from 31 July to 6 August, underwater irradiance dropped to near zero at all three sites (DS-11, E-1, and W-1). These low values were coincident with a series of intense storms that generated winds in excess of 10 m s<sup>-1</sup> from the southwest and southeast. Extremely low underwater PAR concentrations continued through 9 August followed by four days of slightly higher values, at which point the dataloggers were removed. Prior to the storm, underwater scalar irradiance at DS-11 ranged from 180 to 200 µmol m<sup>-2</sup> s<sup>-1</sup> compared to less than 20 µmol m<sup>-2</sup> s<sup>-1</sup> during the storm,

TABLE 2. Average temperature, salinity, dissolved oxygen, and pH measurements for 30 sites measured annually in July and August 2004, 2005, and 2006. Samples were collected at 2 and 4 m water column depths. Values are means ± SE. ND indicates no data.

| YEAR                 | Temp<br>(°C)<br>2 m                       | Temp<br>(°C)<br>4 m                                   | Salinity<br>(‰)<br>2 m                                   | Salinity<br>(‰)<br>4 m                                   | Dissolved $O_2 \text{ (mg L}^{-1}\text{)}$ 2 m     | $\begin{array}{c} Dissolved \\ O_2 \ (mg \ L^{-1}) \\ 4 \ m \end{array}$ | $\begin{array}{c} pH\\ (m^{-1})\\ 2\ m \end{array}$ | $\begin{array}{c} pH \\ (m^{-1}) \\ 4 \ m \end{array}$ |
|----------------------|---|---|--|--|--|--|---|--|
| 2004<br>2005<br>2006 | 2.11 ± 0.55<br>2.62 ± 1.07<br>4.64 ± 0.16 | $0.88 \pm 0.75$<br>$1.97 \pm 1.32$<br>$4.21 \pm 0.22$ | $23.80 \pm 0.99$<br>$23.85 \pm 1.66$<br>$16.91 \pm 0.35$ | $26.81 \pm 1.16$<br>$26.65 \pm 1.36$<br>$20.67 \pm 0.49$ | $13.18 \pm 0.35$ $11.48 \pm 0.45$ $11.45 \pm 0.02$ | $14.22 \pm 0.38$ $11.53 \pm 0.39$ $11.57 \pm 0.05$                       | $8.19 \pm 0.05$<br>ND<br>$7.90 \pm 0.01$            | 8.22 ± 0.04<br>ND<br>7.88 ± 0.01                       |

TABLE 3. Average Laminaria solidungula basal blade length from nine sites in Stefansson Sound. Blade lengths were measured during summers 2004–2007. A growth year (GWYR) is defined as the period beginning 15 November one year and ending 15 November the following year. Values are means  $\pm$  SE. ND is no data.

| GWYR | DS-11 cm         | E-1 cm           | E-2 cm           | E-3 cm           | L-1 cm           | L-2 cm           | B-1 cm           | W-1 cm           | W-3 cm           |
|------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|
| 2003 | $7.20 \pm 0.50$  | $4.38 \pm 0.36$  | $7.85 \pm 0.40$  | $5.24 \pm 0.40$  | $6.56 \pm 0.54$  | $6.53 \pm 0.86$  | $7.16 \pm 0.60$  | $7.93 \pm 0.51$  | $10.45 \pm 0.94$ |
| 2004 | $25.46 \pm 0.93$ | $10.93 \pm 0.37$ | $9.98 \pm 0.38$  | $22.79 \pm 0.76$ | $18.03 \pm 0.59$ | $14.67 \pm 0.59$ | $18.59 \pm 0.69$ | $13.73 \pm 0.53$ | $20.88 \pm 1.04$ |
| 2005 | $27.65 \pm 0.85$ | $18.97 \pm 0.53$ | $19.10 \pm 0.76$ | $28.54 \pm 0.93$ | $23.77 \pm 0.91$ | $21.82 \pm 0.84$ | $24.76 \pm 1.02$ | $18.49 \pm 0.71$ | $24.94 \pm 1.05$ |
| 2006 | $47.32 \pm 1.64$ | $16.71 \pm 0.71$ | $18.04 \pm 0.96$ | $25.84 \pm 1.07$ | $18.85 \pm 0.75$ | $36.77 \pm 1.72$ | $20.70 \pm 1.00$ | ND               | ND               |

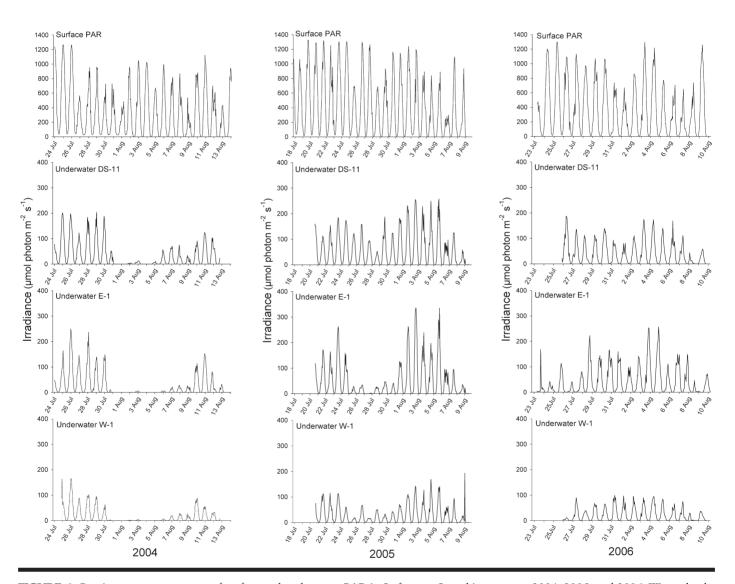


FIGURE 6. Continuous measurements of surface and underwater PAR in Stefansson Sound in summers 2004, 2005, and 2006. Water depths ranged from 5 m (E-1) to 6.5 m (DS-11 and W-1). Missing surface PAR data in 2004 and 2005 were obtained from an irradiance sensor maintained 5 km distant at SDI by Veltkamp and Wilcox (2007).

before rebounding to about 100  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. In 2005, underwater PAR was lowest at E-1 and W-1 from 26–31 July in response to a storm event that generated winds in excess of 9 m s<sup>-1</sup> from the east-northeast but which had little effect on underwater PAR at DS-11.

Overall, water transparency, as reflected by consistently low k values (generally <1.0 m<sup>-1</sup>) and high light transmission (>55% m<sup>-1</sup>) at all three sites, was highest in 2006 as reflected by the absence of significant storm events during the study period (Figure 7). In all three years, mean irradiance was significantly (p < 0.05) lower at site W-1 compared to all other sites (Table 4) for the period 26 July to 10 August although the surface irradiance was high on most days. Values recorded from both surface and underwater PAR sensors are similar to irradiance measurements made in Stefansson Sound during previous studies (Dunton, 1990). Lowest light transmission (<10% m<sup>-1</sup>) and highest k values (2–3 m<sup>-1</sup>) were observed at all three sites in

2004. Conditions in 2005 improved considerably, with just one peak in water turbidity occurring in late July as noted earlier. The shallower depth at E-1, compared to W-1 and DS-11 amplifies the *k* values at this site for similar levels of underwater PAR recorded at all three sites.

#### **DISCUSSION**

The relatively uniform and low water column chlorophyll *a* concentrations measured across Stefansson Sound from 2004–2006 (Figure 5) agree well with earlier assessments made through the same area in 2001, but were lower than those recorded in 2002 by Aumack (2003). Chlorophyll was consistently lower at 2 m than at 4 m depths, which may reflect the consistently higher availability of inorganic nutrients at depth in all three years for silicate, ammonium, phosphate, and nitrate + nitrite (Table 1). Water

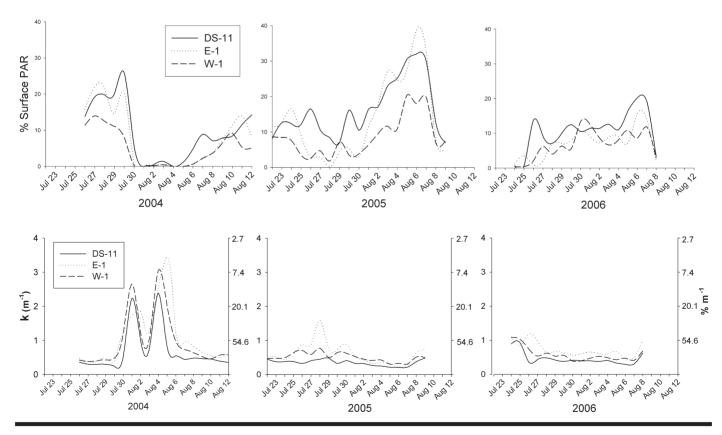


FIGURE 7. Measurements of water transparency at various sites in Stefansson Sound from 2004 to 2006. Top panel: percentage of surface irradiance (%SI). Bottom panel: diffuse attenuation coefficient expressed as k-values (left axis) and as % m<sup>-1</sup> (right axis). Underwater measurements were made at kelp canopy levels at E-1 (4.6 m), W-1 (5.8 m), and DS-11 (6.1 m) with a spherical quantum sensor.

TABLE 4. Mean PAR for each site for the period 26 July–10 August (n = 1071 hourly measurements for each site) from 2004–2006. Asterisks denote site means that are significantly different (p < 0.05) within years. Average surface PAR for the same period is provided for reference.

| Mean PAR (μmol m <sup>-2</sup> s <sup>-1</sup> ) |       |       |       |         |  |  |  |
|--|-------|-------|-------|---------|--|--|--|
| Year   | W-1   | E-1   | DS-11 | Surface |  |  |  |
| 2004   | 15.3* | 23.3  | 28.0  | 314.9   |  |  |  |
| 2005   | 28.3* | 45.1* | 59.2* | 356.0   |  |  |  |
| 2006   | 23.3* | 48.1  | 42.0  | 347.9   |  |  |  |

temperatures were about 2°C warmer in 2006 compared to 2004 and 2005, which was coincident with a 6–7‰ drop in surface and bottom water salinities in 2006. Decreased salinities and pH in 2006 likely reflect freshwater input from the nearby Sagavanirktok River, which produced a distinct brackish water layer to 4 m depths that was not evident in 2004 or 2005. Measurement of bottom salinity at depths exceeding 6 m at various sites (data not reported here) indicate that this brackish water layer seldom extended to the seafloor, sparing benthic organisms at depths greater than 5 m exposure to widely fluctuating salinities and temperatures. However, vertical gradients in temperature and/ or salinity were apparent all three years, producing a clear pycnocline.

Based on in situ frond length measurements made on Laminaria solidungula plants in summers 2005 and 2006, we were able to make new calculations of kelp biomass at sites DS-11 (n = 226) and E-1 (n = 53). Areal biomass at each site was calculated using a correlation coefficient between basal blade dry weight (gdw) and basal blade length (cm) developed for the Stefansson Sound Boulder Patch using specimens collected between 1980 and 1984 (n = 912; Figure 8). Biomass at DS-11 (>25% rock cover) ranged from 5 to 45 gdw m<sup>-2</sup> (mean 23 gdw m<sup>-2</sup>) compared to a range of 0.5 to 2.7 gdw  $m^{-2}$  (mean 1.7 gdw  $m^{-2}$ ) at site E-1 (10-25% rock cover). Intermediate levels of biomass were recorded at sites W-3 (10.1 gdw m<sup>-2</sup>) and E-3 (14.8 gdw  $m^{-2}$ ), both designated as sites with >25% rock cover by Toimil (1980). The range in biomass at DS-11 is within the estimates reported by Dunton et al. (1982). Estimates of benthic biomass at sites in Stefansson Sound are critical for calculation of realistic basin-wide benthic production models in relation to changes in PAR.

Blade elongation in *Laminaria solidungula* displays large spatial and temporal variability as reflected in mea-

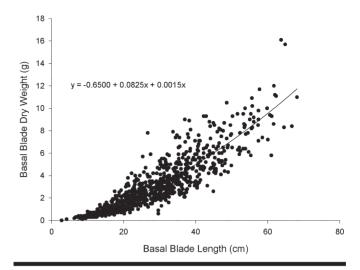


FIGURE 8. Correlation between basal blade dry weight (g) and basal blade length (cm) in *Laminaria solidungula*.

surements from nine sites over the past decade (Figure 9). In addition, mean blade growth at two sites, DS-11 and E-1, made since 1977 and 1981, respectively, reveal some interesting long-term interannual variations (Figure 10). The two years of lowest growth (1999 and 2003) occurred relatively recently and coincide with summers characterized by intense storm activity that likely produced extremely turbid water conditions resulting in extremely

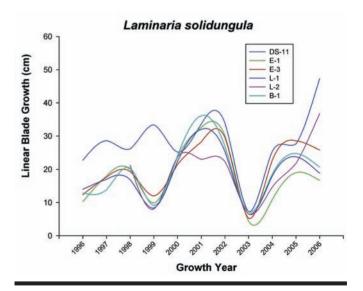


FIGURE 9. Variation in annual growth in *Laminaria solidungula* from 1996 to 2006 at sites occupied in the Stefansson Sound Boulder Patch. Measurements are based on blade lengths of plants collected between 2001 and 2006. Values are means  $\pm$  SE.

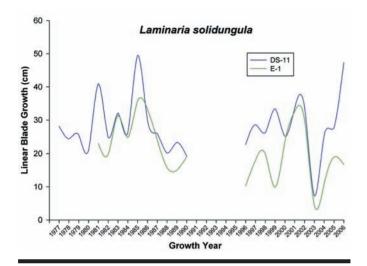


FIGURE 10. Mean annual linear growth of *Laminaria solidungula* from 1977 to 2006 at sites DS-11 (blue) and E-1 (green) in Stefansson Sound Boulder Patch.

low levels of ambient light. Wind speed data collected at SDI by Veltcamp and Wilcox (2007) from 2001 to 2006 revealed that 2003 was marked by the highest maximum wind speeds and lowest light levels in July and August when compared to all other years (Table 5). In addition, since light attenuation was lowest in offshore waters and increased with proximity to the coastline, kelp growth at site E-1 was consistently much less than at DS-11 (Table 3). Changes in local climatology clearly has an important role in regulating kelp growth as a consequence of increased cloud cover and sustained winds that negatively impact kelp growth (Figure 11).

The exceptionally low growth of kelp in 2003 (4–7 cm) indicates that kelp in the Boulder Patch are living close to their physiological light limits and might die if subjected to multiple years of low water transparency. Other factors

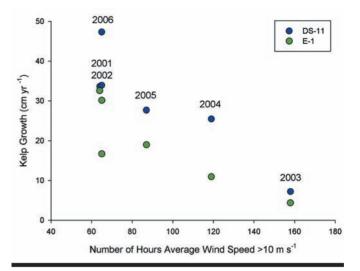


FIGURE 11. Annual mean linear growth of *Laminaria solidungula* as a function of the number of hours that wind speed exceeded 10 m s<sup>-1</sup> at SDI in July and August, from 2001 to 2006. Wind speed data from Veltcamp and Wilcox, 2007. Sites DS-11 (blue) and E-1 (green) are located in the Stefansson Sound Boulder Patch.

that could exacerbate light limitation include increases in temperature and lower salinities. As noted above, between 2004 and 2006 mean water temperature over the study area more than doubled and salinity measurements dropped significantly to depths of 4 m. Since much of the Boulder Patch occurs at depths less than 6 m, kelp could be exposed to periods of lower salinities and higher temperatures during periods of higher than normal precipitation and/or freshwater inflows. Thus, continuous monitoring of kelp growth in Stefansson Sound provides valuable insights into the role of local climate in affecting water transparency through processes that suspend and/or promote phytoplankton (chlorophyll) production.

**TABLE 5.** Open-water meteorological data collected at SDI from 2001–2006 for the period 10 July–9 September (from Veltkamp and Wilcox, 2007).

|      | Wind Speed m s <sup>-1</sup> |         | Number of Hours            | Average Wind Direction | Average Solar Radiation |  |
|------|------------------------------|---------|----------------------------|------------------------|-------------------------|--|
| Year | Average                      | Maximum | $> 10 \; meters \; s^{-1}$ | °Mag                   | $ m W~m^{-2}$           |  |
| 2001 | 5.10                         | 7.18    | 64                         | 157                    | 133.7                   |  |
| 2002 | 4.67                         | 6.50    | 65                         | 174                    | 145.8                   |  |
| 2003 | 5.62                         | 7.98    | 158                        | 172                    | 123.3                   |  |
| 2004 | 5.46                         | 7.37    | 119                        | 149                    | 150.6                   |  |
| 2005 | 5.57                         | 7.47    | 87                         | 125                    | 145.8                   |  |
| 2006 | 5.12                         | 6.94    | 65                         | 148                    | 131.5                   |  |

We derived measures of light attenuation from both synoptic measurements collected at the 30 survey sites, and continuously from dataloggers deployed on the seabed. These coincident measurements of surface and underwater light exhibited distinct geographical patterns and interannual variations between 2004 and 2006 (Figures 3 and 7). Attenuation was consistently elevated in coastal zones, with highest values observed near Endicott Island and SDI indicating more turbid water closer to shore. Lower values were recorded offshore along the eastern and northeastern sides of Stefansson Sound. Attenuation coefficients were also highest in shallower water depths as reflected by site E-1, compared to the lower k values at the deeper sites (W-1 and DS-11). The higher *k* values recorded at the permanent sites reflect the value of continuously recording instruments; during major storms it is virtually impossible to conduct field measurements, but these events are perhaps the most interesting and important in computing an accurate assessment of benthic production. We noted that k values were nearly three times higher at the three permanent sites than at any point during synoptic sampling at 30 sites, despite the use of a scalar sensor in the calculation of k at the permanent sites. The application of cosine measurements of PAR from the permanent sites would have resulted in still higher values for k.

Our data and that of Aumack et al. (2007) strongly suggest that both the spatial and interannual variations in water transparency are correlated with TSS. In general, the majority of the Boulder Patch, including areas with dense kelp populations (>25% rock cover), was found predominantly in clear offshore waters where attenuation measurements were consistently less than 1.0 m<sup>-1</sup>. Our data show that years characterized by frequent storm activity are likely to have significant impacts on annual kelp growth and production. Local climatic change that results in more frequent storm events are thus likely to have a significant and detrimental impact on nearshore kelp bed community production, and could lead to large scale losses of these plants and their associated diverse epilithic and epiphytic fauna.

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#### LITERATURE CITED

- Aumack, C. F. 2003. Linking Water Turbidity and TSS Loading to Kelp Productivity within the Stefansson Sound Boulder Patch. M.S. thesis. University of Texas at Austin, Marine Science Institute, Port Aransas.
- Aumack, C. F., K. H. Dunton, A. B. Burd, D. W. Funk, and R. A. Maffione. 2007. Linking Light Attenuation and Suspended Sediment Loading to Benthic Productivity within an Arctic Kelp Bed Community. *Journal of Phycology*, 43:853–863.
- Ban, S. M., J. Colonell, K. H. Dunton, B. Gallaway, and L. Martin. 1999. Liberty Development: Construction Effects on Boulder Patch Kelp Production. Report to BP Exploration Alaska, Inc., Anchorage.
- Dunton, K. H. 1984. "An Annual Carbon Budget for an Arctic Kelp Community." In *The Alaska Beaufort Sea—Ecosystems and Environment*, ed. P. Barnes, D. Schell, and E. Reimnitz, pp. 311–326. Orlando, Fla.: Academic Press.
- 1985. Growth of Dark-Exposed Laminaria saccharina (L.) Lamour and Laminaria solidungula (J.) Ag. (Laminariales, Phaeophyta) in the Alaskan Beaufort Sea. Journal of Experimental Marine Biology and Ecology, 94:181–189.
- 1990. Growth and Production in *Laminaria solidungula*: Relation to Continuous Underwater Light Levels in the Alaskan High Arctic. *Marine Biology*, 106:297–304.
- . 1992. Arctic Biogeography: The Paradox of the Marine Benthic Fauna and Flora. *Trends in Ecology and Evolution*, 7:183–189.
- Dunton, K. H., and C. M. Jodwalis. 1988. Photosynthetic Performance of *Laminaria solidungula* Measured in situ in the Alaskan High Arctic. *Marine Biology*, 98:277–285.
- Dunton, K. H., E. Reimnitz, and S. Schonberg. 1982. An Arctic Kelp Community in the Alaskan Beaufort Sea. *Arctic*, 35(4):465–484.
- Dunton, K. H., and D. M. Schell. 1986. A Seasonal Carbon Budget for the Kelp *Laminaria solidungula* in the Alaskan High Arctic. *Marine Ecology Progress Series*, 31:57–66.
- Dunton, K. H., and S. V. Schonberg. 2000. "The Benthic Faunal Assemblage of the Boulder Patch Kelp Community." In *The Natural History of an Arctic Oil Field*, ed. J. C. Truett and S. R. Johnson, pp. 338–359. *San Diego*, *Calif*.: Academic Press.
- Henley, W. J., and K. H. Dunton. 1995. A Seasonal Comparison of Carbon, Nitrogen, and Pigment Content in *Laminaria solidungula* and *L. saccharina* (Laminariales, Phaeophyta) in the Alaskan Arctic. *Journal of Phycology*, 31:325–331.
- . 1997. Effects of Nitrogen Supply and Seven Months of Continuous Darkness on Growth and Photosynthesis of the Arctic Kelp,

- Laminaria solidungula. Limnology and Oceanography, 42(2): 209-216.
- LGL Ecological Research Associates, Inc., and K. H. Dunton. 1992. Endicott Beaufort Sea Boulder Patch Monitoring Program (1984–1991). Final Report to BP Exploration (Alaska) Inc., Anchorage, Alaska.
- Martin, L. R., and B. J. Gallaway. 1994. The Effects of the Endicott Development Project on the Boulder Patch, an Arctic Kelp Community in Stefansson Sound, Alaska. *Arctic*, 47(1):54–64.
- McClelland, J. W. 2006. A Pan-Arctic Evaluation of Changes in River Discharge during the Latter Half of the 20th Century. Geophysical Research Letters, 33:L06715, doi:10.1029.
- McKinney, M. L. 1998a. On Predicting Biotic Homogenization: Species-Area Patterns in Marine Biota. *Global Ecology and Biogeography Letters*, 7:297–301.
- ——. 1998b. Is Marine Biodiversity at Less Risk? Evidence and Implications. Diversity and Distributions, 4:3–8.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What Is the Observed Relationship between Species Richness and Productivity? *Ecology*, 82:2381–2396.
- Paine, R. T. 2002. Trophic Control of Production in a Rocky Intertidal Community. *Science*, 296(5568):736–739.
- Parsons, T. R., Y. Maita, and C. M. Lalli. 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Oxford: Pergamon.

- Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The Maintenance of Species Diversity by Disturbance. *Quarterly Review of Biology*, 64:393–418.
- Rosenzweig, M. L. 2001. Loss of Speciation Rate Will Impoverish Future Diversity. *Proceedings of the National Academy of Sciences*, 98: 5404–5410.
- SAS Institute Inc. 1985. SAS/STAT Guide for Personal Computers. Version 6 ed. SAS Institute Inc., Cary, North Carolina.
- Toimil, L. J. 1980. Investigation of Rock Habitats and Sub-Sea Conditions, Beaufort Sea, Alaska. Volume 2. Report to Exxon Company, USA, by Harding-Lawson Associates, Novato, California.
- Veltkamp, B., and J. R. Wilcox. 2007. Nearshore Beaufort Sea Meteorological Monitoring and Data Synthesis Project. Final Report to U.S. Department of the Interior Minerals Management Service Alaska OCS Region, Anchorage, Alaska.
- Welschmeyer, N. A. 1994. Fluorometric Analysis of Chlorophyll *a* in the Presence of Chlorophyll *b* and Pheopigments. *Limnology and Oceanography*, 39(8):1985–1992.
- Worm, B., H. K. Lotze, C. Bostroem, R. Engkvist, V. Labanauskas, and U. Sommer. 1999. Marine Diversity Shift Linked to Interactions among Grazers, Nutrients and Propagule Banks. *Marine Ecology Progress Series*, 185:309–314.