Biomass and Productivity of Intertidal Rockweeds (*Ascophyllum nodosum* LeJolis) in Cobscook Bay

ROBERT L. VADAS, SR.[1,*], WESLEY A. WRIGHT[2], AND BRIAN F. BEAL[3]

Abstract - Rockweeds dominate much of the New England and Canadian Maritime coasts and serve as food and habitat for numerous species. Cobscook Bay is unique in New England for its high tidal amplitude, wide intertidal expanse, diverse flora and fauna, and presumed high intertidal productivity, much of which is thought to be related to extensive intertidal fucoid populations. The goals of this study were: 1) to estimate intertidal rockweed biomass and productivity, 2) to quantify the variation in rockweed productivity over a range of temporal and spatial scales (high- vs low-flow sites at headlands and coves, respectively), and 3) to estimate the contribution of rockweeds to detrital pools. Net productivity was determined by separately weighing growth in the current year vs growth from preceding year classes. Sampling the same populations in both the fall and following spring allowed adjustment for winter mortality of thallus structures and productivity at two sites.

Variation in the length of apical tips of canopy shoots was high, and differences among sites were not significant. However, growth of tips of sub-canopy and lateral shoots was site-specific. Standing crop at low-flow sites ranged from 11.4 kg wet weight m^{-2} at Bar Island to 28.9 kg wet weight m^{-2} at Bell Farm. Standing crop at high-flow sites ranged from 8.5 kg wet weight m^{-2} at Birch Point to 26.7 kg wet weight m^{-2} at Mahar Point. Adjusted productivity estimates ranged from 22 to 105% greater than unadjusted values. Highest productivity estimates for *Ascophyllum* (14.9 kg wet weight m^{-2} yr^{-1} or 894 g C m^{-2} yr^{-1}) occurred at Mahar Pt., a high-flow site. This unadjusted estimate was 50% higher than the average value (594 g C m^{-2} yr^{-1}) from the two sites adjusted for winter losses, Bell Farm and Bar Island. Turnover rates of *Ascophyllum* ranged from 29 to 71% (mean over all sites = 54%) indicating that the biomass of this alga turns over approximately every two years. About 60% of the standing biomass (3.96 x 10^6 g C yr^{-1}) is added to detrital pools, contributing large amounts of energy for secondary consumers. Rockweeds in Cobscook Bay are among the most productive cold-water intertidal assemblages and contribute substantial amounts of carbon to this large embayment.

Introduction

A fundamental dimension of most ecosystems is their capacity to convert carbon into organic matter. Rate of carbon fixation, or

[1]Department of Biological Sciences and School of Marine Sciences, University of Maine, Orono, ME 04469. [2]Department of Biological Sciences, University of Maine, Orono, ME 04469. [3]Division of Environmental and Biological Sciences, University of Maine at Machias, Machias, ME 04654. *Corresponding author - vadas@maine.edu.

productivity, and available organic matter are the key components that drive the trophic linkages of a community or ecosystem (Whittaker 1970). In most aquatic communities, macrophytes and phytoplankters are responsible for primary production. In boreal-temperate marine eco-systems, macroalgae and seagrasses comprise two potentially important benthic groups that contribute substantial amounts of carbon to nearshore communities (Mann 1973). Macroalgae take the form of algal filaments, simple corticated or foliose thalli, encrusting fleshy or calci-fied crusts, and complex and massive rockweeds and kelps. Early studies and syntheses (Kanwisher 1966) suggested that productivity was inversely related to thallus size or mass (see also Littler and Littler 1980, Steneck and Dethier 1994, Vadas 1979). However, convergence of thallus forms does not necessarily dictate similarity of metabolic function (Dudgeon et al. 1995).

Relatively slow-growing rockweeds, such as *Ascophyllum nodosum* Le Jol. and *Fucus vesiculosus* L., dominate the New England and Cana-dian Maritime coasts (Sharp and Semple 1990, Vadas and Elner 1992). These algae are conspicuous throughout North Atlantic shores (Baardseth 1970, Stengel and Dring 1997), and are present in both high and low-flow velocity habitats (Hardwick-Witman and Mathieson 1983). On many shores, they dominate the entire vertical gradient. *Ascophyllum* is abun-dant on moderately exposed and sheltered shores (Keser et al. 1981; Topinka et al. 1981; Vadas and Wright 1986; Vadas et al. 1976, 1978) and often forms a monoculture (sensu Paine 1984) on Maine shores. Both species provide valuable habitat and are important sources of food for several food webs in coastal ecosystems. Because of their height, branched structure, and mass, they serve as nursery areas or habitat during both low and high tide for numerous sessile and mobile organisms including algae, invertebrates, and larval and juvenile fish (Bertness et al. 1999; Fegley 2001; Mathieson et al. 1976; Menge 1978; Rangeley and Kramer 1995a,b). Rockweed beds are also important foraging areas for wildfowl (Hamilton 2000). Clearly, understanding what controls the abundance and productivity of fucoids, especially *Ascophyllum nodosum*, is important at several trophic and functional levels.

A number of methods exist to assess biomass and production in the field, however, most are destructive or indirect estimates. Destructive harvest measurements are typically used in *Ascophyllum* assessment (Baardseth 1970, Keser et al. 1981), but non-destructive measurements of changes in the length of apical branches have also been employed for growth (MacFarlane 1932; Stengel and Dring 1997; Vadas et al. 1976, 1978). Also, the length and slopes of site-index curves have been used to estimate growth and production in *Ascophyllum* (Vadas and Wright 1986). Bundled volumes of small patches of *Ascophyllum* have been used as a non-destructive predictor of biomass and productivity in the

field (Aberg 1990, Cousens 1984). We developed a modified version of the volume technique to rapidly predict biomass in the field. Our field sampling procedures (below) were designed for estimating volume, but here we report on only the wet weight analyses. A detailed study on the volumetric technique will appear elsewhere (Wright et al., in prep.).

The overall goal of the present study was to estimate intertidal biomass and productivity in several locations and establish a temporal baseline for *Ascophyllum* growth and productivity in Cobscook Bay. A secondary consideration was to quantify the variation in net productivity of *Ascophyllum* over a range of temporal and spatial scales. Selection of study sites reflects the spatial variability in hydrodynamic regimes at headlands and coves (high- vs low-flow sites). Because of its dominance intertidally, *Ascophyllum* was used to estimate the contribution of fucoid algae to the biomass and productivity of Cobscook Bay.

Study Sites and Methods

Sites, field collections, and general measurements

Ascophyllum was sampled at headlands (high-flow) and coves (low-flow) at five intertidal sites in Cobscook Bay in 1995 and 1996 (Fig. 1). Two low-flow sites in Whiting Bay (Bar Island and Bell Farm) and one high-flow site in the Central, or South, Bay (Garnet Point) were sampled in October 1995, following the termination of vegetative growth (Vadas et al. 1976). Two additional high-flow sites, Birch Point in South Bay and Mahar Point in Inner Bay (Denny's Bay), were sampled in May 1996 prior to gamete release. Our choice of sampling times was designed to occur after the completion of annual vegetative growth (fall) and before the release of gametes and the dehiscence of receptacles in the spring. To estimate overwintering losses of both vegetative and reproductive tissues, Bar Island and Bell Farm were sampled during both winter and spring, which resulted in a refined (adjusted) estimate of productivity.

All analyses were based on haphazardly tossed 10-cm x 10-cm quadrats in the mid-intertidal, near the mid-range and most productive region (Stengel and Dring 1997) of the *Ascophyllum* band. Quadrat size was based, in part, on the ability to determine readily the circumference of the bundled thalli, and thereby the volume of *Ascophyllum* within the same quadrat (cf., Aberg 1990, Cousens 1984). Samples were taken during low tide until twenty quadrats containing *Ascophyllum* were recorded. Total number of tosses at each site was recorded so that null quadrats would be included in standing crop estimates. All *Ascophyllum* thalli within each of the 20 quadrats were scraped from the substrate, bagged, wet weighed, labeled, stored on ice, and transported in coolers to the laboratory.

In the laboratory, samples were placed in a strainer and rinsed in tap water, and all epiphytes, rocks, and sediment attached to holdfasts removed. The number of holdfasts per quadrat was recorded and the longest thallus was used to determine maximum length. When possible, the longest unbroken thallus was used to estimate the minimum age of thalli in each sample by counting the annually produced air bladders along the main axis from the distal tip to the holdfast. An extra year was added to each age count because the segment from the holdfast to first bladder is conservatively estimated to be two years old (Keser and Larson 1984a; Vadas and Wright, unpubl. data). The sample was blotted dry with paper towels and the total wet weight recorded.

To distinguish between the current and previous year's vegetative growth (and contribution to annual productivity), growing tips were
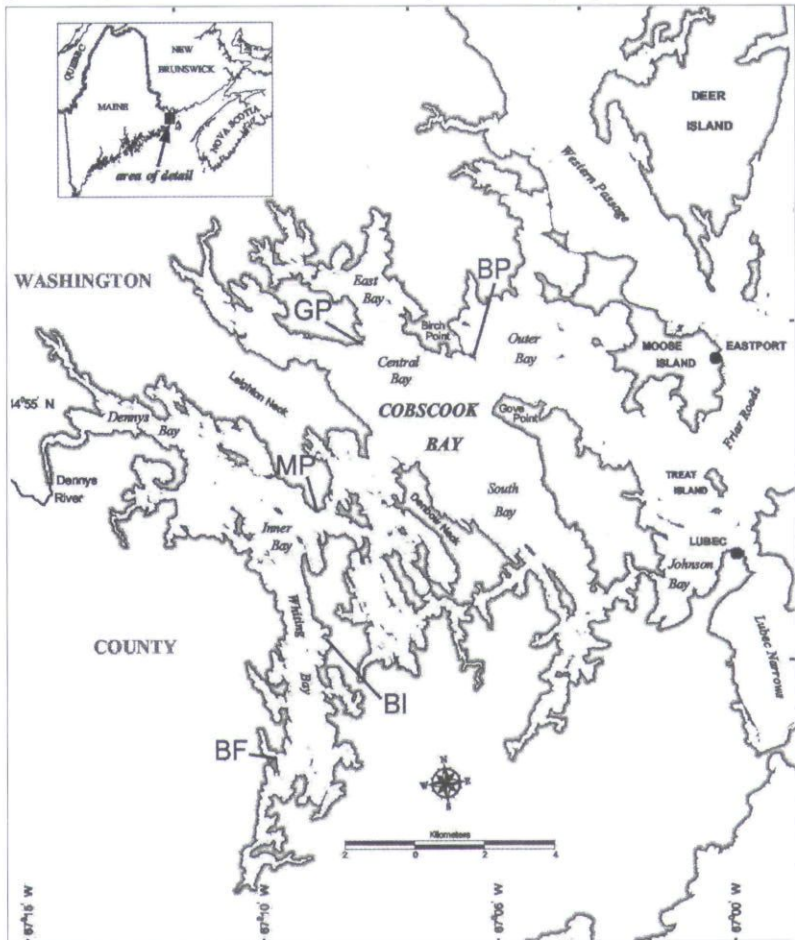

Figure 1. Map of Cobscook Bay rockweed study sites during 1995–96. BF = Bell Farm, BI = Bar Island, BP = Birch Point, GP = Garnet Point, MP = Mahar Point.

excised directly below the most distal air bladder. Air bladders are initiated annually in spring, and provide a convenient marker for annual growth. Excised apical tips sampled during fall represented annual linear vegetative growth during 1995. Because thalli sampled in (March–April, 1996) had recently formed an additional air bladder and the vegetative growth of interest occurred in 1995, shoots were cut in two places, immediately below the first and below the second most distal bladders. The second (lowermost) segment represented linear vegetative growth during 1995. Growth of *Ascophyllum* tips is affected by shading, and the vertical position of the growing tips in the canopy or understory determines length (Cousens 1981, Vadas and Wright 1986). Apical or distil tips (segments) representing 1995 growth were categorized as canopy, subcanopy, or suppressed tips. Apical tips on the longest thalli, e.g., shoots not shaded by *Ascophyllum* thalli, were defined as canopy tips. Tips on shoots that were 50 to 80 percent of the length of canopy shoots and at least partially shaded by the canopy were defined as subcanopy tips. Tips on shoots that were shaded and were shorter than 50 percent of the length of canopy shoots were defined as suppressed tips. Short lateral branches within the subcanopy or understory were also classified as suppressed tips.

Up to twenty-five 1995 growth segments, if available, were sampled randomly from each quadrat, and the length and number of bifurcations recorded. For spring samples exceeding 100 g, growth segments were subsampled from the longest thallus. We estimated the wet weight of the three tip types in the quadrat by dividing the wet weight of each tip type by the total wet weight of the longest thallus. This value was multiplied by the total wet weight in the quadrat. In quadrat samples of 100 g or less, all thalli were used to generate 25 samples of the three tip types. Total growth (wet weight) of all tips from 1995 was estimated by summing the weight of the three types of tips.

To determine reproductive growth and contribution to annual productivity in the current year, receptacles were removed, counted, and weighed. For spring samples exceeding 100 g, receptacles were subsampled from the longest thallus. We estimated receptacle wet weight by dividing the receptacle wet weight from the longest shoot in each quadrat by the total wet weight of the longest thallus and multiplying by the total wet weight in the quadrat. In quadrat samples of 100 g or less, all receptacles were weighed.

Analysis of apical tip growth

Lengths of canopy, sub-canopy, and suppressed growing tips for 1995 were analyzed to determine if spatial differences exist in growth patterns among sites and between seasons. Student t-tests were used to determine if significant differences in tip length within each canopy

type were detectable between fall and spring samples from the same site. Because variances were heterogeneous, ANOVA on rank-transformed data and orthogonal contrasts based on flow considerations were used to test for differences in tip length of each canopy type among sites within each sampling period.

Standing crop estimates

Standing crop of *Ascophyllum* was estimated by two methods, only one of which (harvesting) is presented here. The harvest technique involved detaching holdfasts and weighing all thalli within quadrats. The mean wet weight and standard error for all samples from a site, including null quadrats, was calculated and converted to g wet wt m^{-2}. For each sampling period, ANOVA on rank-transformed data with orthogonal contrasts was used to test for differences in mean standing crop between and within flow regimes. The Wilcoxon rank sums test was used to compare mean standing crop between the two sampling periods for Bar Island and Bell Farm.

Annual productivity estimates

Productivity was determined in two ways: 1) an "unadjusted" estimate taken in the fall or spring that included both vegetative and reproductive structures and, 2) an "adjusted" estimate that included overwintering vegetative and reproductive losses by sampling the same populations in fall and spring. At sites sampled in the fall, vegetative growth was determined by calculating the mean wet weight of the apical growing tips. At sites sampled in the spring, vegetative growth was determined by calculating the mean wet weight of the segments produced in 1995. Reproductive growth was determined by calculating the mean wet weight of the receptacles. For sites sampled twice (Bar Island and Bell Farm), the letters and formulae (explained below) were used to estimate changes in weight and production. Overwintering loss of vegetative growth was calculated for each tip type by subtracting the mean tip count in the spring of 1996 (B: tips produced in 1995) from the mean tip counts of fall (A). Mean tip wet weight in the fall (C) was divided by the mean tip count in the fall (A) and multiplied by the number of tips lost or (C/A)(A-B). This overwintering wet weight loss was then added to the spring tip wet weight (D) and converted from g /100 cm^2 to kg m^{-2} by multiplying by 0.1. Thus, the adjusted productivity of vegetative tips (kg m^{-2} yr^{-1}) is equal to [(C/A)(A-B) + D] x 0.1. The three tip types (canopy, subcanopy, and suppressed) were summed to determine total adjusted (for winter losses) annual vegetative productivity.

The contribution of reproductive receptacles to productivity was calculated in a manner similar to vegetative analysis. Overwintering loss of reproductive tissue in the two populations was estimated by

subtracting the mean number of receptacles in the spring (B) from the mean in the fall (A) or (A-B). The mean receptacle wet weight in the fall (C) was divided by the mean receptacle count in the fall (A) and multiplied by the number of receptacles lost or (C/A)(A-B). The over-wintering wet weight loss of receptacles was added to the spring receptacle wet weight (D) and adjusted to kg m^{-2} by multiplying by 0.1.

Estimates of total annual productivity were determined by adding the vegetative and reproductive components. These wet weight esti-mates of *Ascophyllum* were converted into dry weight by multiplying by 0.2 and converted into grams carbon by multiplying by 0.3 (Mann 1972, Smith 1988, Westlake 1963).

Turnover estimates

Turnover rates of *Ascophyllum* thalli were calculated from each of the five sites. Turnover can be expressed as turnover time, and is the inverse of turnover rate expressed as years or days (x 365). At sites sampled once, estimates were based on unadjusted productivity values. At sites sampled both in fall 1995 and spring 1996 (Bar Island and Bell Farm), turnover rates were generated according to season. This was done at each site by dividing the average annual productivity by average annual biomass for the year.

Results

Analysis of apical tip growth

Differences in the growth of the three tip types reflect differences in canopy location, as those higher in the canopy grew at significantly faster rates. Mean canopy tip lengths ranged from 59.6 mm at a low-flow site, Bell Farm (fall 1995), to 87.1 mm at a high-flow site, Mahar Point (spring 1996) (Fig. 2). Mean length of subcanopy tips ranged from 37.2 mm at Bell Farm (fall 1995) to 52.3 mm at a high-flow site, Birch Point (spring 1996),
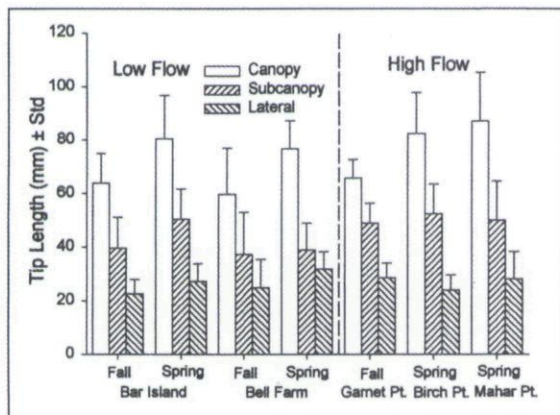
Figure 2. Mean tip length of *Ascophyllum nodosum* for three canopy heights at five sites in Cobscook Bay from October 1995 and May 1996 samples. Sites are de-noted as low- or high-flow.

whereas mean length of lateral tips ranged from 22.6 mm at a low-flow site, Bar Island (fall 1995), to 31.8 mm at Bell Farm (spring 1996).

Table 1. Comparisons of mean tip lengths (mm) between two sampling periods (years) at Bar Island and Bell Farm for three canopy types (t-tests).

Site	Type	Year	n	Mean	95% CI	t	df	P > |t|
Bar Island								
	Canopy	1995	16	63.89	5.37	-3.3559	29	0.0022
		1996	15	80.50	8.23			
	Subcanopy	1995	19	39.62	5.20	-2.8785	35	0.0068
		1996	18	50.41	5.18			
	Lateral	1995	18	22.55	2.43	-2.2122	32	0.0342
		1996	16	27.12	3.30			
Bell Farm								
	Canopy	1995	19	59.68	7.82	-3.1557	30	0.0036
		1996	13	76.75	5.71			
	Subcanopy	1995	20	37.22	6.91	-0.4035	37	0.6889
		1996	19	38.93	4.47			
	Lateral	1995	19	24.74	4.83	-2.2203	32	0.0336
		1996	15	31.75	3.30			

Table 2. Comparisons of mean tip lengths from three canopy types among all sites sampled in 1995 (ANOVA with orthogonal contrasts).

A. Canopy tips[1]

Source	df	SS	MS	F	P > F
Site[2]	2	258.52	129.26	0.49	0.6129
BI and BF vs. GP	1	168.49	168.49	0.64	0.4259
BF vs BI	1	77.49	77.49	0.30	0.5886
Error	52	13601.48	261.57		
Total	54	13860.00			

B. Subcanopy tips[1]

Source	df	SS	MS	F	P > F
Site[2]	2	2053.35	1026.68	4.15	0.0211
BI and BF vs. GP	1	2051.27	2051.27	8.28	0.0057
BF vs BI	1	0.62	0.62	0.00	0.9602
Error	54	13374.65	247.68		
Total	56	15428.00			

C. Lateral tips[1]

Source	df	SS	MS	F	P > F
Site[2]	2	1906.47	953.23	3.97	0.0247
BI and BF vs. GP	1	1638.76	1638.76	6.83	0.0117
BF vs BI	1	288.90	288.90	1.20	0.2776
Error	53	12723.03	240.06		
Total	55	14629.50			

[1]Because the variances of the tip length means were heterogeneous, values were rank transformed.
[2]Site abbreviations: BF = Bell Farm, BI = Bar Island, GP* = Garnet Point. *High-flow site.

Comparison of mean tip lengths at Bar Island and Bell Farm, the two sites sampled in fall 1995 and spring 1996, revealed a general pattern of increased length over winter. With the exception of subcanopy tips at Bell Farm, mean tip lengths representing growth during 1995 were significantly longer in spring 1996 (Table 1). Comparisons of mean canopy tip lengths among the three sites sampled in 1995 were not significant (P > 0.05). However, site differences were evident for subcanopy and lateral tips (Table 2). A similar pattern occurred for sites sampled in 1996 (Table 3).

Comparison of mean lengths for sub-canopy and lateral tips from the high-flow site, Garnet Point, were significantly greater than mean tip lengths at the low-flow sites, Bar Island and Bell Farm (Table 2, Fig. 2). In 1996, lengths of sub-canopy tips at the high-flow sites, Birch Point and Mahar Point, were greater than the low-flow sites, Bar Island and Bell Farm (Table 3). There were no significant differences in mean lateral tip lengths among sites sampled in 1996.

Table 3. Comparisons of mean tip lengths from three canopy types among all sites sampled in 1996 (ANOVA with orthogonal contrasts).

A. Canopy tips

Source	df	SS	MS	F	P > F
Site[1]	3	837.08	279.03	1.15	0.3384
BI and BF vs. BP and MP	1	568.48	568.48	2.34	0.1321
BF vs. BI	1	98.15	98.15	0.40	0.5280
BP vs. MP	1	166.25	166.25	0.68	0.4120
Error	56	13629.13	243.38		
Total	59	14466.20			

B. Subcanopy tips

Source	df	SS	MS	F	P > F
Site[1]	3	2064.21	688.07	4.96	0.0036
BI and BF vs. BP and MP	1	754.33	754.33	5.44	0.0226
BF vs. BI	1	1217.26	1217.26	8.78	0.0042
BP vs. MP	1	47.50	47.50	0.34	0.5603
Error	68	9428.68	138.66		
Total	71	11492.90			

C. Lateral tips

Source	df	SS	MS	F	P > F
Site[1]	3	496.76	165.59	2.91	0.0413
BI and BF vs. BP and MP	1	196.06	196.06	3.45	0.0681
BF vs. BI	1	166.14	166.14	2.92	0.0924
BP vs. MP	1	142.90	142.90	2.51	0.1180
Error	63	3583.53	56.88		
Total	66	4080.29			

[1]Site abbreviations: BF = Bell Farm, BI = Bar Island, BP* = Birch Point, GP* = Garnet Point , MP* = Mahar Point.
*High-flow sites.

Standing crop estimates

Estimates of standing crop were highly variable (Fig. 3). The standing crop at low-flow sites ranged from 11.4 kg wet weight m^{-2} in the spring at Bar Island to 28.9 kg wet weight m^{-2} in the fall at Bell Farm. Standing crop at high-flow sites in spring ranged from 8.5 kg wet weight m^{-2} at Birch Point to 26.7 kg wet weight m^{-2} at Mahar Point. Variation was high, and the 95% confidence intervals overlapped when all sites were compared to each other. Differences in mean standing crops between high- and low-flow sites sampled in 1995 were not significant (Table 4). Similarly, biomass comparisons for sites sampled in 1996 revealed no significant differences between flow regimes (Table 5). Also, comparisons within

Table 4. Comparisons of mean standing crop[1] of *Ascophyllum* among all sites sampled in 1995 (ANOVA with orthogonal contrasts).

Source	df	SS	MS	F	P > F
Site[2]	2	2477.27	1238.64	2.19	0.1182
BI and BF vs. GP	1	937.26	937.26	1.66	0.2014
BF vs BI	1	1467.75	1467.75	2.60	0.1109
Error	81	45757.73	564.91		
Total	83	48235.00			

[1]Because the variances for standing crop were heterogeneous, values were rank transformed.
[2]Site abbreviations: BF = Bell Farm, BI = Bar Island, GP* = Garnet Point.
*High-flow site.

Table 5. Comparisons of mean standing crop[1] of *Ascophyllum* among all sites sampled in 1996 (ANOVA with orthogonal contrasts).

Source	df	SS	MS	F	P > F
Site[2]	3	5279.14	1759.71	1.51	0.2163
BI and BF vs. BP and MP	1	132.90	132.90	0.11	0.7364
BF vs. BI	1	1647.36	1647.36	1.41	0.2373
BP vs. MP	1	3460.11	3460.11	2.96	0.0878
Error	117	136600.86	1167.53		
Total	120	141880.00			

[1]Because the variances of the tip length means were heterogeneous, values were rank transformed.
[2]Site abbreviations: BF = Bell Farm, BI = Bar Island, BP* = Birch Point, GP* = Garnet Point , MP* = Mahar Point.
*High-flow sites.

Table 6. Comparisons of mean standing crop (kg wet weight m^{-2}) of *Ascophyllum* between two years at Bar Island and Bell Farm (non-parametric Wilcoxon Rank Sums Test).

Site	Year	n	Mean	95% CI	Z	P > |Z|
Bar Island	1995	30	13.11	8.66	0.4251	0.6707
	1996	32	11.43	19.07		
Bell Farm	1995	27	28.94	16.33	-0.8155	0.4148
	1996	26	17.86	12.68		

flow regimes were not significant. Comparisons between sampling periods (fall 1995, spring 1996) within sites (Bar Island and Bell Farm) revealed no significant seasonal differences (Table 6).
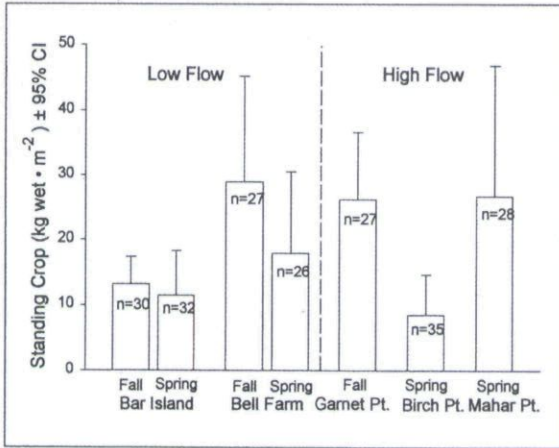

Figure 3. Mean standing crop (based on harvest method) of *Ascophyllum nodosum* at five sites in Cobscook Bay from October 1995 and May 1996 samples. Sites are denoted as low- or high-flow.
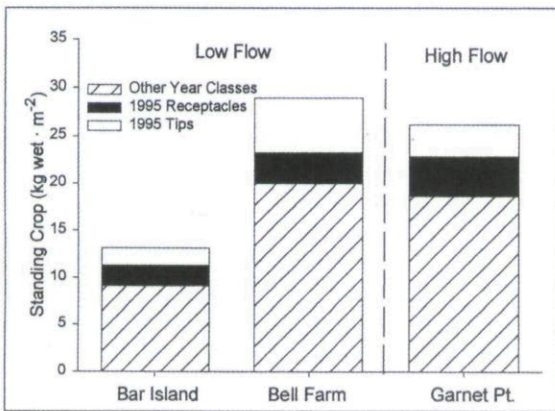

Figure 4. Allocation of 1995 standing crop components (annual vegetative growth and reproductive tissue) and of other year classes of *Ascophyllum nodosum* for three sites sampled in October 1995.
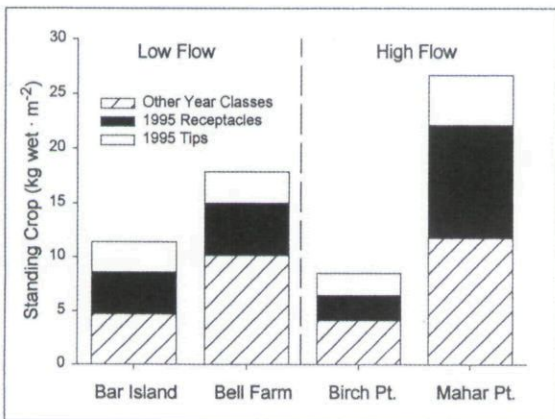
Figure 5. Allocation of 1995 standing crop components (annual vegetative growth and reproductive tissue) and of other year classes of *Ascophyllum nodosum* for four sites sampled in May 1996.

Allocation of standing crop components

Standing crop for each site sampled in 1995 and 1996 was divided into three components: 1995 vegetative growth, reproductive tissue, and "other" year classes (Figs. 4 and 5). In October, more than 50% of the biomass was in reproductive tissues at two of the three sites sampled. The percentage of reproductive tissue to 1995 vegetative biomass during May 1996 was greater than 50% at every site. The amount of "other" (pre- and post-1995) tissues decreased over the winter at Bar Island and Bell Farm. At the same time, standing crop of receptacles increased at these two sites (Fig. 5).

Annual productivity estimates

Our estimate of annual productivity of *Ascophyllum* includes weight of both vegetative and reproductive tissues. A considerable range of productivity estimates occurred at the five sites covering two seasons. Annual productivity during 1995 ranged from 4.0 kg wet weight m^{-2} at Bar Island in October 1995 to 14.9 kg wet weight m^{-2} at Mahar Point in May 1996 (Table 7).

To refine the harvest estimates of productivity, we adjusted for overwintering shoot (tip) losses. This refined estimate was possible only at Bar Island and Bell Farm, because both were sampled during fall and spring, thereby permitting seasonal comparisons of changes in the number and weight of shoots (tip types). At Bar Island, the adjusted vegetative productivity nearly doubled the fall (unadjusted) estimate, 1.8 to 2.9 kg wet wt m^{-2} yr^{-1}. At Bell Farm, the adjusted value decreased slightly from 5.7 to 5.5 kg wet wt m^{-2} yr^{-1} (Tables 7, 8).

Adjusted reproductive estimates of productivity for Bar Island and Bell Farm also nearly doubled the unadjusted estimates Table 9. At Bar Island, the adjusted value increased from 2.2 to 5.2 kg wet wt m^{-2} yr^{-1}. At Bell Farm, the adjusted value went from 3.3 to 6.2 kg wet wt m^{-2} yr^{-1} (Tables 7, 9). The combined adjusted values for net annual productivity are 8.2 and 11.7 kg wet wt m^{-2} yr^{-1} for Bar Island and Bell Farm, respectively (Table 10). The highest productivity estimate for the five

Table 7. Mean unadjusted annual productivity (kg wet weight m^{-2} ± 95% confidence interval) estimates for 1995 and 1996 divided into reproductive and vegetative components.

Site	n	Reproductive		Vegetative		Total	
		mean	95% CI	mean	95% CI	mean	95% CI
Fall 1995							
Bar Island	30	2.17	1.79	1.82	1.33	3.99	3.06
Bell Farm	27	3.25	2.88	5.70	3.60	8.94	5.90
Garnet Point	27	4.17	2.22	3.38	1.36	7.54	3.25
Spring 1996							
Bar Island	32	3.87	3.97	2.83	2.04	6.70	4.61
Bell Farm	26	4.91	4.04	2.81	2.19	7.72	6.14
Birch Point	35	2.34	2.51	2.05	2.03	4.39	4.53
Mahar Point	28	10.29	10.95	4.62	3.26	14.90	14.04

sites in Cobscook Bay (14.9 kg wet wt m^{-2} yr^{-1}) was for an unadjusted, spring value at a high-flow site, Mahar Point (Table 7). For comparative

Table 8. Mean adjusted vegetative annual productivity estimates for Bar Island and Bell Farm. Adjusted values are based on seasonal changes in tip counts and wet weights.

Site	Canopy (shoot) type	Fall tip count (a)	Spring tip count (b)	Fall tip wet weight[1] (c)	Spring tip wet weight[1] (d)	Adjusted vegetative productivity[2]
Bar Island						
	Canopy	27.80	27.60	7.83	15.08	1.51
	Sub-canopy	61.23	47.47	7.13	8.75	1.03
	Lateral	62.10	82.21	2.18	4.51	0.38[3]
	Total					2.93
Bell Farm						
	Canopy	42.96	28.27	22.47	15.16	2.28
	Sub-canopy	103.56	46.77	24.96	8.31	2.20
	Lateral	113.63	50.38	9.53	4.68	1.00
	Total					5.48

[1] Wet weights are in grams.
[2] Adjusted productivity calculation (kg m^{-2}) = [(c/a)(a-b)+d] x 0.1.
[3] Because there was no detected over-wintering loss, (a-b) was treated as zero.

Table 9. Mean adjusted reproductive annual productivity estimates for Bar Island and Bell Farm.

Site	Fall recep count (a)	Spring recep count (b)	Fall recep wet weight[1] (c)	Spring recep wet weight[1] (d)	Adjusted reproductive productivity[2]
Bar Island	414.26	155.75	21.68	38.69	5.22
Bell Farm	584.08	357.42	32.47	49.06	6.17

[1] Wet weights are in grams.
[2] Adjusted productivity calculation (kg m^{-2}) = [(c/a)(a-b)+d] x 0.1.

Table 10. Unadjusted and adjusted annual productivity for Bar Island and Bell Farm expressed as daily and yearly weights and as grams carbon per year.

Site	Method of estimation	Total productivity[1] (g wet m^{-2} d^{-1})	Total productivity[2] (kg wet m^{-2} y^{-1})	Total productivity (gC m^{-2} y^{-1})
Bar Island				
Fall	Unadjusted	10.93	3.99	239
Spring	Unadjusted	18.36	6.70	402
	Adjusted	22.33	8.15	489
Bell Farm				
Fall	Unadjusted	24.49	8.94	536
Spring	Unadjusted	21.15	7.72	463
	Adjusted	31.92	11.65	699

[1] Daily rates provided for comparative purposes with other macrophytes.
[2] Calculated by adding total adjusted vegetative productivity from Table 8 to adjusted reproductive productivity in Table 9.

purposes, adjusted productivity estimates were also converted to carbon and expressed as g C m^{-2} yr^{-1}. The value for Mahar Point was 894 g C m^{-2} yr^{-1}. The adjusted carbon-based productivity estimates for Bar Island and Bell Farm were 489 g C m^{-2} yr^{-1} and 699 g C m^{-2} yr^{-1}, respectively (Table 10). Adjusted values at these two sites ranged from 22 to 105% higher than the unadjusted estimates.

Turnover estimates

The proportion of *Ascophyllum* standing biomass lost annually and expressed as turnover rates, ranged from 29 to 71% (mean pooled across all sites = 54%; Table 11). Mean turnover rates for Bar Island were similar for the two seasons sampled, and ranged from 62 to 71%. At Bell Farm, the rates were slightly lower (40 to 65%) and more variable. Estimates for the three sites sampled only once (Birch Point, Mahar Point, Garnet Point) ranged from 29 to 56%. On average, the biomass of these perennial plants is turning over in less than two years. Of the seven turnover times calculated for the five sites, only two, Garnet Point and the fall estimate at Bell Farm, exceeded two years.

Discussion

These studies were undertaken to estimate rockweed production in the intertidal region of Cobscook Bay. *Ascophyllum nodosum* and *Fucus vesiculosus* are the dominant species in the Bay, and *Ascophyllum* was used as a surrogate of productivity for the rockweed zone. Although individual *F. vesiculosus* thalli grow at faster rates than *Ascophyllum* (Keser and Larson 1984a,b; Mathieson et al. 1976), the greater proportional coverage and biomass of *Ascophyllum* (Vadas et al. 2004) more than compensates for the higher growth rate of *Fucus*.

Estimates of standing crop and productivity, like all other estimates, are highly variable, even within the same species, and usually involve one or more assumptions. For example, Cousens (1984) reviewed the various methods used to estimate productivity in *Ascophyllum* and applied the same data set to the four published methods. He obtained a range of estimates, some yielding either much higher or lower values. In this study,

Table 11. Mean turnover rates and turnover times for *Ascophyllum* in Cobscook Bay, ME.

Site	Date	Standing crop[1]	Unadjusted productivity[2]	Adjusted productivity[2]	Turnover rate (P/B)	Turnover time (B/P)[3]
Bar Island	1995	13.11	3.99	8.15	0.622	1.579
	1996	11.43	6.70	8.15	0.713	1.402
Bell Farm	1995	28.94	8.94	11.65	0.403	2.484
	1996	17.86	7.72	11.65	0.653	1.533
Birch Point	1996	8.51	4.39	-	0.516	1.938
Mahar Point	1996	26.71	14.90	-	0.558	1.793
Garnet Point	1995	26.20	7.54	-	0.288	3.475

[1]kg wet weight m^{-2}. [2]kg wet weight m^{-2} yr^{-1}. [3]years.

the estimates of *Ascophyllum* production based on fall sampling alone exclude the large production of maturing receptacles during winter and spring. Conversely, the single spring value excludes the lost production due to winter storms or ice scouring (Chock and Mathieson 1983). Thus, both methods underestimate productivity. Our adjusted estimates, which take into account winter vegetative and reproductive losses, were variable, but generally higher than the estimates based only on fall sampling. Adjusted productivity values increased fall and spring mean estimates by 22 to 105% (Table 10). Accounting for winter losses presumes that the receptacles present in the fall would have all survived and attained the "average" size exhibited by receptacles in spring. In addition, there is at least one other source of error in these estimates. Productivity measurements of macrophytes, especially brown algae, usually fail to account for the large amount of carbon devoted to the production of mucilage and dissolved organic matter (Dring 1982). These carbon sources have not been considered in this study.

The estimates of total algal standing crop were highly variable between sites and seasons (Table 11) and ranged from 8.5 kg wet weight m^{-2} at Birch Point to 28.9 kg wet weight m^{-2} in the fall at Bell Farm. We observed temporal differences in standing crop estimates at Bell Farm (-12.8%) and Bar Island (-38.3%) between fall and spring sampling. These seasonal differences are likely due to mortality of vegetative and reproductive tissue. In addition to Bell Farm, two high-flow sites (Garnet and Mahar Points) also had standing crop estimates greater than 25 kg wet weight m^{-2}. The Mahar Point value is among the higher estimates (kg wet weight m^{-2}) of *Ascophyllum* in the northwest Atlantic ($\approx$ 32 and 20 from southwestern Nova Scotia, MacFarlane 1952 and Sharp 1987; 19.8 from eastern Nova Scotia, Cousens 1981; 32 and 19.5 from southwestern Maine, Topinka et al. 1981 and Keser et al. 1981; 7 from New Hampshire, Chock and Mathieson 1983), and among the higher estimates in the northeast Atlantic (26 in Norway, Baardseth 1970; 24.7 in Spain, Soneira and Niell 1975).

There are some recognizable patterns in the growth and productivity of *Ascophyllum* in Cobscook Bay. First, is a strong pattern of seasonal growth and shoot mortality, being highest in summer and winter, respectively. These observations are consistent with earlier studies (Chock and Mathieson 1983; Cousens 1984; Vadas et al. 1976, 1978). Second, our data suggest that fucoid productivity in Cobscook Bay is greater at high- vs. low-flow sites. However, variability among sites was high and differences between sites with different flow regimes were not significant. In *Durvillea*, a sublittoral fringe brown alga, density and standing crop doubled in high-flow (turbulent) conditions (South and Hay 1974). Also, *Ascophyllum* growth rates in the Northwest Atlantic Ocean were highest at intermediate exposures where water motion was moderately high (Cousens 1981, 1982; Topinka et al. 1981; Vadas and Wright 1986).

The current study reinforces the concept that rockweeds form a highly productive belt on intertidal shorelines. Highest productivity estimates for *Ascophyllum*, 14.9 kg wet wt m^{-2} yr^{-1} (894 g C m^{-2} yr^{-1}) occurred at Mahar Point, a high-flow site. This constricted area has flows approaching 2 m sec^{-1} (Brooks et al. 1999). The production estimate for Mahar Point is two to three times higher than other sites in the Bay, but is probably conservative because it is based on a single, unadjusted spring sample (n ≈ 20).

The annual estimates of *Ascophyllum* productivity (239 to 894 g C m^{-2} yr^{-1}) observed in Cobscook Bay are within the range of some but not all estimates for rockweeds from this biogeographic region. Generally, productivity estimates for fucoids from Nova Scotia and the northeast coast of North America ranged from 300 to 600 g C m^{-2} yr^{-1} (Brinkhuis 1977, Cousens 1981, Mann 1973, Roman et al. 1990). However, earlier estimates from eastern Canada ranged from 700 to 1400 g C m^{-2} yr^{-1} (Bakus 1969, cited in Dawes 1981). Also, Chock and Mathieson (1983) reported an average daily productivity for *A. nodosum* in the Great Bay, NH, system of 8 g dry m^{-2} dy^{-1} (876 g C m^{-2} yr^{-1}). Our mean adjusted estimates (≈ 600 g C m^{-2} yr^{-1}) are in the upper range of productivity estimates for fucoid algae from these and other boreal and cold water intertidal shores (≈ 630 g C m^{-2} yr^{-1}, Cousens 1981). For example, net productivity of *Fucus vesiculosus* in the Tagus Estuary, Portugal was 405 g C m^{-2} yr^{-1} (Ferreira and Ramos 1989). Similar rates of production (480–495 g C m^{-2} yr^{-1}) were observed for unattached forms of *Ascophyllum* and/or *Fucus* by Chock and Mathieson (1983) and Roman et al. (1990).

Total (areal) productivity estimate for *A. nodosum* in Cobscook Bay was high and was based on various habitat measurements made by Larsen et al. (2004) and Campbell (2004). We combined several of their classes (#16 + #17+ half of #15) for a total fucoid area of 1060 hectares. Based on the average annual productivity (594 g C m^{-2} yr^{-1}) of our two seasonally adjusted sites (Bar Island and Bell Farm; Table 10), total rockweed production in Cobscook Bay is estimated to be 6.3 x 10^9 g C yr^{-1}. Comparative estimates for fucoids in the Nauset Marsh, MA, is 1.95 x 10^8 g C yr^{-1} (Roman et al. 1990). A slightly different expression of production encompassing all seaweeds (fucoids not separated) in St. Margaret's Bay, NS, is 6.48 x 10^5 g C m^{-1} of shore line (Mann 1972).

Ascophyllum is dynamic and contributes considerable amounts of organic matter into Cobscook Bay. Although it has a relatively slow (for algae) turnover time (2.03 years—mean of seven estimates [Table 11]; 3–11 years, Sharp 1987), its widespread abundance on all rocky shores accounts for its large annual input into the Bay. Stengel and Dring (1997) argued that its ubiquitous intertidal distribution is related to its morphological and physiological plasticity. Based on average fall and spring turnover rates at Bar Island and Bell Farm, *Ascophyllum* annually contributes ≈ 60 % of the standing biomass (6.3 x 10^9 g C yr^{-1}) x (0.598)

= 3.8 x 10^6 g C yr^{-1} directly into Cobscook Bay. In addition, fucoid algae are well recognized for their exudation of dissolved organic matter (Dring 1982) that accounts for ≈ 5% of net productivity (Lüning 1990). Thus, a conservative estimate for the input of carbon from the fucoid belt in Cobscook Bay amounts to (3.8 x 10^6 g C yr^{-1}) + ([.05] x [3.8 x 10^6 g C yr^{-1}]) ≈ 4.0 x 10^6 g C yr^{-1}.

It is clear that the fucoids are important, perhaps critical, to the productivity and energy flow in Cobscook Bay. Our calculations indicate that a large portion of the fixed carbon goes through detrital pathways. Although we did not evaluate grazing, with the possible exception of *Littorina obtusata* (L.), there were few grazers feeding directly on *Ascophyllum*. However, episodic outbreaks of *Lacuna vincta* (Montagu) have periodically devastated the thalli of *Fucus* in Cobscook Bay (R.L. Vadas and B.F. Beal, pers. observ.; cf., Thomas and Page 1983). Also, dislodged (drift) fucoids may contribute directly to grazers, e.g., sea urchins and some gastropods. Nonetheless, the disproportionate abundance and productivity of *Ascophyllum* ensures that most of the carbon goes into detrital food webs (cf., Josselyn and Mathieson 1980). It is possible that the productivity of fucoids may play a large role in the impressive secondary productivity of filter-feeders in the Bay, e.g., scallops and soft-shell clams (see also Campbell 2004). Cobscook Bay has a large and diverse community of both infaunal (bivalves, polychaetes, holothurians, sipunculids, echiurids) and epifaunal (bivalves, tunicates, sponges, hydrozoans, anthozoans) filter feeders (Larsen and Gilfillan 2004, Larsen et al. 1980, Trott 2004). Perhaps, as Gili and Coma (1998) suggest for suspension-feeding communities in general, this complexity, which appears to be greater than that of marine invertebrates in nearby Machias and Englishman's Bay (adjacent, and south of Cobscook Bay), is due to the available and seemingly excess energy generated by macroalgae such as *Ascophyllum* within Cobscook Bay.

Acknowledgments

Literature Cited

Aberg, P. 1990. Measuring size and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum*. Marine Ecology Progress Series 63:281–287.

Baardseth, E. 1970. Synopsis of biological data on knobbed wrack *Ascophyllum nodosum*. FAO Fisheries Synopsis No. 38, Rev. 1. Food and Agriculture Organization, Rome, Italy. 41 pp.

Bakus, G.J. 1969. Energetics and feeding in shallow marine waters. International Review of Genetics and Experimental Zoology 4:273–369.

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

Brinkhuis, B.H. 1977. Comparisons of salt-marsh fucoid production estimated from three different indices. Journal of Phycology 13:328–335.

Brooks, D.A., M.W. Baca, and Y.-T. Lo. 1999. Tidal circulation and residence time in a macrotidal estuary: Cobscook Bay, Maine. Estuarine, Coastal, and Shelf Science 49:647–665.

Campbell, D.E. 2004. Evaluation and emergy analysis of the Cobscook Bay Ecosystem. Northeastern Naturalist 11(Special Issue 2):355–424.

Chock, J.S., and A.C. Mathieson. 1983. Variations of New England estuarine seaweed biomass. Botanica Marina 26:87–97.

Cousens, R. 1981. Variation in annual production by *Ascophyllum nodosum* (L.) Le Jolis with degree of exposure to wave action. Proceedings of the International Seaweed Symposium 10:253–258.

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. Botanica Marina 25:191–195.

Cousens, R. 1984. Estimation of annual production by the intertidal brown alga *Ascophyllum nodosum* (L.) Le Jolis. Botanica Marina 27:217–227.

Dawes, C.J. 1981. Marine Botany. John Wiley & Sons, Inc, New York, NY. 605 pp.

Dring, M.J. 1982. The Biology of Marine Plants. Edward Arnold, London, UK. 199 pp.

Dudgeon, S.R., J.E. Kubler, R.L. Vadas, and I.R. Davison. 1995. Physiological responses to environmental variation in intertidal red algae: Does thallus morphology matter? Marine Ecology Progress Series 117:193–206.

Fegley, J.C. 2001. Ecological implications of rockweed, *Ascophyllum nodosum* (L.) Le Jolis, harvesting. Ph.D. Thesis, University of Maine, Orono, ME.

Ferreira, J.G., and L. Ramos. 1989. A model for the estimation of annual production rates of macrophyte algae. Aquatic Botany 33:53–70.

Gili, J., and R. Coma. 1998. Benthic suspension feeders: Their paramount role in littoral marine food webs. Trends in Ecology and Evolution 13:316–321.

Hamilton, D.J. 2000. Direct and indirect effects of predation by Common Eiders and abiotic disturbance in an intertidal community. Ecological Monographs 70:21–43.

Hardwick-Witman, M.N., and A.C. Mathieson. 1983. Intertidal macroalgae and macroinvertebrates: Seasonal and spatial abundance patterns along an estuarine gradient. Estuarine, Coastal, and Shelf Science. 16:113–129.

Josselyn, M.N., and A.C. Mathieson. 1980. Seasonal influx and decomposition of autochthonous macrophyte litter in a north temperate estuary. Hydrobiologia 71:197–208.

Kanwisher, J.W. 1966. Photosynthesis and respiration in some seaweeds. Pp. 407–420, *In* H. Barnes (Ed.). Some Contemporary Studies in Marine Science. George Allen Unwin. London, UK.

Keser, M., and B.R. Larson. 1984a. Colonization and growth of *Ascophyllum nodosum* (Phaeophyta) in Maine. Journal of Phycology 20:83–87.

Keser, M., and B.R. Larson. 1984b. Colonization and growth dynamics of three species of *Fucus*. Marine Ecology Progress Series 15:125–134.

Keser, M., R.L. Vadas, and B.R. Larson. 1981. Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, U.S.A. Botanica Marina 24:29–38.

Larsen, P.F., and E.S. Gilfillan. 2004. A preliminary survey of the subtidal macrobenthic invertebrates of Cobscook Bay, Maine. Northeastern Naturalist 11(Special Issue 2):243–260.

Littler, M.M., and D.S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: Field and laboratory tests of a functional form model. American Naturalist 116:25–44.

Larsen, P.F., L.F. Doggett, C. Garside, J. Topinka, T. Mague, T. Garfield, R. Gerber, S. Fefer, P. Shettig, and L. Thornton, 1980. The Estuarine System. An Ecological Characterization of Coastal Maine. Newton Corner, MA, US Fish and Wildlife Service. FWS/OBS-80/29. US Department of Interior, Washington, DC.

Larsen, P.F., S. Barker, J. Wright, and C.B. Erickson. 2004. Use of cost effective remote sensing to map and measure marine intertidal habitats in support of ecosystem modeling efforts: Cobscook Bay, Maine. Northeastern Naturalist 11(Special Issue 2):225–242.

Lüning, K. 1990. Seaweeds: Their Environment, Biogeography, and Ecophysiology. John Wiley & Sons, Inc., New York, NY. 527 pp.

MacFarlane, C. 1932. Observations on the annual growth of *Ascophyllum nodosum*. Transactions of the Nova Scotian Institute of Science, Proceedings 18:27–33.

MacFarlane, C. 1952. The seaweed resources of the Atlantic provinces of Canada. Proceedings of the International Seaweed Symposium 1:104–106.

Mann, K.H. 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada: I. Zonation and biomass of seaweeds. Marine Biology 12:1–10.

Mann, K.H. 1973. Seaweeds: Their productivity and strategy for growth. Science 182:975–981.

Mathieson, A.C., J.W. Shipman, J.R. O'Shea, and R.C. Hasevlat. 1976. Seasonal growth and reproduction of estuarine fucoid algae in New England. Journal of Experimental Marine Biology and Ecology 25:273–284.

Menge, B.A. 1978. Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action, and desiccation on predator feeding rates. Oecologia 34:17–35.

Paine, R.T. 1984. Ecological determinism in the competition for space. Ecology 65:1339–1348.

Rangeley, R.W., and D.L. Kramer. 1995a. Tidal effects on habitat selection and aggregation by juvenile pollock *Pollachius virens* in the rocky intertidal zone. Marine Ecology Progress Series 126:19–29.

Rangeley, R.W., and D.L. Kramer. 1995b. Use of rocky habitats by juvenile pollock *Pollachius virens*. Marine Ecology Progress Series 126:9–17.

Roman, C.T., K.W. Able, M.A. Lazzari, and K.L. Heck. 1990. Primary productivity of angiosperm and macroalgae dominated habitats in a New England USA salt marsh: A comparative analysis. Estuarine, Coastal, and Shelf Science 30:35–46.

Sharp, G.J. 1987. *Ascophyllum nodosum* and its harvesting in eastern Canada. Pp. 3–48, *In* M.S. Doty, J.F. Caddy, and B. Santelices (Eds.). Case Studies of Seven Commercial Seaweed Resources. FAO Fisheries Technical Paper 281, Rome, Italy. 311 pp.

Sharp, G.J., and R.E. Semple. 1990. An assessment of *Ascophyllum nodosum* resources in Scotia/Fundy 1990. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 91/52. 30 pp.

Smith, B.D. 1988. Comparison of productivity estimates for *Laminaria* in Nova Scotia. Canadian Journal of Fisheries and Aquatic Sciences 45:557–562.

Soneira, A., and X. Niell. 1975. Sobre la biologia de *Ascophyllum nodosum* (L.) Le Jolis en Galicia I. Distribucion y abundancia en la Ria de Vigo. Investigacion Pesquera 39:43–59.

South, G.R., and C.H. Hay. 1974. Variation in morphology and standing crop in New Zealand *Durvillea antarctica* (Chamisso) Hariot in relation to exposure and latitude. Proceedings of the International Seaweed Symposium 8:489–498.

Steneck R.S., and M.N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:1–18.

Stengel D.B., and M.J. Dring. 1997. Morphology and in situ growth rates of plants of *Ascophyllum nodosum* (Phaeophyta) from different shore levels and responses of plants to vertical transportation. European Journal of Phycology 32:193–202.

Thomas, M.L.H., and F.H. Page. 1983. Grazing by the gastropod, *Lacuna vincta*, in the lower intertidal area at Musquash Head, New Brunswick, Canada. Journal of the Marine Biological Association of the United Kingdom 63:725–736.

Topinka, J., L. Tucker, and W. Korjeff. 1981. The distribution of fucoid macroalgal biomass along central coastal Maine. Botanica Marina 24:311–319.

Trott, T.J. 2004. Cobscook Bay inventory: A historical checklist of marine invertebrates spanning 162 years. Northeastern Naturalist 11(Special Issue 2):261–324.

Vadas, R.L. 1979. Seaweeds: An overview: Ecological and economic importance. Experientia 34:435–437.

Vadas, R.L., and R.W. Elner. 1992. Plant-animal interactions in the north-west Atlantic. Pp. 33–60, *In* D.M. John, S.J. Hawkins, and J.H. Price (Eds.). Plant Animal Interactions in the Marine Benthos. Systematics Association Special Volume No. 46, Clarendon Press, Oxford, UK. 570 pp.

Vadas, R.L., and W.A. Wright. 1986. Recruitment, growth, and management of *Ascophyllum nodosum*. Actas Segundo Congreso Nacoinal Sobre Algas Marinas Chilenas 2:101–113.

Vadas, R.L., M. Keser, and P.C. Rusanowski. 1976. Influence of thermal loading on the ecology of intertidal algae. Thermal Ecology 2:202–212.

Vadas, R.L., M. Keser, and B. Larson. 1978. Effects of reduced temperatures on previously stressed populations of an intertidal alga. Pp. 434–451, *In* J.H. Thorp III, and J.W. Gibbons (Eds.). Energy and Environmental Stress in Aquatic Systems. ERDA Symposium Series, Augusta, GA. 854 pp.

Vadas, R.L., Sr., B.F. Beal, W.A. Wright, S. Emerson, and S. Nickl. 2004. Biomass and productivity of red and green algae in Cobscook Bay, Maine. Northeastern Naturalist 11(Special Issue 2):163–196.

Westlake, D.F. 1963. Comparisons of plant productivity. Biological Reviews 38:385–425.

Whittaker, R.H. 1970. Communities and Ecosystems. Collier-Macmillan Canada, Ltd., Toronto, ON, Canada. 162 pp.