



## Population ecology of *Palmaria palmata* (Palmariales, Rhodophyta) from harvested and non-harvested shores on Digby Neck, Nova Scotia, Canada

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Population ecology of *Palmaria palmata* is described from the intertidal zone of Digby Neck and adjacent islands of Nova Scotia. The primary objectives were: to evaluate the difference in habitat specialization and population structure of *P. palmata* between harvest and non-harvest shores, and to characterize differences in thallus structure and frond sizes between epilithic and epiphytic populations. Harvest shores were gently sloping boulder fields with boulders typically about 0.5-1.0 m with dense cover of *P. palmata* on many of the rocks. Non-harvest shores (with or without *P. palmata*) consisted of boulders that were smaller or larger than harvest shores, or bedrock; when *P. palmata* was present on non-harvest sites it was typically epiphytic on other algae (e.g., *Fucus* spp., *Mastocarpus stellatus*, *Devaleraea ramentacea*). Harvestable epiphytic populations occurred only in high current areas. While there was little difference in average cover of *P. palmata* harvest and non-harvest shores ( $31.2 \pm 13.7\%$  vs.  $19.4 \pm 7.3\%$ , mean  $\pm$  standard deviation [SD]), the cover of *P. palmata* on harvest shores was highly skewed such that individual boulders often had >90% cover while adjacent rocks had little. Frond length of large fronds was greater on harvested shores, and mean frond density ( $\text{g m}^{-2}$ ) was three times higher than the mean density on the non-harvested shores. Frond lengths of entire epiphytic and epilithic frond complements of 119 thalli from harvest beaches showed no difference in mean size of the largest fronds, and no difference in frond number per holdfast when epiphytic and epilithic thalli were compared.

**Key Words:** Digby Neck; Dulse; Nova Scotia; *Palmaria palmata*; Palmariales; population ecology; seaweed harvesting

### INTRODUCTION

The red alga *Palmaria palmata* (Linnaeus) Weber et Mohr is widely distributed in the cold waters of the North Atlantic and Arctic Oceans (Irvine and Guiry 1983, Bird and Van der Meer 1993, Guiry and Guiry 2011). Despite its cold water affinities, *P. palmata* occurs in warm temperate waters far south as New Jersey in the western Atlantic Ocean (Taylor 1957) and Portugal in Europe, with localized large populations in northern Spain (Faes and Viejo 2003). Throughout its range *P. palmata* may be an epiphyte, and it typically occurs in the low intertidal and

subtidal zones to depths of about 20 m (Irvine and Guiry 1983, Faes and Viejo 2003, Vadas et al. 2004).

In eastern Canada *P. palmata* occurs from the Bay of Fundy through to the Gulf of St. Lawrence and the island of Newfoundland (Taylor 1957, Edelstein et al. 1970, Wilson et al. 1979, South and Hooper 1980, South et al. 1988). In the outer reaches of the Bay of Fundy, this species can become abundant, and it forms the basis of commercial harvests (MacFarlane 1964, 1966, Ffrench 1974, Chopin and Ugarte 2006). *P. palmata* has a long history

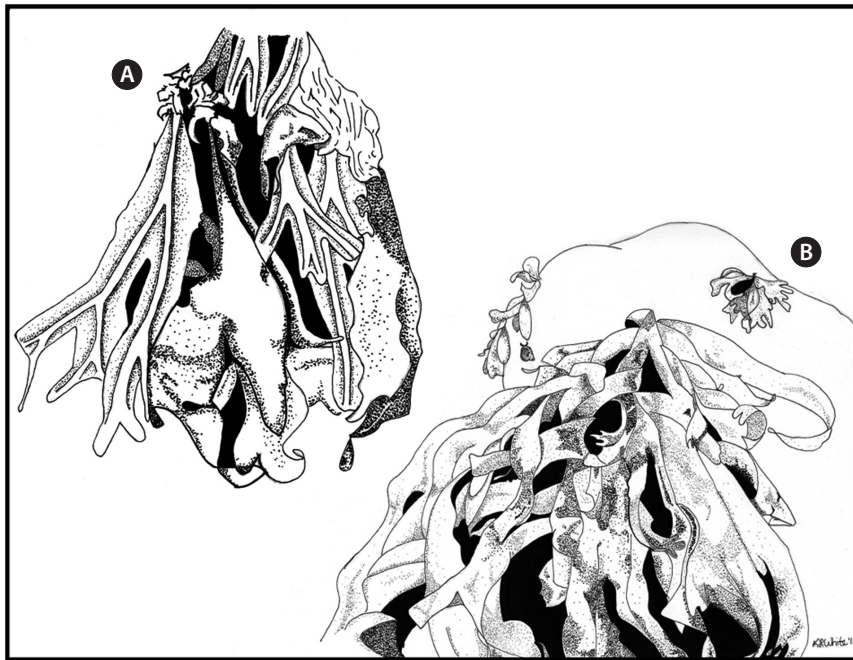
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**Fig. 1.** Habits of *Palmaria palmata* when epiphytic (A) and epilithic (B). In (A) thalli with sparse fronds are epiphytic on *Fucus*; in (B) partially denuded boulder with dense clump of Dulse thalli and several smaller thalli (A & B,  $\times 1/3$ ).

of human utilization (see Guiry and Guiry 2011), and in eastern Canada is widely known and referred to as Dulse. The alga is highly nutritious (Galland-Irmouli et al. 1999), and mostly consumed as a dried product of whole fronds (e.g., MacFarlane 1966, Bird and Van der Meer 1993). More recently, its use as flakes and in various cooked foods is becoming more widespread (e.g., Rhatigan 2009). Various aspects of chemical composition have been evaluated including lipid content (Mishra et al. 1993) and antioxidants (e.g., Yuan et al. 2009, Cornish and Garbary 2010).

There are two traditional areas for the commercial harvesting of *P. palmata* in eastern Canada: Grand Manan Island in New Brunswick, and Digby Neck in Nova Scotia (e.g., Ffrench 1974). In both areas commercial collection of *P. palmata* is carried out by hand picking at low tide. The exploited sites in Nova Scotia are clustered on a series of beaches at the northern end of Digby Neck facing the Bay of Fundy (Lukeman et al. 2012) and on adjacent shores in Annapolis County (MacFarlane 1966). While there is increasing global interest in the aquaculture of *P. palmata* (e.g., Browne 2001, Martínez et al. 2006, Pang and Lüning 2006), the research has mostly focused on tank cultivation and physiological studies (e.g., Morgan et al. 1980, Morgan and Simpson 1981, Martínez and Rico 2002, Corey et al. 2011). Despite the economic and cultural importance of the wild harvest, there have been no

regional studies of *P. palmata* ecology in Nova Scotia. In fact, among commercially exploited seaweeds in eastern Canada, *P. palmata* is the least understood either as a resource or from its ecology in the intertidal community.

This study was undertaken to fill a gap in knowledge in the basic ecology of *P. palmata* in the area where the species is commercially harvested on Digby Neck and adjacent islands of Nova Scotia. The two key objectives were to: 1) clarify the differences (if any) in the structure of populations on harvest and non-harvest shores, and 2) to examine differences in population structure between epilithic and epiphytic habits.

## MATERIALS AND METHODS

Twenty-eight shores including 10 harvested beaches for *P. palmata* (Fig. 1) were visited during the summers of 2010 and 2011 (Table 1). Locations of all shores were established using a hand held GPS unit (Garmin etrex, Olathe, KS, USA). General observations of the algal community were made as well as the nature of the substratum. Although some beaches were visited several times beginning in May 2010, most data was gathered during the July-August spring tides.

Where extensive intertidal populations of *P. palmata*

occurred, a 60 m transect was placed parallel to the shore through the middle of the *P. palmata* population, and cover of *P. palmata* and associated dominant species were recorded in two vertically adjoining 0.5 × 0.5 m quadrats nested randomly within 5 m intervals along the transect (12 pairs in total). For statistical evaluation, the paired quadrats were averaged to give a single cover value. At each of the harvested sites, a sufficient sample of fronds was collected so that the size frequency distribution could be established for the harvested fronds. At some sites, whole thalli were removed from their rock substratum or collected still attached to their basiphyte host. For each thallus, frond length of every frond was measured to the nearest mm. At sites where *P. palmata* was primarily epiphytic on *Fucus* spp., *Mastocarpus stellatus*

(Stackhouse) Guiry, or *Devaleraea ramentacea* (Linnaeus) Guiry, whole host fronds were collected, every frond of *P. palmata* was removed and length was measured. Frond lengths of an additional population of *P. palmata* from Sandy Cove epiphytic on stipes of *Alaria esculenta* (Linnaeus) Greville were also determined. To compare frond lengths from harvest and non-harvest sites, we measured frond lengths from the harvest samples (next paragraph) and the 50 largest fronds taken from the non-harvest sites. The subtidal fronds epiphytic on *A. esculenta* were considered a separate category in the one-way ANOVA that was carried out.

Cover of *P. palmata* at 10 sites was determined before and after commercial harvesting by a Dulse harvester (Wanda Vantassel), and fresh biomass of the *P. palmata*

**Table 1.** List of study sites on Digby Neck and adjacent Islands examined for *Palmaria palmata*

No.	Beach	GPS coordinates	Comments
1	Digby Gut <sup>a</sup>	Zone 20T 0280648 4951432	Harvested
2	Bay View <sup>a</sup>	Zone 20T 0279902 4952075	Harvested
3	Point Prim East <sup>a</sup>	Zone 20T 0279370 4952510	Harvested
4	Point Prim	Zone 20T 0279086 4952433	Harvested
5	Point Prim West	Zone 20T 0278685 4952329	Harvested
6	Haye's Cove <sup>a</sup>	Zone 20T 0276990 4950546	Harvested
7	East Culloden <sup>a</sup>	Zone 20T 0274345 4948449	Harvested
8	Culloden West	Zone 20T 0272885 4947639	Harvested
9	Gulliver's Cove	Zone 20T 0267753 4944315	Harvested
10	Gulliver's Cove Central #1	Zone 20T 0267228 4944131	Harvested
11	Gulliver's Cove Central #2	Zone 20T 0267255 4944171	Harvested
12	Gulliver's Cove West	Zone 20T 0266539 4943789	Harvested
13	Calvin's Beach <sup>a</sup>	Zone 20T 0266682 4943852	Harvested
14	Trout Cove East	Zone 19T 0735938 4937920	No Dulse
15	Trout Cove West	Zone 19T 0735762 4937395	No Dulse
16	Sandy Cove	Zone 19T 0730635 4931387	Not harvested, Dulse present
17	Sandy Cove South	Zone 19T 0729802 4931137	Not harvested, Dulse present
18	Tommy Beach	Zone 19T 0725573 4925348	Not harvested, Dulse present
19	East Ferry, north	Zone 19T 0722617 4919175	Harvested
20	East Ferry, south	Zone 19T 0722655 4918537	Harvested once a year
21	Bear Cove, Long Island	Zone 19T 0719877 4917951	No Dulse
22	Flour Cove, Long Island	Zone 19T 0717447 4913962	Not harvested, Dulse present
23	Cow Ledge, Long Island	Zone 19T 0712869 4906501	Not harvested, Dulse present
24	Freeport South, Long Island	Zone 19T 0713053 4904236	Nor harvested, Dulse present
25	Lighthouse East, Brier Island	Zone 19T 0712079 4907224	Not harvested, Dulse present
26	Lighthouse West, Brier Island	Zone 19T 071183x 4907238	Not harvested, Dulse present
27	Gull Rock Cove, Brier Island	Zone 19T 0709856 4901365	No Dulse
28	Gull Rock Cove, Brier Island	Zone 19T 0709654 4900688	Not harvested, Dulse present

<sup>a</sup>Harvested sites not visited in this study but mapped from an offshore cruise.

was weighted using a 2,000 g spring scale (Stansci Scientific, Chicago, IL, USA) with a resolution of 25 g. At Cow Ledge (historically harvested but not currently used) and two unexploited sites on Brier Island, commercial harvest was simulated (LB and AF), and equivalent data were obtained.

### FronD structure of whole thalli

Morphometric features of complete thalli were examined from 119 thalli from eight harvest sites during June and July 2011 of which 68 were epilithic and the remainder epiphytic on *Fucus* spp. (49 thalli) and *M. stellatus* (2 thalli). For all thalli the minimum size of the largest frond was about 15 cm, and thus potentially harvestable. For each thallus, the length of every frond 1 mm or greater was measured. Holdfast diameter was measured for *P. palmata* using a vernier caliper to the nearest 0.1 mm. These data were used to evaluate possible morphometric differences in frond structure of epilithic and epiphytic thalli at harvest sites. Epiphytic thalli at these eight sites had low abundance (except East Ferry north and Cow Ledge), and typically at the upper end of the elevation gradient occupied by *P. palmata*.

## RESULTS

### General observations

The Dulse harvest shores of Digby Neck and Islands range from 50-500 m in length and regularly experience tidal amplitudes of 5-8 m. When present, *P. palmata* on these shores primarily occupies the lower 1.5 m of the tidal elevation, and when low tides do not retreat below 1.3 m, insufficient *P. palmata* is exposed to warrant harvesting. Thus, the *P. palmata* zone on harvest beaches largely replaces the shore elevations occupied by *Chondrus crispus* Stackhouse and *M. stellatus* on non-harvest beaches. Our surveys of 28 sites allowed us to distinguish several physically and biologically defined shore types.

The cover values for *P. palmata* from all shores showed a continuous gradient (Fig. 2). There was no gradient in abundance of *P. palmata* on the harvest shores - all these sites had high cover and density of *P. palmata* relative to non-harvest shores. The only exception was at Freeport (Cow Ledge) that was historically harvested, but has not been commercially used for many years. This site had the highest cover in the study.

### Habitat differences of harvested and non-harvested beds

Harvest shores had several characteristic features - they were all gently sloping boulder fields with boulders typically 50-75 cm diameter. These shores were wave-exposed with long fetches (most shores) or with strong tidal currents (i.e., two shores at East Ferry). These shores were often weakly indented shores (i.e., shallow coves) in which the boulder fields were bounded by outcrops of bedrock on adjoining headlands. All harvest shores were associated with adjacent kelp beds with a mixture of one or more kelp species [e.g., *Laminaria digitata* (Hudson) J. V. Lamouroux, *Saccharina longicuris* (Bachelot de la Py-laie) Kuntz, *Alaria esculenta*].

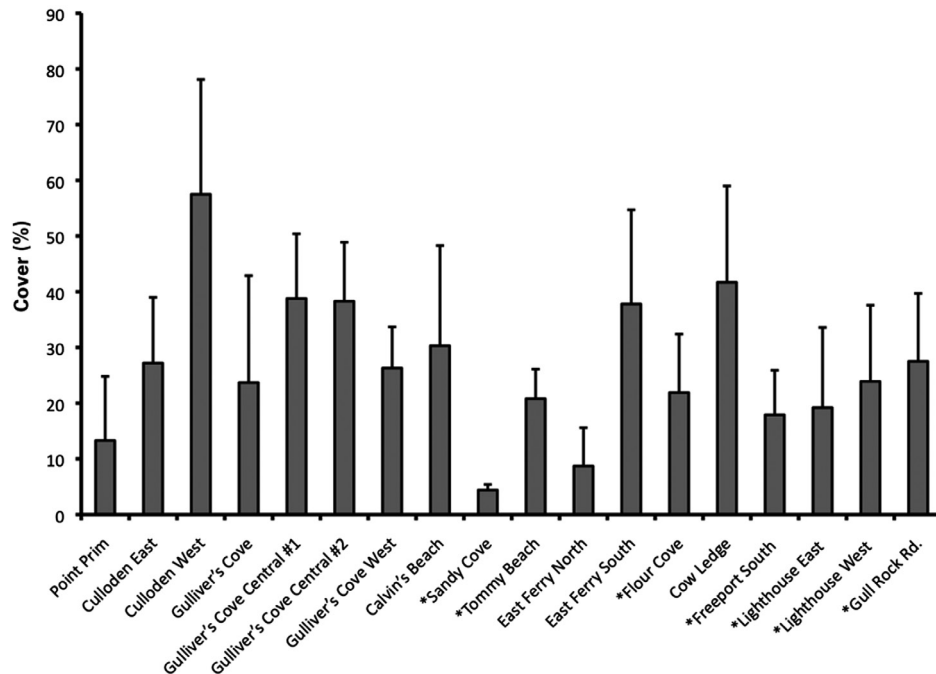
Non-harvest shores, however, were mostly bedrock with narrow ledges and channels with steep walls. Even if *P. palmata* was common, it would be difficult (and dangerous) to harvest. Where boulder fields were present, these often had high accumulations of wrack (e.g., Flour Cove), small boulders (i.e., <50 cm diameter) or high sediment loads.

### Community ecology of harvested and non-harvested beds

There was a major difference in abundance of *P. palmata* on harvested and non-harvested shores. Of the 28 shores we examined, the lower intertidal shore had low cover of other species, in particular fucoids, kelps, *C. crispus*, or *M. stellatus*. These species tended to predominate on rock ledges or the sides of channels. *Devaleraea ramentacea* also occupied the tidal elevation of *P. palmata* on ledges or sites with extensive sand and calcified debris (e.g., Cow Ledge).

### Cover of *Palmaria*

While there is a key difference in cover of intertidal shores with and without *P. palmata*, it is harder to distinguish among shores with and without harvestable amounts of *P. palmata*. Accordingly, average cover values between the two best non-harvested shores (Lighthouse east and west on Brier Island) are equivalent to those of the two harvest shores with the lowest cover (21.6% vs. 18.5%, respectively). These means are not significantly different based on a student's t-test ( $p > 0.05$ ). The cover values of all other harvest shores are significantly greater than the cover of all the non-harvest shores at  $p < 0.01$  ( $31.2 \pm 13.7\%$ ,  $19.4 \pm 7.3\%$ , respectively). The key differ-



**Fig. 2.** Cover of *Palmaria palmata* on shores of Digby Neck and adjacent islands based on transects through the Dulse zone on each shore. Sites presented on an east to west basis. Asterisks (\*) indicate non-exploited shores (bars indicate mean  $\pm$  standard deviation,  $n = 12$ ).

ence between harvest and non-harvest shores is not the overall cover on the shore, but the concentration of *P. palmata* in harvestable patches.

These cover values provide only limited insight into whether or not harvestable quantities are present. The width of the zone where *P. palmata* occurs is critical. The cover values are based on values from a transect parallel to the water through the densest part of the *P. palmata* population. On non-harvest shores, this zone was very narrow (i.e., ca. 0.5-2.0 m), and often on vertical or steep faces that made access difficult. Harvest shores were always gently sloping and the width of the zone was typically 5-8 m. Thus, higher cover was also extended across a greater area. A key feature of harvest shores is that in addition to having high cover (i.e., >70%), following harvest, the cover values remained at about 40% (Fig. 3). At the non-harvest sites, experimental harvesting reduced the cover to about 20% (Fig. 3).

On harvested shores, cover values show a strong correlation with harvestable biomass ( $r = 0.630$ ,  $p < 0.05$ ). The two lowest cover values were for Point Prim (actively harvested but considered a poor site - Wanda Vantassel personal communication), and East Ferry north which was considered to have a poor harvest in May when our sampling took place, but was excellent in August when at least eight harvesters were on the shore (DG personal

observation, Wanda Vantassel personal communication).

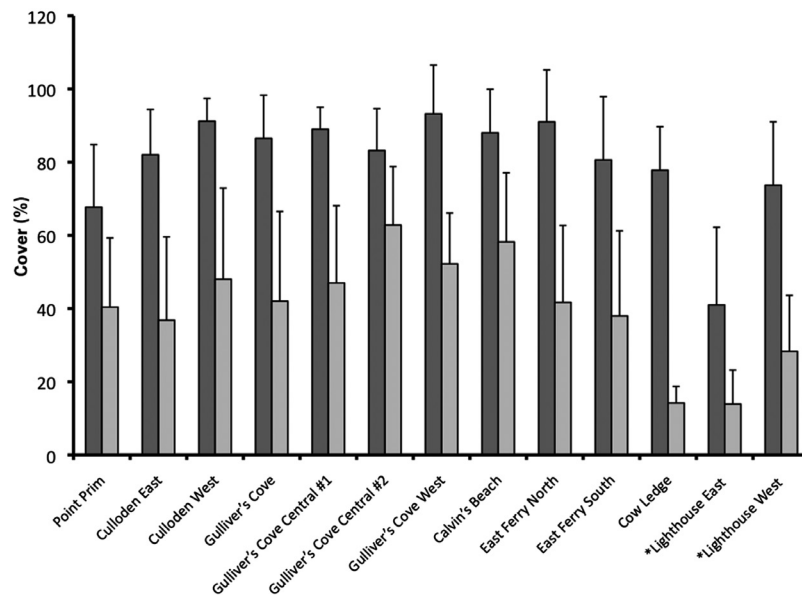
A straightforward comparison of biomass on harvest and non-harvest shores is difficult given our field methodology. Density is critical; the *P. palmata* must be sufficiently aggregated to make it worthwhile to harvest, and those aggregations must be sufficiently numerous to give harvesters return on time.

### Frond length

Of the 3,749 fronds of *P. palmata* measured from 45 host fronds of *Fucus* and *Mastocarpus* at four non-harvest sites, 2,278 fronds (60.8%) were greater than 1 mm long and 727 fronds (19.4%) were >10 cm long. The latter may be considered comparable to the size distribution of epiphytic fronds of *P. palmata* from three regularly harvested sites, where 1,554 fronds (65.0%) were greater than 1 mm long, and 19.9% were >10 cm. At Cow Ledge, 133 epiphytic fronds (56.6%) were greater than 1 mm long and 39 fronds (16.6%) were greater than 10 cm.

Mean length of fronds between harvest and non-harvest sites, and between epiphytic and non-epiphytic populations (Fig. 1) is difficult to compare directly. To compensate for the bias towards small fronds in populations where we counted fronds of all sizes down to 1 mm, we used only the 50 largest fronds from each sample. In all





**Fig. 3.** Cover values of *Palmaria palmata* before and after harvest from individual rocks at sites where Dulse was collected using traditional harvesting effort. Sites presented on an east to west basis. Asterisks (\*) indicate non-exploited (bars indicate mean  $\pm$  standard deviation,  $n = 25$  for each site).

sites, fronds greater than 31 cm long were coded as 31 cm. This minimized the influence of very large fronds on the final 'mean' calculation. These data are shown in Fig. 4. A one-way ANOVA based on sites indicated that sites were significantly different ( $F$  ratio = 99.5,  $p < 0.001$ ). The three non-harvest sites on Brier and Long Island had the smallest fronds, and these were significantly different from other sites. The only non-harvest site to group with the harvest sites was the sample of epiphytic fronds on *Alaria esculenta* at extreme low water from Sandy Cove (Fig. 4). Conversely, the only sample from a harvest site to group with the non-harvest samples was from Cow Ledge, where only 135 fronds  $>10$  mm were measured. The similarity of epiphytic and epilithic populations was shown at Gulliver's Cove West where fronds were not significantly different in length ( $23.9 \pm 3.9$  cm vs.  $25.8 \pm 2.9$  cm) based on Tukeys post-hoc test. When the epiphytic sample from Sandy Cove was considered in a distinct category, a one-way ANOVA separated all of the remaining samples from harvest and non-harvest sites (overall means 15.5 cm vs. 25.1 cm [ $p < 0.001$ ]).

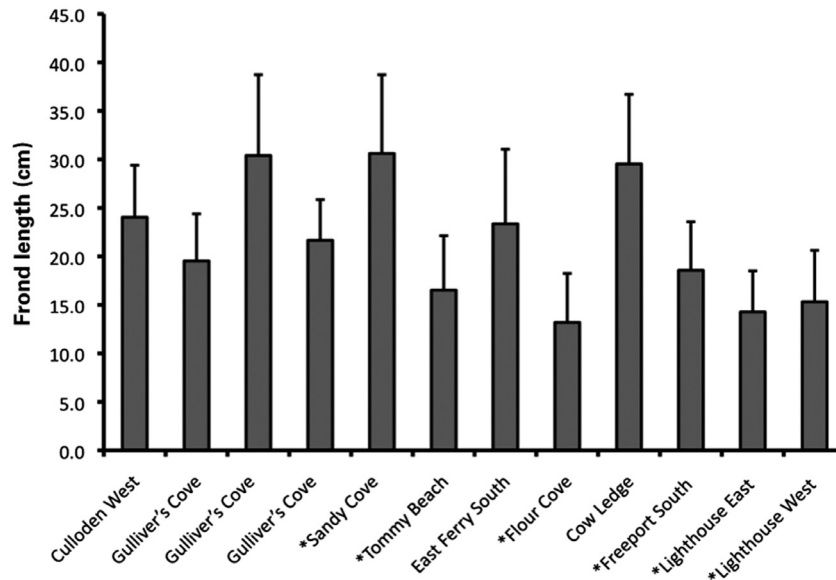
In both harvest and non-harvest sites 1.4% of all fronds were  $>30$  cm long. Thus sites with epiphytic *P. palmata* can produce large fronds, and there is little apparent difference between harvest and non-harvest sites in terms of the potential to produce large epiphytic fronds.

### Frond density

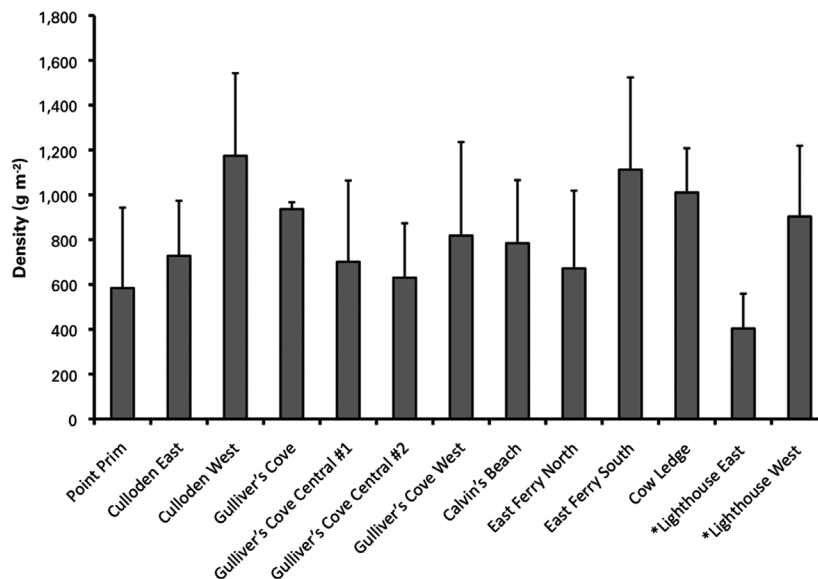
It was beyond the scope of this work to determine the number of fronds per unit area, and frond densities at most non-harvest sites were not carried out because of obviously low values and concerns regarding conservation. Instead, we determined harvestable biomass per unit area at ten harvest sites and three sites not currently harvested commercially (Fig. 5). *P. palmata* on boulders had high density with numerous fronds growing from single holdfasts (Fig. 1). Epiphytic populations on *Fucus* spp. (Fig. 1), *M. stellatus* and *D. ramentacea* tended to have only a few large fronds, and a limited density of small fronds. Regardless, a single frond of *Fucus* can host over 100 fronds of *P. palmata* over 1 mm long, with an additional 78 fronds  $<1$  mm long.

### Whole thalli frond structure at harvest sites

The 119 thalli (68 epilithic and 51 epiphytic) for which all fronds were measured consisted of 1,627 fronds 1 mm long or greater. Thalli of *P. palmata* consist of one to many fronds 0.1 mm to about 30 cm in length, with the smallest maximum frond size of 15 cm. These thalli had between 1 and 54 fronds with median values of 11 and 10 for epiphytic and epilithic thalli respectively. Size distribution frequencies were virtually identical between epiphytic and epilithic thalli (Fig. 6), although the mean size of epilithic fronds were 2.5 cm longer. When a single large epiphytic frond was removed from the analysis



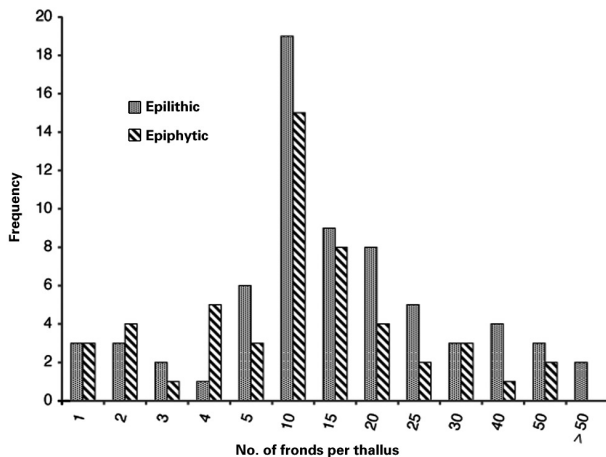
**Fig. 4.** Frond length of the largest fronds collected at exploited and non-exploited sites of *Palmaria palmata* on Digby Neck and adjacent Islands. Sites presented on an east to west basis. Asterisks (\*) indicate non-exploited sites; bars indicate means  $\pm$  standard deviation (n variable, always greater than 25).



**Fig. 5.** Density (as g m<sup>-2</sup>) of *Palmaria palmata* on sample harvest rocks on exploited and non-exploited beaches. Sites presented on an east to west basis. Asterisks (\*) indicate non-exploited beaches. Bars indicate means  $\pm$  standard deviation (n = 25).

(5 standard deviation [SD] away from the mean), the difference between the two habits was 3.2 cm, and the size difference was highly significant ( $p < 0.005$ ). Median frond length was 20.1 cm (epilithic) and 15.5 cm (epiphytic), supporting a general perception from the intertidal zone

that epiphytic fronds of *P. palmata* were smaller than epilithic ones. There was no significant difference in frond number per thallus or holdfast size (Students t-test at  $p < 0.05$ ) (Table 2).



**Fig. 6.** Frequency distribution of frond number per thallus of *Palmaria palmata* from epiphytic (n = 51) and epilithic (n = 68) thalli at harvest sites on Digby Neck based on fronds > 1 mm long.

**Table 2.** Morphometric comparison of epilithic and epiphytic thalli collected from Dulse harvest beaches

Feature	Habit	Mean ± SD	Significance
No. of frond	Epilithic	15.0 ± 13.1	p = 0.189
	Epiphytic	12.0 ± 11.0	
Frond length (cm)	Epilithic	19.2 ± 6.4	p = 0.060
	Epiphytic	16.7 ± 7.8	
Holdfast diameter (mm)	Epilithic	3.5 ± 1.6	p = 0.94
	Epiphytic	3.5 ± 1.7	

Values indicate mean ± standard deviation. Significance based on Students t-test.

## DISCUSSION

Three primary conclusions can be derived from this study: 1) the sites that host harvestable beds of Dulse are distinct in terms of their physical structure from the typical basaltic bedrock seashores that predominate along the north shore of Digby Neck, 2) the population ecology of *P. palmata* from harvest shores is quantitatively different from those that are not, and 3) the algal community of the harvest beds differs from that at other sites, even independent of the occurrence of *P. palmata*. The harvestable *P. palmata* occurs on shores with mostly epilithic populations rather than the epiphytic populations at the non-harvest sites. In aggregate, harvest shores have greater cover of *P. palmata*, with larger fronds and greater biomass. We observed minimal size difference in the size frequency distribution of *P. palmata* growing epiphytically or epilithically at harvest sites or between epiphytic

fronds at harvest and non-harvest sites when considering only the larger fronds (Fig. 4). Thus, once a thallus of *P. palmata* has become established, the environmental differences from one site to another in terms of nutrients, wave action etc., or biotic factors, do not appear to be limiting the capacity for growth. However, when median size of all fronds was compared, epilithic fronds were almost 5 cm larger. We attribute this to increased removal of the largest epiphytic fronds by higher drag forces from the impact of equivalent wave action on the epiphytic fronds.

We are left with nature of the substratum (i.e., boulder fields in appropriate size range) as the primary explanation that accounts for differences in production between harvest and non-harvest shores. That some sites (e.g., Gull Rock Cove) with apparently suitable substrata (i.e., boulder fields) were devoid of *P. palmata* may be attributed to other factors, e.g., siltation, freshwater runoff, excessive littorine populations, wrack accumulation, or frequency of major physical disturbance. Two harvest shores (East Ferry north and south) had extensive epiphytic populations, and these were in high current areas. Cow Ledge also had an extensive epiphytic population and was also in a high current area. *P. palmata* at the remaining harvest sites was primarily epilithic, and these epilithic populations formed the basis of the commercial harvest.

While most harvest shores have a long history, some shores have been abandoned because of decline of *P. palmata* (Wanda Vantassel personal communication). This apparently results from storm damage where violent wind and waves can move the rocks on which the alga grows. The proportion of rocks disturbed by wave action may be the primary determinant for the development of a harvestable Dulse population: too few rocks disturbed, and insufficient space may be created for colonization of *P. palmata*, and succession may proceed to longer lived perennials (i.e., *C. crispus* and *M. stellatus*). Disturbance of too many rocks may keep the habitat in short-lived, early succession species (e.g., filamentous green algae, *Ulva* spp.). Hence maintenance of *P. palmata* on boulder fields may provide another demonstration of the intermediate disturbance hypothesis (Sousa 1979). Alternatively, the gradient of abundance and the overall species richness of these communities may reflect the environmental stress model of Menge and Sutherland (1987) in which interactions with the wider biota are key to understanding abundance. Distinguishing between either of these models requires additional details of both the physical and biotic factors, and their influence on the success of *P. palmata* at particular sites.

These causal factors need to be further explored to



determine if the number of Dulse beaches could be enlarged through artificial seeding of the sites. Seeding of shores would require a small investment of financial resources relative to that required for actual aquaculture operations, such as that being carried out in Europe (e.g., Martínez et al. 2006). One constraint on artificial seeding, however, is associated with the *Palmaria*-type life history (Van der Meer and Todd 1980, Gabrielson and Garbary 1986) in which female gametophytes mature within days and must be fertilized by spermatia from male gametophytes that take a full year to mature. Thus seeding of shores with tetraspores may need to be carried out in successive years, or mature male fronds would have to be added to the mature tetrasporophytes to ensure spermatial and tetraspore 'rain' so that rapidly maturing female gametophytes became fertilized (see discussion in Guiry and Guiry 2011).

While Lukeman et al. (2012) provided a mathematical model to suggest that current harvesting is sustainable, the Dulse industry is limited by resource availability. Additional sites on Digby Neck and adjacent Long and Brier Islands would appear to be equally suitable for dense populations of *P. palmata*. The requisite boulder fields and kelp beds are present, but rocks are devoid of *P. palmata*. Several sites with continuous bedrock but with the kelp beds either had no intertidal *P. palmata*, or it was restricted to an epiphytic population on *Fucus* spp. or *M. stellatus*. Sites were either harvestable or non-harvestable. Thus, there did not seem to be a transition from harvestable to nearly harvestable to unharvestable. The only exception was Cow Ledge on Long Island where, despite high cover and large thalli, this site may not bear the monthly summer harvest regime of other sites (Lukeman et al. 2012).

In addition to *P. palmata*, Digby Neck hosts populations of the two other intertidal algal species that are commercially harvested in Nova Scotia: *Ascophyllum nodosum* (Linnaeus) Le Jolis and *C. crispus*. While only *P. palmata* is commercially harvested on Digby Neck, establishment of new harvest sites would not interfere with future exploitation of the other species. This is a consequence of *A. nodosum* occurring at a higher tidal elevation (Novacek and McLachlan 1989), and the fact that *C. crispus* is not abundant on the boulder fields from which *P. palmata* is harvested. The snail, *Littorina littorea* (Turton) is also commercially exploited on Digby Neck (Anonymous 1998), often from the same shores as *P. palmata*. The extent to which interactions of these species enhance or detract from commercial exploitation of the other, remains to be studied.

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