Developmental and Environmental Sources of Variation on Annual Growth Increments of *Ascophyllum nodosum* (Phaeophyceae)

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Annual growth segments of *Ascophyllum nodosum* (L.) Le Jolis (Fucales, Fucaceae) are denoted by air bladders that form each spring. By examining annual growth segments, it may be possible to infer information about the physical conditions during the growth period; however, it is uncertain whether the annual segments will expand in size after the initial growth. We examined *A. nodosum* segments from three populations in Nova Scotia, and statistically evaluated whether the annual growth (length, mass, and maximum diameter) of segments was independent of the age of the frond, whether the segments increased in size after the initial growth, and whether the segment lengths were correlated with mean water temperatures and mean air temperatures when the segments were formed. We found that the growth in length of *A. nodosum* is dependent on the age of the frond, but frond age explained less than 12 % of the overall variation in length. However, the mass and maximum diameter of segments were independent of the age of the frond. Differences occurred between the lengths of segments formed in different years, but there was no significant correlation with regional mean water or air temperatures. This study indicates that the length of *A. nodosum* segments may be an indicator of the annual physical characteristics of a site, but future studies are needed to identify which factors have the strongest influence on growth patterns.

Key Words: *Ascophyllum nodosum*, development, Nova Scotia, Phaeophyceae, temperature

INTRODUCTION

Ascophyllum nodosum (L.) Le Jolis (hereafter *Ascophyllum*) is a perennial brown alga that, together with *Fucus vesiculosus* L., dominates sheltered to moderately exposed rocky intertidal shores of the temperate North Atlantic (David 1943; Adey and Hayek 2005). Populations of *Ascophyllum* consist of a small number of large plants (genets), where modular fronds grow from a common holdfast (David 1943; Moss 1971; Cousens 1985; Lubchenko 1986; Åberg 1992). Frond densities in the mid-intertidal region can reach many hundreds per square meter, and completely cover a large proportion of rocky shores in overlapping layers (Garbary *et al.* 2006). Besides being a dominant food source, this alga influences the local community structure by reducing heat and desiccation stress, by providing habitat for underlying benthic organisms (Bertness *et al.* 1999), and by being the basis for a complex symbiotic community (Deckert and Garbary 2005; Garbary *et al.* 2005). In Nova Scotia,

where *Ascophyllum* is particularly prevalent, it is commercially harvested for various applications (Sharp 1987; Lazo *et al.* 1994).

Fronds of *Ascophyllum* have apical, meristematic growth of approximately 100 mm y^{-1} in Nova Scotia (Cousens 1982). The majority of primary fronds are dichotomously branched, although monopodial and trichotomous branching have been reported (David 1943). Air bladders, which keep the plants afloat at high tide, are produced after one to several years of growth (Keser and Larson 1984; Cousens 1986) and are a more or less permanent feature of each frond (Garbary *et al.* 2006). In the spring, growth is initiated with the formation of an air bladder, which is complete by June. Assuming annual production of bladders, a minimum age of fronds can be determined by counting the number of air bladders on the longest unbroken axes (Cousens 1986; Sharp 1987; Brackenbury *et al.* 2006). The extent to which growth occurs between air bladders is unknown. Growth rates of fronds of *Ascophyllum* have been shown to depend on the size class of the frond, degree of interference and algal canopy, amount of sunlight, population from which the fronds originate (Cousens 1982, 1985; Lazo *et al.* 1994;

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Stengel and Dring 1997), and water temperature (Strömgren 1983; Vadas and Wright 1986; Sharp 1987). Here we focus on growth of frond segments (= internodes of Cousens 1982) that are at least one year old, and attempt to distinguish age-related and environmental-related influences on growth. Thus if little to no growth occurs in segments subsequent to their formation, then differences in segment size might be attributed to environmental factors. By examining annual growth segments in *Ascophyllum*, it may therefore be possible to infer past environmental conditions. Analogous morphologies which result in annual growth increments occur in the stipes of certain Laminariales, including species of *Laminaria*, *Ecklonia* and *Pterygophora* (Kain 1963, 1979; Novaczek 1981; De Wreede 1984). While annual growth rings are formed in these taxa that allow for aging of the fronds, these fronds are typically shorter lived than *Ascophyllum* and growth increments are highly variable. Consequently, *Ascophyllum* may be a better model system for examining differential annual growth associated with year to year differences in environmental conditions.

In this study, we examine the following hypotheses:

1) the amount of annual growth (length, mass, and maximum diameter) of *Ascophyllum* is independent of the frond age,

2) the annual segment does not elongate after the initial growth, but increases in width and mass, and

3) the annual growth (length, mass, and diameter) is dependent on water temperature and air temperature.

The first hypothesis is based on the fact that a cursory inspection of *Ascophyllum* fronds from a particular population shows a more or less regular placement of bladders along thalli, regardless of frond age. Hypothesis two is based on a similar observation, but also the fact that the branch widths are usually minimal at the frond apex and reach a maximum at some older position on the frond. The third hypothesis addresses the issue that if segment size is not dependent upon developmental integration in the thallus, then it is likely dependent upon environmental conditions existing when that segment actually grew. Here we use mean monthly air and water temperatures as factors that might explain differential segment size.
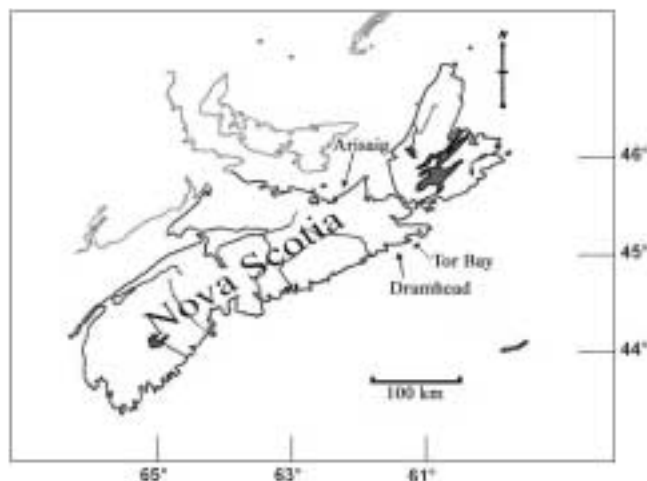

Fig. 1. Map of Nova Scotia, showing the locations of sampling sites.

MATERIALS AND METHODS

Frond Collection

Three populations of *Ascophyllum* were selected from the Gulf of St. Lawrence (Arisaig, 45°46'N, 62°10'W) and Atlantic (Tor Bay, 45°11'N, 61°21'W, and Drumhead, 45°08'N, 61°36'W) coasts of Nova Scotia (Fig. 1). The three sites are moderately protected from wave exposure (maximum at Tor Bay, minimum at Arisaig) by off-shore islands or rock outcrops. Moderate ice scouring occurs at Arisaig, although we were able to collect undamaged fronds with moderate difficulty. The Arisaig population grew on granite bedrock, whereas the substratum at Tor Bay and Drumhead were granitic boulder fields. The slope at the three sites varied from very steep (> 60° at Arisaig) to shallow (< 15° at Drumhead and Tor Bay). Salinity at Arisaig is typically 28 psu, whereas at Tor Bay and Drumhead it is ca. 33 psu.

Approximately 120 fronds were haphazardly collected from each site, from the middle of the *Ascophyllum* zone between October 5 and 18, 2006. Fronds were collected with holdfasts intact, during low tides. Heavily epiphytized fronds were avoided as epiphytes affect growth patterns (e.g., Kraberg and Norton 2007). Specimens were stored in plastic bags for transport to maintain moisture, and stored at 5°C prior to processing.

Laboratory Techniques

Only fronds with an unbroken primary axis with three or more air bladders were included in the analyses. The longest unbroken axis of the frond was selected, and all lateral branches and receptacles were cut off with a razor

blade. We isolated annual segments by making an incision below each air bladder. By doing so, we were able to identify the time-period during which each segment was formed. Fronds were processed within 20 minutes of removing them from the plastic bags in which they were stored, to avoid dehydration. Frond segments were blotted with paper towels before weighing. The following measurements were made for each segment: length (to the nearest mm) with a metric ruler, mass (to the nearest 0.0001 g) using an Ohaus Explorer Pro balance, and maximum diameter (to the nearest 0.1 mm) using a vernier caliper.

Statistical Analyses

To determine whether or not the *Ascophyllum* fronds came from populations with different morphological characteristics, we first examined data with non-metric multidimensional scaling (nMDS) ordination. Distinctions among populations were statistically confirmed with ANOSIM, based on Bray-Curtis similarities on untransformed data, using segment length, maximum segment diameter and segment mass as defining criteria. The ANOSIM is a randomization test, which is an analogue to an ANOVA for multivariate data (Clarke and Gorley 2006; Clarke *et al.* 2006).

To determine whether the growth in length of *Ascophyllum* is a function of the age of the frond, we did Type I linear regression analyses with frond age as a fixed independent variable, and the metrics for the 2006, 2005, 2004, or 2003 segment sizes as the dependent variable in each regression (e.g., Howell 1992). This was repeated for each of the populations. In each case, we tested the significance of the Pearson's product-moment correlation coefficient (r). We also carried out similar regression analyses and significance tests to determine whether growth in width, mass, or tissue density (g mm^{-1}) is dependent on the frond age.

To determine whether there is variation in growth between years, we compared the mean length, width, maximum diameter, and tissue density (g mm^{-1}) between successive segments using ANOVA tests and Tukey HSD multiple comparison tests. By looking at the average length, width, mass, and tissue density (g mm^{-1}) of segments successively towards the frond holdfast, we were able to determine whether the segments became longer, wider, and thicker with age. Because Tukey HSD tests did not always reflect differences in successive years when ANOVAs indicated significance, we also compared means with 95% confidence intervals.

Differences in the results predicted by each method likely reflects the Bonferroni adjustment for the family-wise error rate; this is accounted for in the Tukey HSD calculations, but not in the confidence intervals (see Moran 2003 for discussion).

We did Type II linear regression analyses with the average air temperature between April and October, or sea surface temperature between April and August of each growing season, as the random, independent variable, and the average segment length, mass, width, or tissue density (g mm^{-1}) for each year as the dependent variable. Temperatures were averaged for April-October, and not the rest of the year because the majority of *Ascophyllum* growth occurs from the late spring until early autumn (David 1943). Air temperature data from Deming, Nova Scotia (45°13' N, 61°10' W, elevation 15.8 m) were obtained from Environment Canada National Climate Data and Archive (2006). Water temperature data are from the Bedford Basin, Halifax Co. (41°04' N, 63°39' W) for which long-term temperature records are available (Li *et al.* 2006). Water temperature averages were calculated by averaging mean temperatures of the upper three meters of the water column from April to October. While other environmental factors (e.g., light and nutrients) may have similar or even greater impact on growth (Lobban and Harrison 1994), we do not have access to the relevant data on which to undertake the analyses.

Regression analyses were computed with Excel (Microsoft Corp., Redmond, WA), and significance tests were calculated manually, using tables and equations found in Zar (1999). ANOVAs and post-hoc Tukey HSD tests were performed in SPSS 13.0 (SPSS Inc., Chicago, IL), while nMDS ordination and ANOSIMs were performed in PRIMER-E 6.1.6 (PRIMER-E Ltd., Plymouth, UK).

RESULTS

There were significant differences in the morphological characteristics (segment length, mass, and maximum diameter) between the populations of *Ascophyllum* at Tor Bay, Arisaig, and Drumhead (Global R = 0.189, p < 0.01). The nMDS ordination indicated that populations from Arisaig and Drumhead were more similar than the population from Tor Bay. The average values for segment length, mass, maximum diameter and tissue density for each of the populations are given in Table 1. Tor Bay had the longest, heaviest and widest yearly growth segments,

Table 1. Average length, and maximum diameter, and tissue density of segment of *Ascophyllum nodosum* segments from Arisaig, Drumhead, and Tor Bay, Nova Scotia. Figures indicate mean ± s.e.

Location	Length (mm)	Mass (g)	Diameter (mm)	Tissue density (g mm^{-1})
Tor Bay	104.2 ± 1.8	1.0712 ± 0.0252	4.66 ± 0.05	0.0103 ± 0.0002
Arisaig	103.6 ± 1.6	0.8512 ± 0.0193	4.12 ± 0.03	0.0082 ± 0.0001
Drumhead	81.8 ± 1.8	0.5584 ± 0.0111	3.57 ± 0.03	0.0070 ± 0.0002
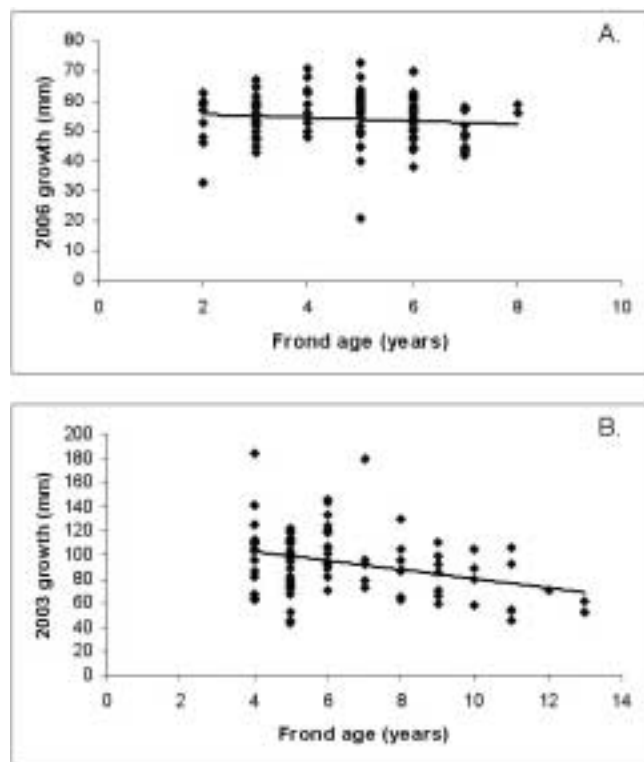
Fig. 2. Examples of regression analyses with extreme low and extreme high coefficients of determination. Regressions are the dependence of the annual growth in length of *Ascophyllum* on the age of the frond when the growth occurred. A. Arisaig segments formed in 2006 (r^2 = 0.011; p of r = 0.287). B. Drumhead segments formed in 2003 (r^2 = 0.110; p of r = 0.001)

Table 2. Summary of regression analyses of the dependence of the annual growth in length of *Ascophyllum* on the age of the frond when the growth occurred. Type I linear regression equations were based on scatterplots of length (dependent variable) and growth year (2006, 2005, 2004, or 2003) during which the segment was formed (fixed, independent variable). The slope refers to the slope of the best fit regression line (regression coefficient), the r^2 value is the coefficient of determination, and r is the Pearson's correlation coefficient.

Year of Segment growth (n)	Slope (mm y^{-1})	r^2	r	p of r
Arisaig				
2006 (115)	-0.538	0.011	0.104	0.287
2005 (115)	-1.588	0.017	0.130	0.164
2004 (107)	0.014	0.012	0.110	0.261
2003 (79)	-0.012	0.082	0.286	0.011
Drumhead				
2006 (102)	-0.745	0.039	0.198	0.046
2005 (102)	-2.125	0.064	0.254	0.010
2004 (100)	-2.659	0.090	0.299	0.003
2003 (94)	-3.777	0.110	0.331	0.001
Tor Bay				
2006 (102)	-1.747	0.018	0.328	<0.001
2005 (102)	-0.007	0.091	0.301	0.002
2004 (98)	-4.003	0.067	0.259	0.010
2003 (84)	-2.789	0.030	0.174	0.113

while Drumhead had the shortest, lightest and narrowest yearly growth segments. The differences in segment length were about 20%, but because of the differences in mass, there was a 30% difference in mass per unit length (g mm^{-1}) between the two extreme populations. The differences between the largest and smallest values (Tor Bay and Drumhead, respectively) were significant for all four metrics (length: F = 91.91, df = 2, p < 0.001; mass: F = 215.85, df = 2, p < 0.001; maximum diameter: F = 230.11, df = 2, p < 0.001; tissue density: F = 114.30, df = 2, p < 0.001) (Table 1). The Arisaig population was intermediate between the others for all metrics, although for segment length it was not significantly different from Tor Bay. For the remaining measures, Arisaig was significantly different from both Tor Bay and Drumhead. Based on these differences, our three hypotheses need to be evaluated separately in each population.

The correlation coefficient was significant in some cases between the annual growth in length of *Ascophyllum* and frond age when the growth occurred, particularly in plants from Drumhead and Tor Bay. These results suggest that the length of segments is slightly dependent on the age of the frond. However, in all cases, frond age explained less than 12% of the variation in segment length (see Figs 2 a and b for examples of scatterplots with extreme coefficients of determination). Even when these regressions were statistically significant, the slopes of the lines are very shallow (Table 2). A summary of these regression statistics from the scatter-

Table 3. Summary of regression analyses of the dependence of the annual tissue density (g mm^{-1}) *Ascophyllum* on the age of the frond when the growth occurred. Type I linear regression equations were based on scatterplots of tissue density (g mm^{-1}) (dependent variable) and growth year (2006, 2005, 2004, or 2003) during which the segment was formed (fixed, independent variable). The slope refers to the slope of the best fit regression line (regression coefficient), the r^2 value is the coefficient of determination, and r is the Pearson's correlation coefficient.

Segment growth year (n)	Slope (g mm^{-1} y^{-1})	r^2	r	p of r
Arisaig				
2006 (115)	0.0002	0.0798	0.2825	0.001
2005 (115)	0.0002	0.0168	0.1296	0.084
2004 (107)	0.0002	0.0369	0.1921	0.024
2003 (79)	0.0003	0.0172	0.1311	0.125
Drumhead				
2006 (102)	0.00006	0.0628	0.2506	0.006
2005 (102)	0.00002	0.0044	0.06633	0.255
2004 (100)	-2E-06	0.00002	0.00447	0.484
2003 (94)	0.00005	0.0063	0.07937	0.225
Tor Bay				
2006 (102)	0.00002	0.0016	0.0400	0.345
2005 (102)	0.00004	0.0027	0.0520	0.302
2004 (98)	0.00030	0.0504	0.2245	0.013
2003 (84)	0.00040	0.0614	0.2478	0.014

Fig. 3. Average length (with 95% confidence intervals) of *Ascophyllum* annual segments from (A) Arisaig, (B) Drumhead, and (C) Tor Bay, Nova Scotia. Letters represent significant differences between years of growth, identified by Tukey HSD post-hoc tests.

plots between length and year of growth is shown in Table 2. There were no significant correlations between the width or mass of each segment and frond age.

In some cases, the correlation coefficient was significant between the annual tissue density of *Ascophyllum* and the frond age during which the growth occurred (Table 3), again suggesting slight dependence of age on the annual growth. In all cases, the age of the frond explained less than 8% of the differences in tissue density. Table 3 summarizes the regression coefficients, coefficients of determination, Pearson's correlation coefficient, and the significance for the relationship between tissue density and year of segment growth for each of the populations.

There were significant variations among segment lengths in each of populations (Fig. 3a-c) (Arisaig: F = 9.40, df = 6, p < 0.001; Drumhead: F = 11.68, df = 11, p < 0.001; Tor Bay: F = 5.59, df = 9, p < 0.001). However, the variation did not follow any apparent pattern, indicating that the segments do not get longer after the initial growth. In the case of the Arisaig population, Tukey HSD tests did not reveal any significant differences in length between successive growth years; however, confi-
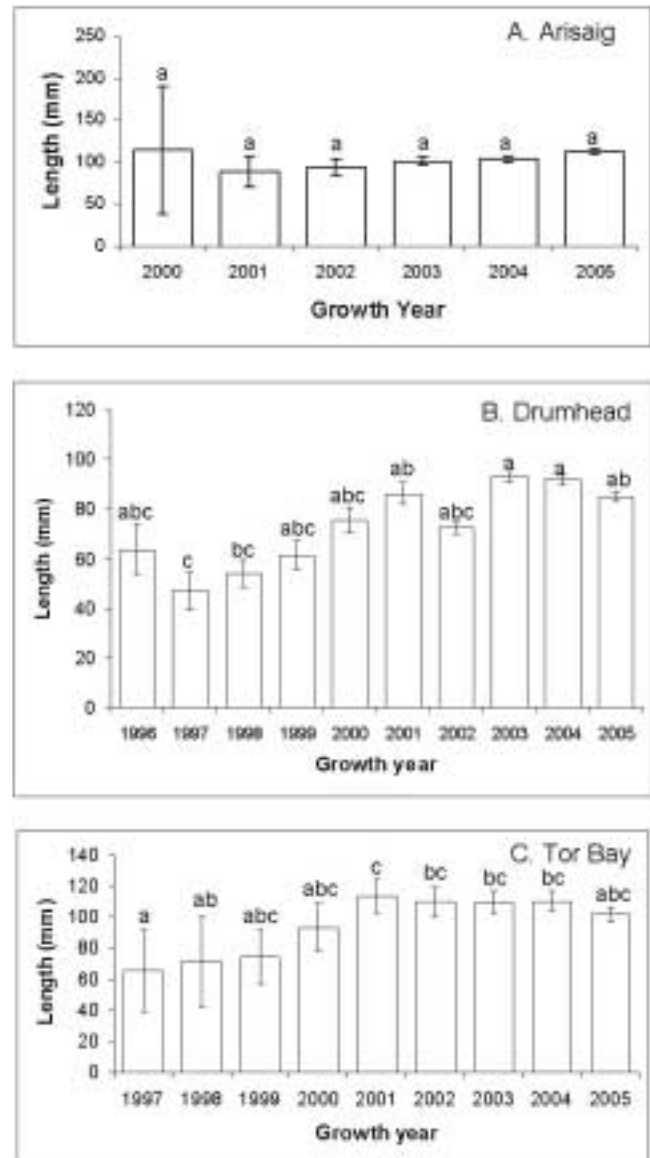
dence intervals suggest a significant difference between the length of segments from 2005 and 2002.

There were significant differences between the mass of segments formed in different years (Fig. 4a-c) (Arisaig: F = 2.074, df = 6, p = 0.055; Drumhead: F = 6.756, df = 11, p < 0.001; Tor Bay: F = 3.464, df = 9, p < 0.001). However, Tukey HSD tests did not separate the groups. Based on 95 % confidence intervals, the segments formed in 2005 had significantly less mass than older segments in populations from Drumhead and Tor Bay. We also found significant differences in the maximum diameter of seg-
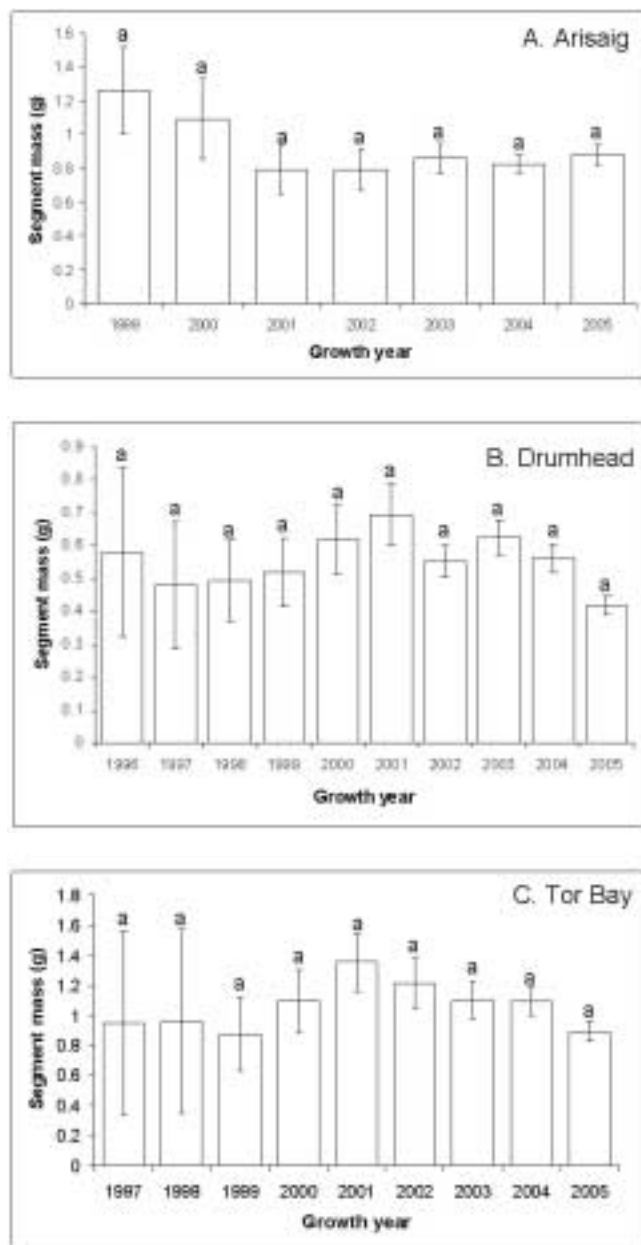
Fig. 4. Average mass (with 95% confidence intervals) of *Ascophyllum* annual segments from (A) Arisaig, (B) Drumhead, and (C) Tor Bay, Nova Scotia. Letters represent significant differences between years of growth, identified by Tukey HSD post-hoc tests.
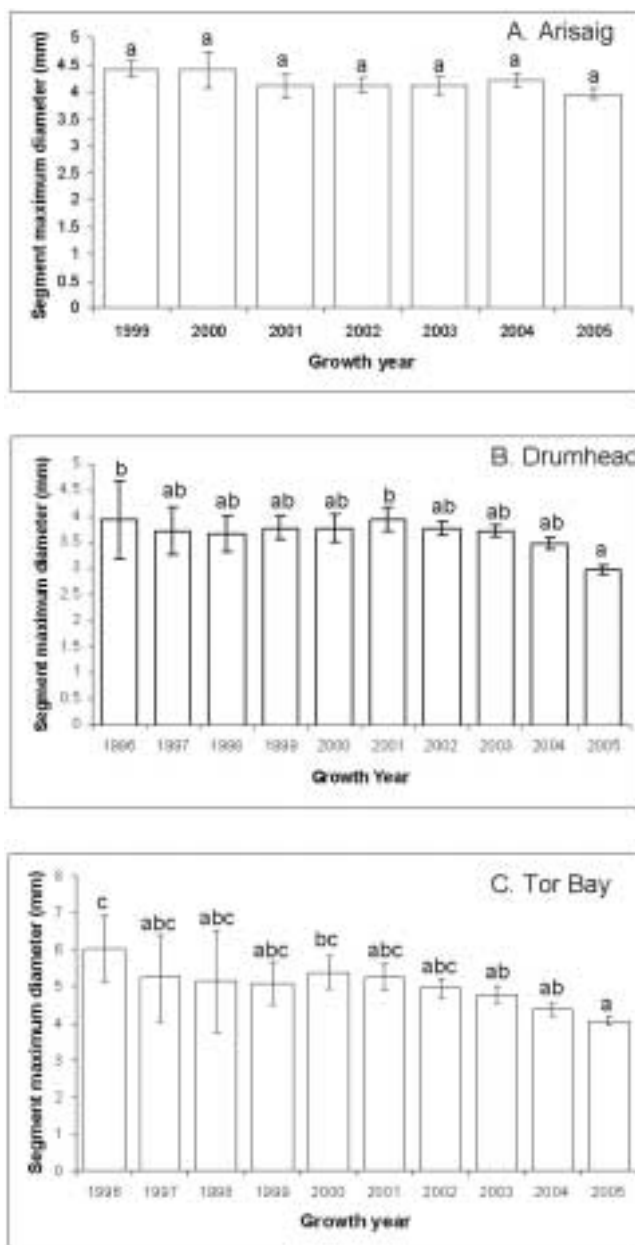

Fig. 5. Average maximum diameter (with 95% confidence intervals) of *Ascophyllum* annual segments from (A) Arisaig, (B) Drumhead, and (C) Tor Bay, Nova Scotia. Letters represent significant differences between years of growth, identified by Tukey HSD post-hoc tests.

ments at each of the sites (Fig. 5a-c) (Arisaig: F = 2.346, df = 6, p = 0.031; Drumhead: F = 14.325, df = 11, p < 0.001; Tor Bay: F = 10.913, df = 9, p < 0.001). In all populations, the 2005 segments were thinner than older segments. There were significant differences in tissue density (g mm^{-1}) between successive years at all of the sites (Fig. 6a-c) (Arisaig: F = 2.67, df = 5, p = 0.022; Drumhead: F = 10.59, df = 9, p < 0.001; and Tor Bay F = 6.182, df = 8, p < 0.001). The tissue density increased with successively

older segments.

There were no significant correlations between the average air temperature between April and October and the length of segments that grew during that time period (Fig. 7). There were also no significant correlations between the average sea surface temperature (top 3 m) between April and October and the length of annual segments (Fig. 8). Furthermore, there were no significant correlations between the average air temperature
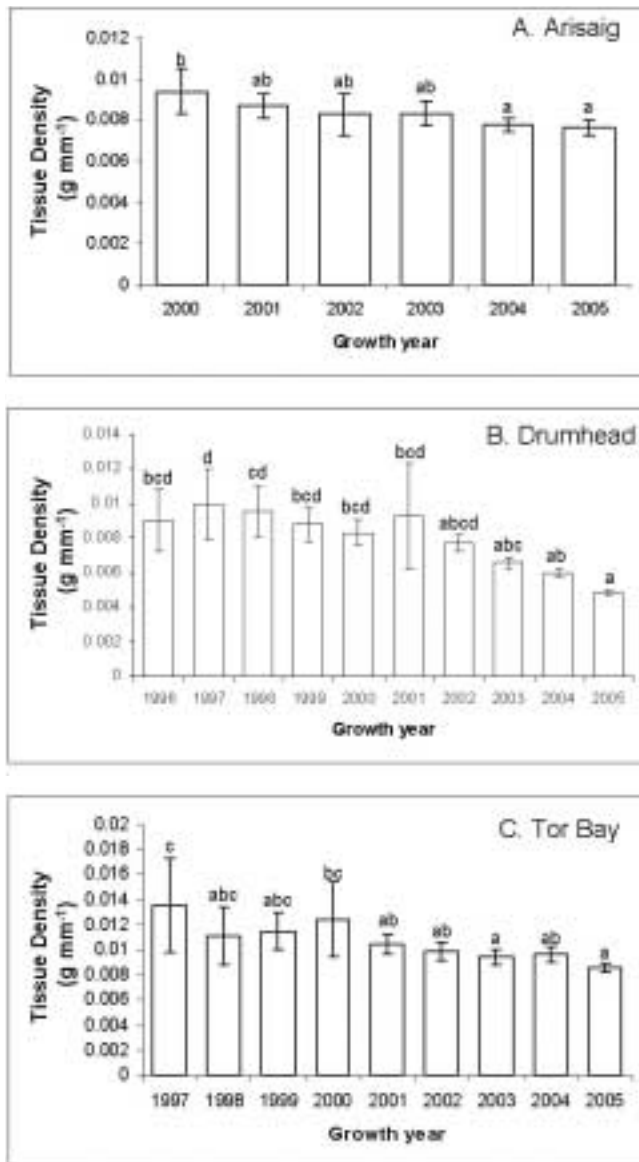
Fig. 7. Correlation between the average air temperature during April-October from Deming, NS and the average segment length of *Ascophyllum* fronds from Arisaig, Tor Bay, and Drumhead, Nova Scotia. The coefficients of determination (r^2) for Arisaig, Drumhead, and Tor Bay were 0.341, 0.078 and 0.0.008, respectively.

Fig. 8. Correlation between the average sea surface temperature from April-October from Bedford Basin, NS and the average segment length of *Ascophyllum* fronds from Arisaig, Tor Bay, and Drumhead, Nova Scotia. The coefficients of determination (r^2) for Arisaig, Drumhead, and Tor Bay were 0.102, 0.017 and 0.017, respectively.

Fig. 6. Average tissue density (g mm^{-1}) of *Ascophyllum* annual segments from (A) Arisaig, (B) Drumhead, and (C) Tor Bay, Nova Scotia. Letters represent significant differences between years of growth, identified by Tukey HSD post-hoc tests.

between April and October (Fig. 9), or the average sea surface temperature and the tissue density of segments (Fig. 10).

DISCUSSION

The significant differences that we detected between the morphological traits of *Ascophyllum* from the three sites indicate that we did indeed examine separate populations of the seaweed. It is interesting to note that the separations suggest that the Drumhead and Arisaig populations ha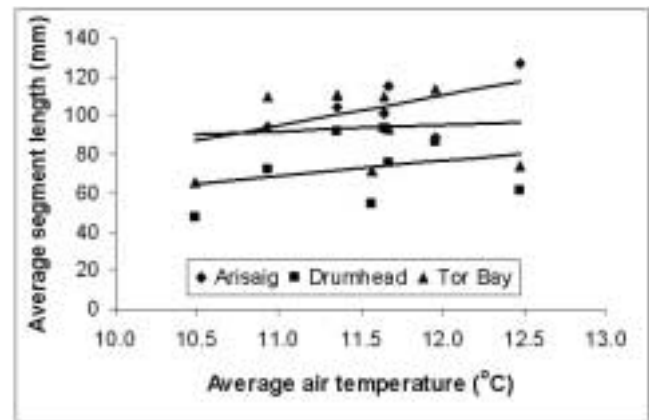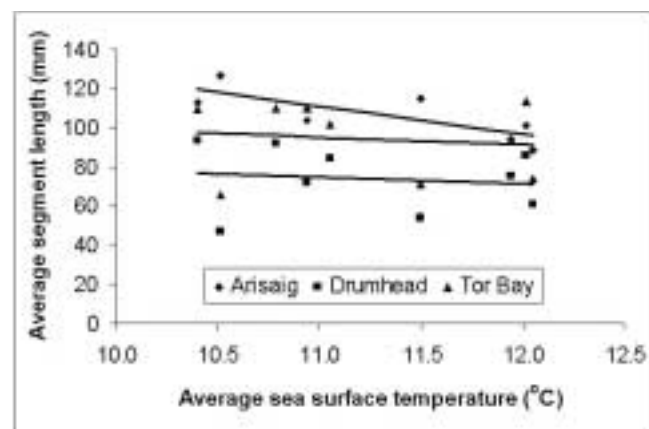ve more similar properties than either does to the Tor Bay population. We may be able to infer that the morphological differences are due to the environment, rather than genetic differences between the populations because of the proximity of sites. One would expect that the sites on the Atlantic coast would be more genetically similar and that this would be reflected in frond morphology, but instead, we found the opposite. The site at Tor Bay is more exposed to wave action than either of the other sites, which may be more important than presumed genetic similarity in determining the morphology of plants based on population proximity. This also suggests a high degree of phenotypic plasticity. This is consistent with a comprehensive study of morphological
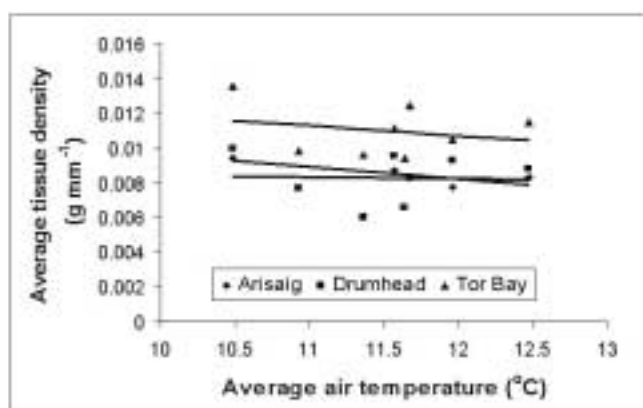
Fig. 9. Correlation between the average air temperature during April-October from Deming, NS and the tissue density (g mm^{-1}) of *Ascophyllum* fronds from Arisaig, Tor Bay, and Drumhead, Nova Scotia. The coefficients of determination (r^2) for Arisaig, Drumhead, and Tor Bay were 0.69, 0.002, and 0.058, respectively.
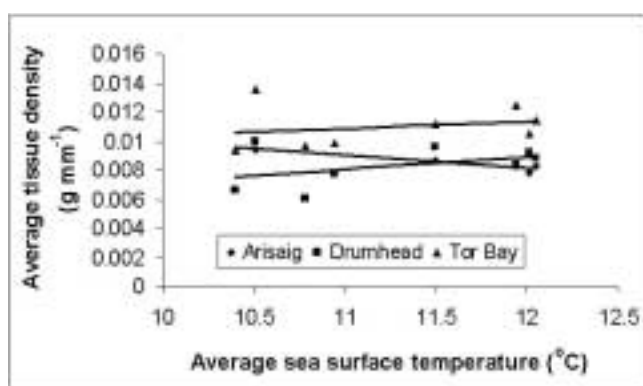

Fig. 10. Correlation between the average sea surface temperature from April-October from Bedford Basin, NS and the average tissue density (g mm^{-1}) of *Ascophyllum* fronds from Arisaig, Tor Bay, and Drumhead, Nova Scotia. The coefficients of determination (r^2) for Arisaig, Drumhead, and Tor Bay were 0.86, 0.18, and 0.43, respectively.

variation of *Ascophyllum* in Nova Scotia (McLean 2007). The current findings that growth rates were highest in more sheltered sites is consistent with observations by Vadas and Wright (1986).

This study indicates that the amount of annual growth is independent of frond age. There were no significant correlations between the mass or maximum diameter of segments, and the age of the segments during the growth period. Furthermore, there were no consistent patterns in the length of segments and the correlation with frond age, and the coefficient of determination was weak (< 12%) in all cases. This suggests that the annual growth is independent of frond age. Because one can assume that older fronds will be larger and therefore have higher

photosynthetic capabilities, it indicates that the fronds may be devoting their energy to other factors, such as annual reproductive output, repairing damaged frond segments (e.g., bladders, Garbary *et al.* 2006), growth of vegetative lateral branches, or increasing production of phlorotannins to deter herbivores (Pavia *et al.* 1999).

Although there were no apparent associations between the age of the fronds and segment growth, there were differences between segments from successive years of growth. Segments added in 2005 were thinner and lighter than older segments at all sites. This indicates that as fronds age, they become wider, and increase in mass, even though length does not increase. The fact that length increase is a small component of developmental changes may indicate that it can be used as an indicator of environmental conditions. Similar to the use of tree rings in dendrochronology (e.g. Schweingruber 2007), there is a potential for the annual growth increments of *Ascophyllum* to integrate environmental conditions during the growth period when segments undergo most of their growth. Thus, in a growing season when conditions are suboptimal, one could expect a smaller annual growth increment than when conditions are closer to optimal. The limited subsequent changes in length suggest that length increments are a permanent record of environmental impacts on growth.

We examined whether the sea surface temperature or air temperature during the peak growing times (April to October) influenced the annual growth of *Ascophyllum* segments. There was no significant correlation between either variable. This is contrary to the findings of Strömgren (1977), who measured *in situ* growth rates of *Ascophyllum*, and found that growth rates were markedly reduced in reduced temperature. Vadas and Wright (1986) also found that warmer water in more southern sites resulted in faster frond growth rates. Keser *et al.* (2005) examined annual increments in *Ascophyllum* at sites with elevated temperature. They found increased growth rates up to 25°C, with mortality when temperatures exceeded 27-28°C.

Based on our results, it would seem that potential impacts of temperature on growth increments in *Ascophyllum* are being masked by other environmental effects. It may be that temperature variation is simply not sufficient to induce large enough changes in growth that we can resolve, or that the temperature data we used is not sufficiently localized to our sites to provide meaningful insight. Alternatively, other aspects of temperature may be more significant (e.g., day- night variation or

degree days above 20°C). Given the non site-specific origin of these data, and the lack of relevant long-term records, we did not attempt to use other descriptors of temperature phenomena to explain our morphological observations. Other aspects of weather and environment during the growing season may have more influence on growth than slight variations in average temperature. For example, differences in nutrient levels among years may lead to differential growth. In addition, differences in the light environment (extent of cloud or fog cover in a given year) may be more significant than temperature variation. Future studies should focus on these variables and the growth of *Ascophyllum*. It is also possible that these and other factors operate in opposing directions, to produce the very limited extent of segment growth differences that we observed in the three populations.

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REFERENCES

Åberg P. 1992. A demographic study of two populations of the seaweed *Ascophyllum nodosum*. *Ecology* **73:** 1473-1487.

Adey W.H. and Hayek L.C. 2005. The biogeographic structure of the western North Atlantic rocky intertidal. *Crypt. Algol.* **26:** 35-66.

Bertness M.D., Leonard G.H., Levine J.M., Schmidt P.R. and Ingraham A.O. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* **80:** 2711-2726.

Brackenbury A.M, Kang, E.J. and Garbary D.J. 2006. Air pressure regulation in air bladders of *Ascophyllum nodosum* (Fucales, Phaeophyceae). *Algae* **21:** 245-251.

Clarke K.R. and Gorley R.N. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd. Plymouth, U.K.

Clarke K.R., Somerfield P.J. and Chapman M.G. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *J. Exp. Mar. Biol. Ecol.* **330:** 55-80.

Cousens R. 1982. The effect of exposure to wave action on the morphology and pigmentation of *Ascophyllum nodosum* (L.) Le Jolis in south-eastern Canada. *Bot. Mar.* **25:** 191-195.

Cousens R. 1985. Frond size distributions and the effects of the algal canopy on the behaviour of *Ascophyllum nodosum* (L.) Le Jolis. *J. Exp. Mar. Biol. Ecol.* **92:** 231-249.

Cousens R. 1986. Quantitative reproduction and reproductive effort by stands of the brown alga *Ascophyllum nodosum* (L.) Le Jolis in south-eastern Canada. Est. Coast. Shelf Sci. 22: 495-507.

David H.M. 1943. Studies in the autecology of *Ascophyllum nodosum* Le Jol. *J. Ecol.* **31:** 178-198.

Deckert R.J. and Garbary D.J. 2005. *Ascophyllum* and its symbionts VI. Microscopic characterization of the *Ascophyllum nodosum* (Phaeophyceae), *Mycophycias ascophylli* (Ascomycetes) symbiotum. *Algae* **20:** 225-232.

De Wreede R.E. 1984. Growth and age class distribution of *Pterygophora californica* (Phaeophyta). *Mar. Ecol. Prog. Ser.* **19:** 93-100.

Garbary D.J., Brackenbury A., McLean A.M. and Morrison D. 2006. Structure and development of air bladders in *Fucus* and *Ascophyllum* (Fucales, Phaeophyceae). *Phycologia* **45:** 557-566.

Garbary D.J. and Deckert, R.J. 2001. Three part harmony – *Ascophyllum* and its symbionts. In: Seckbach J (ed.), *Symbiosis: mechanisms and model systems.* Kluwer, Dortrecht, The Netherlands. pp. 309-321.

Howell D.C. 1992. *Statistical methods for psychology.* Duxbury, Pacific Grove, CA, USA.

Kain J.M. 1963. Aspects of the biology of *Laminaria hyperborea.* II. Age, weight and length. *J. Mar. Biol. Ass. U.K.* **43:** 129-151.

Kain J.M. 1979. A view of the genus *Laminaria. Ann. Rev. Oceanogr. Mar. Biol.* **17:** 101-161.

Keser M. and Larson B.R. 1984. Colonization and growth of *Ascophyllum nodosum* (Phaeophyta) in Maine. *J. Phycol.* **20:** 83-87.

Keser M., Swenarton J.T. and Foertch J.F. 2005. Effects of thermal input and climate change on growth of *Ascophyllum nodosum* (Fucales, Phaeophyceae) in eastern Long Island Sound (USA). *J. Sea Res.* **54:** 211-220.

Kraberg A. and Norton T.A. 2007. Effect of epiphytism on reproductive and vegetative lateral formation in the brown, intertidal seaweed, *Ascophyllum nodosum* (Phaeophyceae). *Phycol. Res.* **55:** 17-24.

Lazo L., Markham J.H. and Chapman A.R.O. 1994. Herbivory and harvesting: effects on sexual recruitment and vegetative modules of *Ascophyllum nodosum. Ophelia* **40:** 95-113.

Li W.K.W., Harrison W.G. and Head E.J.H. 2006. Coherent assembly of phytoplankton communities in diverse temperature ocean ecosystems. *Proc. R. Soc. Ser. B,* **273:** 1953-1960.

Lobban C.S. and Harrison P.J. 1994. *Seaweed ecology and physiology.* Cambridge University Press, Cambridge, UK.

McLean A.M. 2007. Morphological trends in the brown alga *Ascophyllum nodosum* from Nova Scotia, Canada and

Lochmaddy Scotland. BSc Honours Thesis, St. Francis Xavier University, Antigonish, Nova Scotia, Canada.

Moran M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100:** 403-405.

Moss B. 1971. Meristems and morphogenesis in *Ascophyllum nodosum* ecad *mackaii* (Cotton). *Br. Phycol. J.* **6:** 187-193.

Novaczek I. 1981. Stipe growth rings in *Ecklonia radiata* (C.Ag.) J.Ag. (Laminariales). *Br. Phycol. J.* **16:** 363-371.

Pavia H., Toth G. and Åberg P. 1999. Trade-offs between phlorotannin production and annual growth in natural populations of the brown seaweed *Ascophyllum nodosum. J. Ecol.* **87:** 761-771.

Schweingruber F.H. 2007. Wood structure and environment. Springer, Berlin.

Sharp G. 1987. *Ascophyllum nodosum* and its harvesting in Eastern Canada. In: Case studies of seven commercial seaweed resources. *FAO Tech. Rep.* **281:** 3-46.

Stengel D.B. and Dring M.J. 1997. Morphology and in situ growth rates of plants of *Ascophyllum nodosum* (Phaeophyta) from different shore levels and responses of plants to vertical transplantation. *Eur. J. Phycol.* **32:** 193-202.

Strömgren T. 1977. Apical length growth of five intertidal species of Fucales in relation to irradiance. *Sarsia* **63:** 39-47.

Strömgren T. 1983. Temperature-length growth strategies in the littoral alga *Ascophyllum nodosum* (L). *Limnol. Oceanogr.* **28:** 516-521.

Vadas R.L. and Wright W.A. 1986. Recruitment, growth and management of *Ascophyllum nodosum. Actas II Congr. Algas Mar. Chilenas.* pp. 101-113.

Zar, J.H. 1999. Biostatistical Analysis. 4th ed. Prentice-Hall, Inc. Upper Saddle River, NJ.