Recovery following experimental harvesting of *Laminaria longicruris* and *L. digitata* in southwestern Nova Scotia

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ABSTRACT: *Laminaria* population variables and understory community composition were monitored just prior to, and for two summers following, a September 1980 experimental total harvest of *L. longicruris* De la Pylaie and *L. digitata* (L.) Lamouroux within two plots in Lobster Bay, Nova Scotia. Both plots, distinguished mainly by depth, were characterized by high *Laminaria* standing crop and no recent history of extensive sea urchin grazing. Within the shallower plot (2–3 m below MSL), recovery could not be assessed thoroughly due to ice damage, but within the deeper plot (3–4 m below MSL), *L. longicruris* regrew cropped biomass and attained maximum observed abundance within one year. Both *Laminaria* species required two years to mature to pre-harvest population characteristics. Survivorship of 0–1 year old and mature populations of both species was generally low (0–67 % per year); however, the higher maximum life expectancy of *L. digitata* (> 4 years vs 2 years) can result in that species persisting to the disadvantage of *L. longicruris.* Analysis of understory community composition for both harvested plots and their adjacent controls weakly distinguished the harvested plots one summer after harvesting from all others. It is doubtful the distinction is attributable to harvesting and in neither site was there evidence of a critical change in the understory community. Management implications for the commercial harvest of the brown alga *Laminaria* are discussed.

INTRODUCTION

The desire to understand the characteristics and role of the seaweed community in nearshore ecosystems and their implications for eastern Canadian fisheries management has produced several contributions during the past few years (see Pringle et al., 1980; Wharton & Mann, 1981). Nearly all address the role of this community in relation to higher trophic levels, in particular the lobster, and the possible detrimental consequences of lost seaweed production. We still have little information on, and lack an understanding of, the population and community characteristics of seaweeds, the notable exception being *Chondrus crispus* Stackhouse. This species is presently the most economically important seaweed in the region, and has been the subject of intensive resource management research since 1975 (Pringle & Sharp, 1980). More recently attention has started to focus on the kelp species (Laminariales). Kelp is harvested in various parts of the world for dried foodstuffs and for alginate (Pringle & Sharp, 1980). In southwestern Nova Scotia, Canada, *Laminaria* was harvested from 1940–1949 and

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periodically since then. The quantities were relatively small (<3000 MT, wet), and apparently sustainable, but there were reports of harvested populations not recovering (Sharp, 1980).

   To improve our understanding of the dynamics and characteristics of *Laminaria* populations in Nova Scotia, as recommended by Pringle et al. (1980), this study presents the results of a three-year program to assess the impact of a total *Laminaria* harvest at two sites within a *Laminaria* dominated seaweed community in Lobster Bay in the southwestern part of the province. This area was chosen because of no recent history of extensive sea urchin grazing, which has detrimentally affected most kelp beds in Nova Scotia (Chapman, 1981), and it is the area where harvesting is likely to occur. Recent discussions with executives of the marine plant industry in Nova Scotia indicate renewed interest in *Laminaria.* If their corporate plans are realized, they anticipate a demand for large quantities of the resource in the foreseeable future.

SITE DESCRIPTION

   To overcome discontinuities in hard substrate with depth, two study sites located within 3 km of each other in Lobster Bay, Nova Scotia (43° 41' N × 65° 52' W), were chosen for high *Laminaria* standing crop and accessibility (Figure 1). The shallower site (S) is east-facing from a low reef exposed only at low tide and the deeper site (D) faces west off a small island in the bay. The sites are similar in exposure to wave action and are characterized by temperatures and salinities ranging from −1 to 17 °C and 28 to 33 ‰, respectively. Intertidal and shallow subtidal areas occasionally experience lower salinities with an ebb tide during spring melt and suffer from ice scouring during severe winters. The substrate for plants at both sites is rock. Mean substrate relief is 12.4 ± 6.3 cm (n = 320) and 25.3 ± 13.9 cm (n = 1200) for the harvest and control plots at sites S and D, respectively. Below 5 m at site D the substrate becomes gravel. Unperturbated *Laminaria* standing crop distribution with depth is presented in Figure 2.

METHODS

   Figures 3 portrays the layout and sampling format of sites S and D. Precise location of the experimental plots and permanent quadrats for monitoring tagged plants was facilitated by placing flagged aluminum eye-bolts in the substrate. All field maintainance, collections and measuring required the use of SCUBA.

   Harvest and control plot standing crop assessments at sites S and D were obtained for all species in the summers of 1980 and 1981, and for *Laminaria* at site D also the summer of 1982. All *Laminaria* plants greater than 50 cm total length were counted within each of the forty 0.25 m² quadrats comprising each assessment transect. Following *Laminaria* counting, the most representative 0.25 m² quadrat of each 1.0 m² quadrat was collected using an underwater airlift fitted with a 3 mm mesh collecting bag. The choice of collected quadrats was biased when necessary toward obtaining sufficient data on *Laminaria* population statistics. All plant material within each collected quadrat was sorted to species, and weighed both wet and, with the exception of *Laminaria* > 10 cm, dry (24 h at 100 °C). For site D collections, the standing crops of *Phyllophora brodiaei* (Turner) J. Agardh, *Phyllophora membranifolia* (Goodenough & Woodward) J. Agardh,
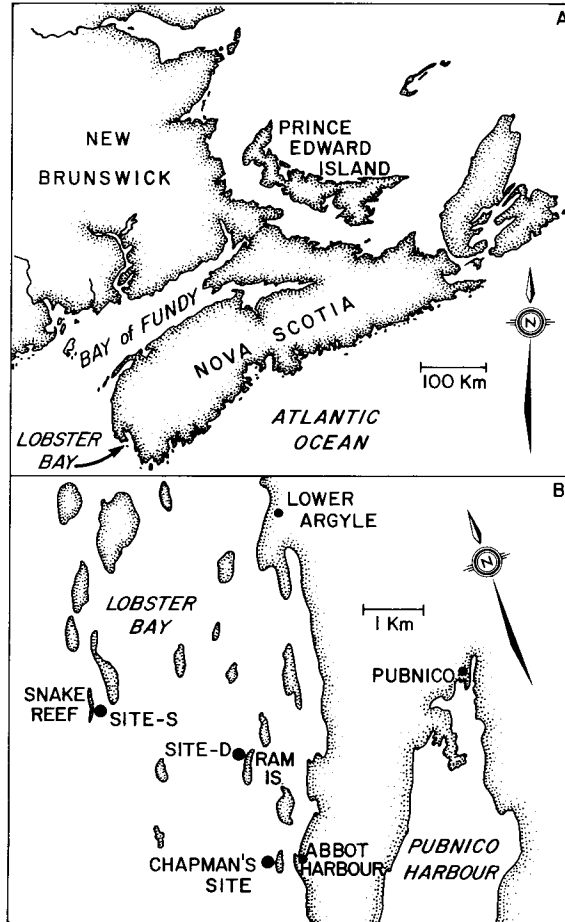
Fig. 1. Location of study sites. (A) Atlantic Canada; (B) Lobster Bay in southwestern Nova Scotia
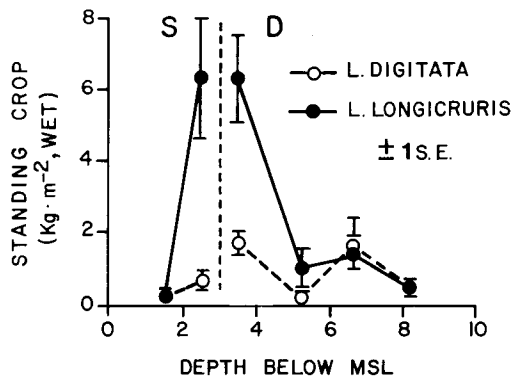

Fig. 2. Standing crop of *Laminaria longicruris* and *L. digitata* over depth (m) below mean sea level (MSL) at sites S and D within Lobster Bay, southwest Nova Scotia
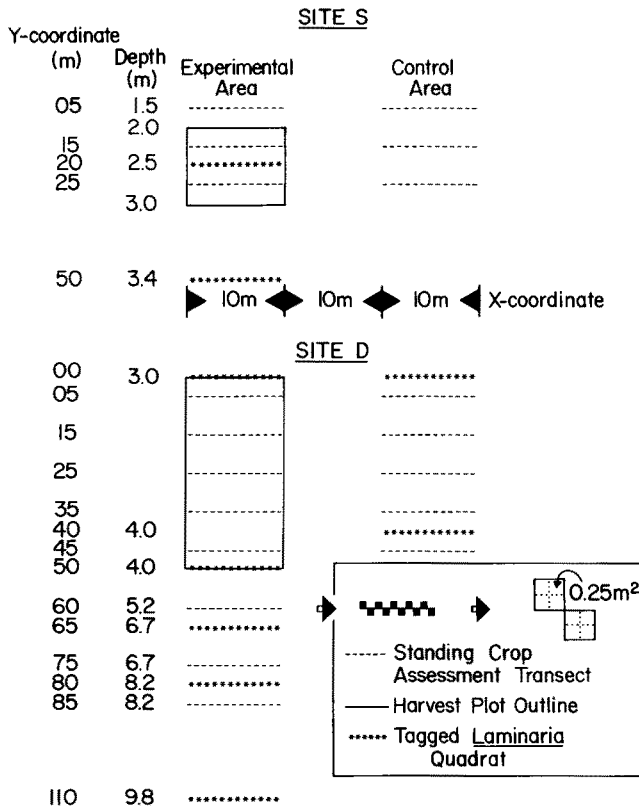
Fig. 3. Diagrammatic representation of sites S and D within Lobster Bay, Nova Scotia; and the locations of the standing crop assessment transects, tagged *Laminaria longicruris* and *L. digitata* quadrats, and the harvest plot outlines

and *Chondrus crispus* Stackhouse were corrected for bryozoan encrustation. *C. crispus* was further separated into fronds greater or less than 10 cm. Individual plants of *L. longicruris* De la Pylaie and *L. digitata* (L.) Lamouroux > 10 cm total length were counted and the following variables measured: stipe length, lamina length, stipe weight, lamina weight, number of lamina, maximum lamina width, reproductive? (Yes or No). Environmental conditions and substrate characteristics for both sites were also recorded. In early September 1980, immediately following the control and harvest plot assessments for both sites, all *Laminaria* plants within and overlapping the harvest plots were detached at or near the holdfast by SCUBA divers using long sharp kitchen knives.

Laminaria growth and mortality data were obtained by regularly counting and measuring tagged plants of each species within two site S and seven site D quadrats (1 m × 10 m). All plants greater than 50 cm total length within one site S and two site D harvest plot quadrats were tagged with individually numbered cable ties and first measured the summer following harvesting (1981). The same procedure, but at different starting dates, was followed for the six quadrats not in the harvest plots. The plant measurements are those listed earlier for the assessment transects with the exception of

weight determinations. Beginning in March 1982, holes (5 mm diameter) were punched 5 cm above the meristem of each remaining plant and some newly tagged plants to measure linear lamina growth and attrition (Mann, 1973). The tagged plant quadrats were monitored until April 1983. Double tagging experiments indicated there was no measurable tag loss.

RESULTS

Understory community

Understory community characteristics were measured and monitored until the *Laminaria* population recovered substantially from harvesting, which was interpreted to be the summer following harvesting (1981). A cluster analysis of all 80 site S and all 200 site D quadrats, without distinction of harvest (H) and control (C) plots or year, in separate analysis produced no recognizable groups. This was not unexpected because of the a priori requirement that the harvest and control plots be similar, and within-plot variability contributed by the patchiness of the more abundant species. This latter consideration was emphasized by the rocky substrate. Considering the plots as entities, Figure 4 distinguishes the harvest plot in 1981, the summer following harvesting, from
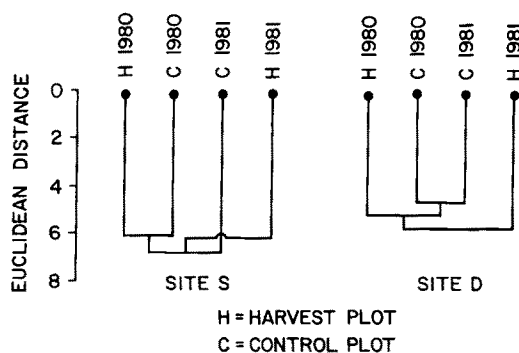

Fig. 4. Cluster diagram of "plot-year" similarity for the understory communities of sites S and D. (C = control plot, H = harvest plot)

all others at both sites using standardized Euclidean distance as a measure of "plot-year" community similarity. Linkage order is the result of a centroid clustering procedure. Standardized Euclidean distance is an appropriate similarity measure because of its equal sensitivity to all species. It is effective in distinguishing plot-year entities by comparing cumulative variation in species standing crop between pairs of entities.

A more rigorous scrutiny of the difference between the 1981 harvest plots and the other plots is presented in Table 1. When analyzed individually, the species which contributed the most to the distinction of H1981 from the other plots at site D in the cluster analysis, specifically *Chordaria flagelliformis* (Muller) C. Agardh and *Polysiphonia* sp., did not have significantly different standing crop distributions for the control versus harvest plots in either 1980 or 1981. This weakens the validity of the distinction in Figure 4. Overall, the trend for site D is a significant decrease in the standing crops of several species relative to the pre-harvest state; however, increases in

Table 1. Taxa recorded in the quantitative quadrat collections within the control and harvest plots of sites S and D in the summer of 1980 and 1981. The variables tabled are those used in judging understory community changes following a 1980 *Laminaria* harvest at each site

Species	Site S					Site D				
	%*	Rank**	CvsH+ 1980	CvsH 1981	Δ++	%	Rank	CvsH 1980	CvsH 1981	Δ
Chlorophyta										
Chaetomorpha atrovirens Taylor	0.02	25	ns	ns		0.02	11	ns	ns	
Cladophora sp.	0.01	13	ns	ns		0.56	5	<.05	ns	—
Phaeophyta										
Asperococcus echinatus (Mertens) Greville	<0.01	24	ns	ns		0.0	•	•	•	
Chordaria flagelliformis (Müller) C. Agardh	0.12	14	ns	ns		<0.01	1	ns	ns	
Desmarestia aculeata (L.) Lamouroux	0.17	18	ns	ns		0.44	12	ns	<.05	—
Desmarestia viridis (Müller) Lamouroux	<0.01	22	ns	ns		0.02	15	ns	<.01	—
Fucus vesiculosus L.	1.06	15	<.05	ns	+	0.0	•	•	•	
Leathesia difformis (L.) Areschoug	<0.01	16	ns	ns		0.0	•	•	•	
Saccorhiza dermatodea (De la Pylaie) Farlow	<0.01	3	ns	ns		0.0	•	•	•	
Scytosiphon lomentaria (Lyngbye) C. Agardh	0.01	23	ns	ns		0.28	18	<.05	ns	—
Rhodophyta										
Ahnfeltia plicata (Hudson) Fries	0.48	26	<.01	ns	+	0.01	13	<.01	ns	—
Ceramium rubrum (Hudson) C. Agardh	0.04	2	<.001	ns	+	1.15	•	•	•	—
Chondrus crispus Stackhouse (fronds >10 cm)	34.27	6	ns	ns		18.06	14	ns	ns	

Species	%	rank	+	+	++	%	rank	+	+	++
Chondrus crispus (fronds <10 cm)	56.46	10	ns	ns		28.81	7	<.001	<.001	
Corallina officinalis L.	1.39	7	ns	ns		10.18	8	<.05	ns	+
Cystoclonium purpureum (Hudson) Batters	1.05	1	ns	<.01	+	0.60	3	<.05	<.001	+*
Dumontia incrassata (Müller) Lamouroux	<0.01	9	ns	ns		0.0	•	•	•	
Euthora cristata (L. ex Turner) J. Agardh	0.01	19	<.05	ns		0.14	•	•	•	
Membranoptera alata (Hudson) Stackhouse	0.01	17	ns	ns	−	1.15	4	<.001	ns	−
Palmaria palmata (L.) Greville	2.77	8	ns	<.01	+	1.40	•	•	•	
Phyllophora brodiaei (Turner) J. Agardh	1.17	12	ns	<.05	+	8.74	6	ns	ns	
Phyllophora membranifolia (Goodenough & Woodward) J. Agardh	0.65	5	ns	ns	+	28.16	10	ns	ns	
Polysiphonia sp.	0.01	19	<.01	<.01	−	<0.01	1	ns	ns	
Polyides caprinus (Gunnerus) Papenfuss	0.29	11	ns	ns		<0.01	17	ns	ns	
Ptilota serrata Kützing	<0.01	19	ns	ns		<0.01	9	ns	ns	
Rhodomela lycopodioides (L.) C. Agardh	0.02	4	ns	ns		0.30	16	<.05	ns	−

• Percentage of total site standing crop (pre-harvest; excluding Laminaria)

•• Ranked decreasing sum of squares contribution by each species to the Euclidean distance measure separating the 1981 harvest plots from all others as presented in Figure 4. Note that *Ceramium rubrum*, *Euthora cristata* and *Palmaria palmata* were not included in the cluster analysis for site D since they occurred mainly as epiphytes on *Laminaria longicruris*

+ Result of a Mann-Whitney U-test for different control (C) plot and harvest (H) plot standing crop distributions. For site S: $n_C = n_H = 20$; for site D: $n_C = n_H = 50$; ns = non-significant result, i.e. p >.05

++ Absolute or relative direction of a detected shift in harvest plot standing crop distribution compared to control plot standing crop distribution from 1980 to 1981

H1981 standing crop significantly greater (p <.05) than H1980 standing crop; C1981 standing crop not significantly different from C1980 standing crop

the standing crops of two species were recognized. The epiphyte *Cystoclonium pur-pureum* (Hudson) Batters displayed the strongest response, with H1981 standing crop increasing 2.7 times over H1980 standing crop (p = .02) compared with only a 1.65 times increase for C1981 relative to C1980 (p = .32). Three other species, *Cladophora* sp. (−), *Corallina officinalis* L. (+) and *Membranoptera alata* (Hudson) Stackhouse (−) are also interpreted as the most apparent indicators of change in the understory community because of their high standing crops and contribution to Euclidean distance. *Ceramium rubrum* (Hudson) C. Agardh, *Euthora cristata* (L. ex Turner) J. Agardh and *Palmaria palmata* (L.) Greville were not included in the cluster analysis presented for site D since they occurred mainly as epiphytes on the larger *L. longicruris* plants and would bias the results of the analysis toward distinction of H1981. Epiphytes were rarely observed on *L. longicruris* in the H1981 collections.

For site S the distinction of H1981 is less equivocal with the epiphytes *C. purpureum* and *C. rubrum* ranking first and second, respectively, in contribution to Euclidean distance. Both species increased considerably in standing crop in H1981. *C. purpureum* was 6.2 times H1980 standing crop and 10.2 times C1981 standing crop, and *C. rubrum* increased 1000 times over H1980 standing crop and 5 times over C1981 standing crop. This dramatic effect for *C. rubrum* is largely an artifact of its very low standing crop (5 mg · m⁻², dry) in H1980. The general trend for those species which demonstrated a significant relative change was an increase in H1981 standing crop. Only two relatively unimportant species decreased in standing crop. Of those which increased, other than the two species previously mentioned, only *P. palmata* increased notably in H1981 to 6.7 times H1980 compared with 1.65 times C1981. It was not necessary to account for epiphytes in the site S analysis since *L. longicruris* at that site was free of epiphytes.

Table 2 presents some ecological parameters for each plot. For site S, H1981 has the highest mean dry weight and species diversity for the understory community. The increased standing crops of *C. purpureum* and *P. palmata* are responsible for the high H1981 standing crop and also the high species diversity by diminishing the dominance of *C. crispus.* For site D no clear distinction of H1981 is evident, the differences in mean dry weight and species diversity being predominantly due to the large between-plot variance in *C. crispus* standing crop.

Laminaria recovery

By December 1980, three months following the experimental harvest, a visual reconnaissance of the harvest plot at site D confirmed that regrowth of *L. longicruris* was well in progress. The plants had recovered to a density that made it difficult to distinguish the harvest plot from the surrounding area, and several plants exceeding 2 m in total length were observed. Soral tissue was evident on only a very small percentage of the plants observed. Site S was not visited because it was not readily accessible at this time of year.

Table 3 summarizes the population characteristics of *L. longicruris* and *L. digitata* at sites S and D during the summers of 1980–82. Figures 5 and 6 present corresponding length histograms describing the population structure of both species. At site S population variables of *L. longicruris* and *L. digitata* were still well under pre-harvest values within H1981 and C1981. The length histograms indicate that the populations of both

Table 2. Ecological parameters for the control (C) and harvest (H) plots of sites S and D in 1980 and 1981

Parameters	Site S				Site D			
	H1980	C1980	H1981	C1981	H1980	C1980	H1981	C1981
Number of quadrats	20	20	20	20	50	50	50	50
Number of species	17	24	21	22	21	16	17	19
Mean dry weight (g · m^{-2})*	266	357	505	457	150	180	181	270
Mean number of species per 0.25 m^2 quadrat	6–7	9	9–10	9–10	10	8–9	7–8	7–8
Species diversity (H′)**								
(1) All species	1.10	1.47	2.08	1.80	1.51	1.33	1.20	1.93
(2) Excluding *Laminaria* and its epiphytes	0.74	0.66	1.55	1.14	2.03	1.78	1.92	1.72

* Excluding *Laminaria*
** Shannon & Weaver (1949)

Table 3. Population characteristics of *Laminaria longicruris* and *Laminaria digitata* within the harvest (H) and control (C) plots of sites S and D during the summers of 1980–82. The data incorporate only those plants greater than 50 cm total length except where otherwise noted

Parameters	Site S			Site D				
	1980 (H+C)	H1981	C1981	1980 (H+C)	H1981	C1981	H1982	C1982
L. longicruris								
Mean standing crop (kg · m^{-2}, wet)*	6.19	0.35	0.60	6.17	5.93	2.83	8.18	4.83
Mean plant length (cm)	288	146	123	270	246	244	332	320
Mean plant weight (g, wet)	373	122	49	406	287	389	692	725
Mean density (n · m^{-2})	16.6	2.6	10.0	15.2	20.7	7.2	11.8	6.7
Percentage reproductive	13.2	0.0	1.8	22.4	15.0	16.7	31.2	29.3
L. digitata								
Mean standing crop (kg · m^{-2}, wet)*	0.69	0.20	0.15	1.77	0.46	2.98	1.97	3.15
Mean plant length (cm)	137	76	87	136	99	139	147	164
Mean plant weight (g, wet)	252	91	110	391	101	372	347	511
Mean density (n · m^{-2})	2.7	2.1	1.3	4.5	4.4	7.8	5.7	6.2
Percentage reproductive	28.6	17.7	44.4	29.3	8.9	35.3	28.9	44.1

* Incorporates all plants and is corrected for sampling bias by adjusting plot standing crop based on the expected ratio of 4 : 1 for 'number of plants counted : number of plants collected' within each plot

species are shifted toward the smallest length interval, and, by comparison of the control and harvest plot distributions, suggest that both are composed mainly of plants less than one year old. There is no evidence that the largest plants in the 1980 plots survived until summer 1981. Site S was not monitored after 1981 because of evidence that the lower standing crop of both species in 1981 is due to ice scouring, not the experimental harvest.

Within site D, *L. longicruris* recovered to pre-harvest standing crop (96 %) the summer following harvesting. Mean plant length and weight were less than pre-harvest values but this was compensated by a 36 % increase in plant density. Within H1982 the
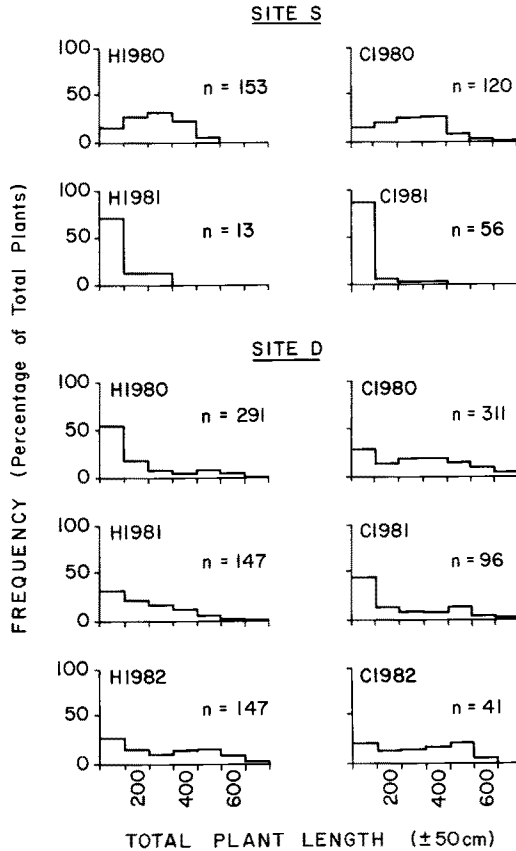
Fig. 5. Total plant length (cm) histograms for *Laminaria longicruris* > 50 cm within the harvest (H) and control (C) plots at sites S and D during the years they were assessed. (1980 = pre-harvest; 1981+ = post-harvest)

population variables for *L. longicruris* exceeded H1980 values. The length distribution for H1982 was substantially similar to that of H1980 with the exception that there were fewer small plants than in H1980. *L. digitata* required two years (H1982) to recover cropped biomass and attain population characteristics substantially similar to H1980.

Noteworthy in Table 3 is the strong recovery of *L. longicruris* in H1981 which continues with the highest observed *L. longicruris* standing crop of $8.18 \text{ kg} \cdot \text{m}^{-2}$ occurring in H1982. This recovery occurs while *L. digitata* standing crop is low relative to the pre-harvest state. Within the unperturbated (control) *Laminaria* populations, *L. longicruris* standing crop was only 46 % and 78 % of 1980 standing crop in C1981 and C1982, respectively, while *L. digitata* standing crop steadily increased to 178 % of 1980 standing crop in C1982. The maximum observed ratios of *L. longicruris*: *L. digitata* standing crop (13:1) and abundance (4.7:1) occurred in H1981. This compares to a pre-harvest ratio of 3.5:1 for both characteristics. A shift toward a more even ratio continued as both the harvest and control plots matured.
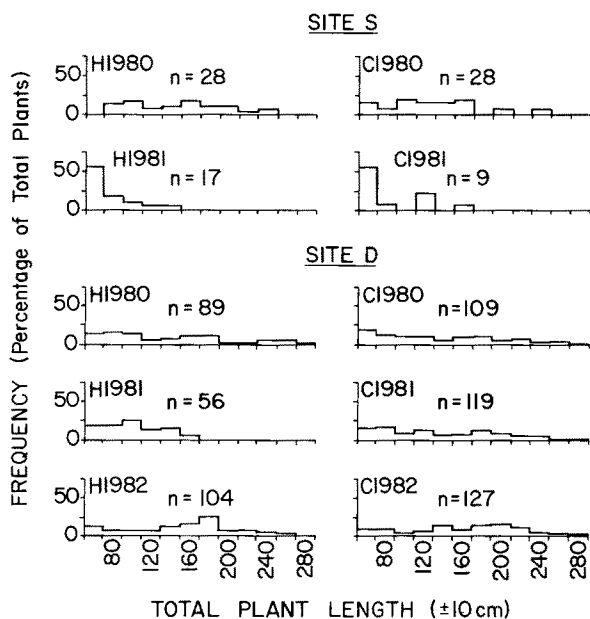
Fig. 6. Total plant length (cm) histograms for *Laminaria digitata* > 50 cm within the harvest (H) and control (C) plots at sites S and D during the years they were assessed. (1980 = pre-harvest; 1981 + = post-harvest)

For both species two years were required for the percentage of reproductive plants within the population to recover to pre-harvest levels. Only *L. digitata* had a continually increasing percentage of reproductive plants within the control plot from 1980–82, with the highest observed percentage occurring in 1982.

Laminaria growth and survivorship

All tagged *L. digitata* plants (n = 43) within one 10 m² quadrat outside of the harvest plot at site S (depth = 3.4 m below MSL) established August 1980 survived less than one year. Total mortality of *L. longicruris* was not confirmed until 20 months following tagging, but annual survivorship was estimated to be 14 %. For neither species was there evidence of a correlation between mortality risk and plant size. Tagged plants of both species within the harvest plot quadrat (10 m²) at site S (depth = 2.5 m below MSL) begun the summer following harvesting (May 1981) also had high population mortalities. There were fewer plants within the harvest plot and they were monitored less often but 100 % mortality of both species was confirmed within 3 months for *L. longicruris* (n = 6) and 10 months for *L. digitata* (n = 18). Because of the short life expectancies of both species at site S, no useful growth data were acquired.

Survivorship curves for *L. longicruris* and *L. digitata* within the tagged plant quadrats at site D are presented in Figure 7. The data are summarized in Table 4. Variability in mean plant total length between quadrats was noted but there was no consistent evidence of a trend in mortality risk with total length for plants greater than
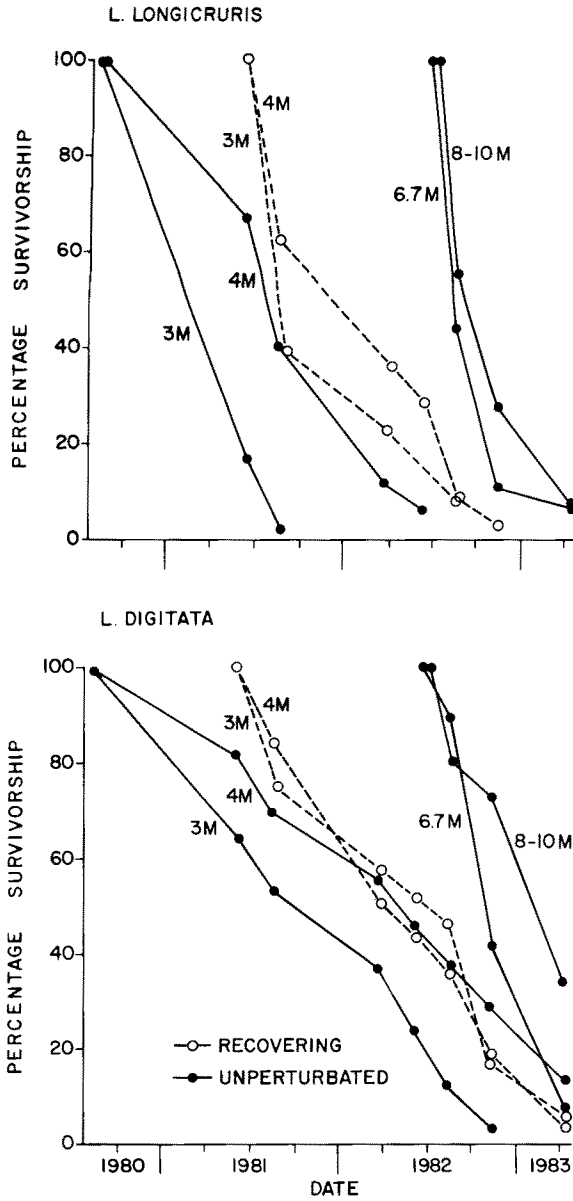
L. LONGICRURIS

L. DIGITATA

Fig. 7. Percentage survivorship of unperturbated and recovering (0–1 year old, harvested September 1980) populations of *Laminaria longicruris* and *L. digitata* at different depths within site D

50 cm in total length. Differences in percentage annual survivorship are thus probably due to depth related effects such as wave action, substrate type, and plant density.

Interpretation of the survival rates indicates longevity of *L. longicruris* and *L. digitata* to be highest at 3–4 m below MSL for both the unperturbated and recovering

Table 4. Survivorship of unperturbated and recovering populations of *Laminaria longicruris* and *Laminaria digitata* for different depths at Site D

	Unperturbated population				Recovering population*	
Depth (m below MSL)	3.0	4.0	6.7	8–10	3.0	4.0
Date monitoring begun	4 Aug 80	12 Aug 80	17 Jun 82	28 Jun 82	27 May 81	1 Jun 81
L. longicruris						
Initial n	138	120	46	111	26	71
Initial plant length (cm)						
(1) Mean	320	230	560	240	210	260
(2) 1 S.D.	160	190	190	190	110	150
Percentage annual survivorship**	7	51	0	0	25	33
L. digitata						
Initial n	63	113	26	51	35	53
Initial plant length (cm)						
(1) Mean	130	100	123	90	110	90
(2) 1 S.D.	60	60	10	50	30	30
Percentage annual survivorship**	57	67	0	15	49	48

* Harvested September 1980
** Calculated assuming a linear mortality rate as interpreted from Figure 7

populations. Within the recovering population no *L. longicruris plants*, and only a few *L. digitata* plants, survived two years. By comparison of the survivorship rates within the unperturbated population, *L. digitata* is the longer-lived of the two species within this depth range, with some plants living nearly three years after being tagged. Based on their total length and Figure 8, some of the plants which survived longest were probably at least one year old when tagged (7 plants > 100 cm total length), suggesting an estimated maximum life expectancy for *L. digitata* of at least four years. No *L. longicruris* plants survived longer than two years and because those surviving longest were small when tagged (< 140 cm total length), the maximum life expectancy for *L. longicruris* is probably about two years. This interpretation is consistent with the evidence of two modes in the unperturbated populations within site D (Figure 5). If these modes represent two year classes, a maximum life expectancy of two years is implied.

The growth curves presented in Figure 8 show that two years are required for individual plants of both species to attain a size equal to those of the pre-harvest population. This substantiates data in Table 3 which indicates two years are required for a full recovery from harvesting. Figure 8 also shows that the biomass of plants more than one year old is lowest during winter months due to reduced lamina area. Analysis of the movement of holes punched just above the meristem of the tagged plants revealed seasonal differences in lamina growth and attrition for both species for the period March 1982 until April 1983. Grown and lost lamina weight was calculated based on the relationship between lamina area and lamina weight determined from measurements on collected *Laminaria:*
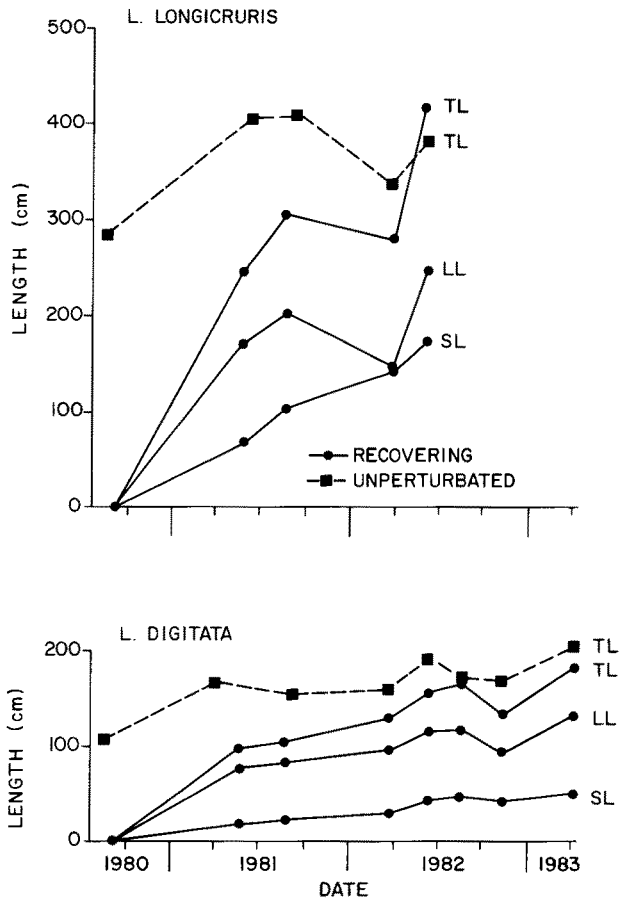
Fig. 8. Mean stipe length (SL), lamina length (LL) and total length (TL) of unperturbated and recovering (0–1 year old, harvested September 1980) populations of *Laminaria longicruris* and *L. digitata* within site D. (Minimum n = 13)

L. longicruris: LB = 0.0730 × LL × LW (n = 2439, r^2 = 95 %)
L. digitata: LB = 0.0699 × LL × LW (n = 1114, r^2 = 92 %)
where: LB = lamina weight (g), LL = lamina length (cm), LW = lamina width (cm).
Figure 9 indicates that maximum lamina growth and increase in plant weight occurred during spring followed by the period of greatest attrition and net weight loss during the summer months. During autumn and winter, the plants are relatively stable, but there is evidence of gradually increasing plant weight.

Cohort weight of the recovering populations of both species for three years following harvesting is presented in Figure 10. The curves are based on the survivorship of both species within the tagged plant quadrats in the harvest plot. Plant weight was calculated based on the relationship between lamina area and plant weight determined from measurements on the previously mentioned collected *Laminaria:*
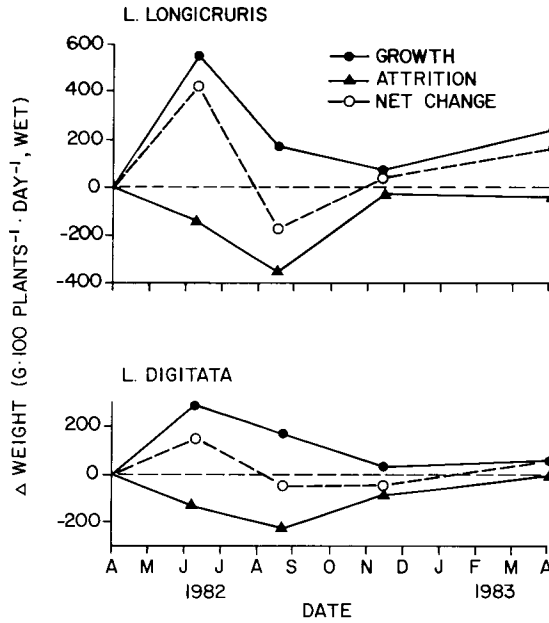
Fig. 9. Seasonal growth and attrition of *Laminaria longicruris* and *L. digitata* lamina within site D for the period March 1982 until April 1983. (Minimum n = 11)
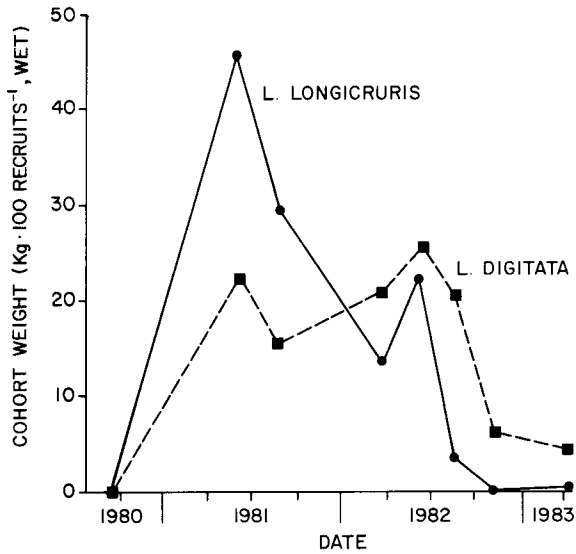

Fig. 10. Cohort weight of 0–1 year old *Laminaria longicruris* and *L. digitata* recovering from a September 1980 harvest within site D and first monitored in May 1981

L. longicruris: PB = 0.0919 × LL × LW (n = 2439, r^2 = 94 %)
L. digitata: PB = 0.0872 × LL × LW (n = 1114, r^2 = 92 %)
where: PB = plant weight (g), LL = lamina length (cm), LW = maximum lamina width (cm).

The maximum yield per recruit for both species occurred the summer following harvesting although for *L. digitata* maximum population standing crop occurred two years after harvesting. Three years following harvesting only a small percentage of the standing crop attained by the monitored cohorts during the first one or two years remained.

DISCUSSION

The importance of large kelps in influencing seaweed community development and characteristics has been noted by Paine & Vadas (1969), Kain (1975) and Foreman (1977). Their studies addressed secondary succession on substrate cleared by divers or intensive sea urchin grazing, but conceivably, harvesting of a *Laminaria* canopy could alter the diversity and stability of the understory community and resilience of the *Laminaria* population. These are the prime considerations for the development of harvest management strategies which emphasize conservation and long-term optimal utilization of the *Laminaria* resource, notwithstanding negative indirect effects on higher trophic levels (Wharton & Mann, 1981).

Within the shallow site (S) there was a clear distinction of the harvested plot in 1981, one year following harvesting, from the control plot. This distinction was characterized particularly by growth of the annual understory epiphytes *C. purpureum* and *C. rubrum*, and also the annual thallus of *P. palmata*. This distinction, however, cannot be attributed only to experimental removal of the kelp canopy in the harvested plot. Kelp biomass was well below pre-harvest levels in both the control and harvest plots in 1981. The winter of 1980–81 was severe with extensive ice formation in Lobster Bay. The most likely cause of the decreased *Laminaria* standing crop at site S, considering its shallow depth and exposure to water movement, is ice scouring during January and February 1981. Since both the control and harvested plots were probably subjected to canopy removal by ice, the distinction of the harvested plot in 1981 cannot be unequivocally attributed to the harvest. This argument is reinforced by considering that the three above-mentioned understory species which contributed the most to the distinction of the harvest plot probably grew during the spring of 1981 by which time there would be no substantial difference in the kelp canopy between the control and harvest plots.

For site D a similar argument applies for *C. purpureum* and *C. officinalis*, which increased in standing crop, and *Cladophora* sp. and *M. alata*, which decreased in standing crop, within the harvest plot in the summer of 1981. *Laminaria* canopy recovery was well in progress by December 1980, four months following harvesting, and had substantially recovered by summer 1981. There was no appreciable difference in canopy between the control and harvest plots when these four species, interpreted as important contributors to the 1981 harvest plot distinction, were undergoing spring growth. No biological explanation is offered for the observed differences in understory standing crop distribution but, alternatively, it is possible that the sampling pattern did not adequately account for within-plot heterogeneity which may be responsible for the significant differences between control and harvest plot standing crop distributions.

Overall, the removal of the *Laminaria* canopy is judged to have only a minor and reversible effect on the understory community within both sites. Within site S, *C. purpureum, C. rubrum* and *P. palmata* are annuals attaining maximum standing crop during late spring and summer. There is no indication that they modify understory composition of the more persistent perennial species. The dominant perennial species within the site, *C. crispus, P. brodiaei, P. membranifolia* and *F. vesiculosus* L. maintained relatively stable standing crop distributions based on the interpretation of Table 1. Similarly, for site D, *C. purpureum, Cladophora* sp. and *M. alata* are annual species which undergo their most rapid growth during spring, and the perennial understory community of *C. crispus, P. brodiaei* and *P. membranifolia* remained stable. One possible exception is *C. officinalis* which decreased in standing crop in both the control and harvest plots but less so in the harvest plot. With the rapid recovery of the *Laminaria* canopy within site D, and the probable potential for its rapid recovery at site S in the absence of ice scouring, no effect on the understory community persisting longer than one year following a single incident of canopy removal in September is anticipated.

The survivorship data presented here are very similar to those recently reported by Chapman (1984) for *L. longicruris* and *L. digitata*, but note that although his site was geographically very close to mine, it was considerably deeper than my harvest plots at 10–12 m below MSL (Figure 1). Chapman observed an increasing mortality risk with increasing plant length for *L. longicruris*, which I did not, possibly because I did not consider plants < 50 cm total length whereas he did. Parke (1948) reported results for *L. saccharina* (L.) Lamouroux, which may be conspecific with *L. longicruris* (Lüning et al., 1978), which agree with results presented here, observing a maximum life expectancy of approximately 2 years. She also observed a similar pattern of seasonal net growth. Gagné et al. (1982) previously observed this pattern for *L. longicruris* in southwestern Nova Scotia. The survivorship data for *L. digitata* are consistent with tagging results of Pérez (1970) who observed some plants (2–5 % of the original number tagged) to live 4 years along the coast of France. He suggested a maximum life expectancy of 5 years because those plants were 30 cm when tagged and culture experiments suggested one year was required to attain that length.

The relative abundance and standing crop of *L. longicruris* and *L. digitata* within the recovering population at site D in 1981 (Table 4) favored *L. longicruris* by ratios of 13:1 (abundance) and 4.7:1 (standing crop). A shift toward a more even ratio as both the harvest and control plots matured was also noted. This pattern is consistent with there being a competitive interaction between *L. longicruris* and *L. digitata* since the relative success (interpreted as summer standing crop) of *L. longicruris* appears to be inversely related to *L. digitata* standing crop. Initially observed is the rapid growth and population recovery of *L. longicruris*. *L. digitata* recovers more slowly but because of its higher life expectancy (> 4 years) compared to *L. longicruris* (2 years) it persists and gradually replaces *L. longicruris*, at least over the short term (i.e. < 4 years). If this interpretation is valid then the development of a mature *L. digitata* population is undesirable because of its slow growth and its inhibition of faster growing *L. longicruris*. I suggest the first hypothesis to test for an explanation of this observation is the effectiveness of shading by *L. digitata* in inhibiting the success of juvenile *L. longicruris*. Similar competitive interactions between species of *Laminaria* and related genera are discussed by Kain (1979).

Chapman (1984) observed no statistically significant enhancement of abundance of either *L. longicruris* or *L. digitata* by canopy removal at 10–12 m below MSL, although a trend toward enhancement is evident in his data. In contrast, I observed considerable enhancement of *L. longicruris* abundance by canopy removal. I suggest this disagreement is partially due to the different site depths, but more likely and more directly, plants at his site were probably not approaching limiting densities. Abundance of unperturbated populations of both species at his site was relatively low at 1.2 plants · m^{-2} and 3.2 plants · m^{-2} for *L. longicruris* and *L. digitata*, respectively. Unperturbated population densities at my site D (3–4 m below MSL) ranged from 6.7–15.2 plants · m^{-2} and 4.5–7.8 plants · m^{-2} for *L. longicruris and L. digitata*, respectively.

All the evidence in Tables 3 and 4 and Figures 5, 6 and 8 support, or are consistent with, the interpretation that both *L. longicruris* and *L. digitata* recover substantially from harvesting within one year although two years are required for both species to reacquire pre-harvest population characteristics. The mortality rates of both species together with their rapid regrowth from harvesting indicate high biomass turnover, and Figure 10, which incorporates this information, clearly shows that harvesting should occur on a yearly basis to maximize yield for both species. The competitive advantage of the longer-lived *L. digitata* over the faster growing *L. longicruris* further indicates a desire for a yearly harvest to prevent establishment of a mature *L. digitata* standing crop. According to Figure 9 harvesting should occur during late spring or early summer to maximize harvest yield since this period follows the rapid growth of the spring and precedes the attrition which occurs during the summer months.

None of the above considerations incorporate the possibility of "recruitment over-harvesting" (Cushing, 1973). This is an important consideration since a yearly harvest could severely reduce the reproductive potential of harvested area. If harvesting were to occur on a yearly basis in spring or early summer the recovering population will have had little opportunity to put much effort into reproduction. Chapman (1981) considered the reproductive potential of *L. longicruris* and *L. digitata* and concluded that if stands of reproductive plants were within 600 m (his maximum experimental distance) of an area barren of kelp substantial recruitment was observed, thus these two species are capable of long distance spore dispersal. Based on this, yearly harvesting of kelp within a particular area is acceptable if only those plants which are easily accessible are harvested, and nearby, less accessible plants are left to provide recruitment.

If recruitment can be assured, and in light of the data presented here, the conventional wisdom that *Laminaria* plants should be harvested by detaching the lamina above the meristem, thereby facilitating lamina regeneration, may be overly conservative. Indeed, there may be no yield advantage by employing such a harvest strategy. Most plants large enough to be harvested in this manner would probably be about one year old with a remaining life expectancy of less than one year. Another year would be required for those plants to attain a harvestable lamina length by which time very few plants would remain. This argument would be weakened by evidence that harvesting above the meristem prolongs life expectancy, but there is presently no reason to suspect this.

In conclusion, this study indicates that a yearly harvest of *Laminaria* within the environs of Lobster Bay, southwest Nova Scotia, would maximize yield. The harvest would yield the largest crop during late spring to early summer (May–July). The data

acquired in this study do not support the conventional wisdom that plants must be cut above the meristem for conservation reasons; rather whole plants may be removed. The removal must be done by cutting, not pulling, because of the potential damage to the rocky substrate resulting in understory community disruption and the death of recruiting *Laminaria*. Two points for caution, however, must be addressed. The effects of successive yearly harvests within a particular area on the seaweed community have not been determined, and many questions remain regarding the effect of *Laminaria* removal on fauna associated with the kelp beds (Breen & Mann, 1976; Pringle & Sharp, 1980).

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