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MORPHOLOGY, GROWTH AND PHENOLOGY OF *Petrocelis middendorffii*[†]

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The non-calcarious red alga *Petrocelis middendorffii* was studied *in situ* in the Bay of Fundy over the period October 1975 - May 1989. This species, widespread throughout the Bay, is found attached to rocks below the *Ascophyllum* zone, downwards to just beyond the *Mastocarpus-Chondrus* zone. In some sites e.g. Gulliver's Cove and Sandy Cove, Digby Co., the crusts occur only in a narrow zone about 1 m above mean low water between the *Mastocarpus-Condrus* and coralline zones. The diameter of crusts varied (0.01-0.5 m), and were generally thicker at the periphery than at the center. The thickness of the perithallium varied with season, the position in the crust, and the presence of developing tetrasporangia. Measurements in permanent quadrats revealed that crusts grew with a radial expansion rate of 1-1.5 mm y^1. This growth occurred from spring to early autumn, and produced a pattern of concentric grooves that may be interpreted as annual growth rings. A coalescence of small crusts into a larger patch of crust exhibiting several concentric grooves was sometimes seen. Tetrasporangia were observed throughout the year. Mature tetraspores arranged cruciately were observed in intercalary perithallial filaments from late November to early March. Following the release of tetraspores during this period, the crusts turned greenish, except at the margins, and the discolored perithallial filaments were regenerated. After more than three years of monthly observations at Gulliver's Cove, we had not detected the germination of sporelings of either *Petrocelis* or *Mastocarpus* on substrates of cleared rocks, glass slides or permanent quadrats. However, *Ulva, Porphyra, Chondrus* and other macrophytes became established from spores at these sites.

On a éxaminé l'algue rouge non-calcaire *Petrocelis middendorfii in situ* dans la Baie de Fundy du mois d'octobre 1975 jusqu'à mai 1989. Cette espéce, largement répandue dans la Baie, s'attache aux roches, en bas du zone *Ascophyllum*, et en sa descente, dépasse le zone *Mastocarpus-Condrus.* Dans quelques lieux, p.ex. Gulliver's Cove et Sandy Cove, comté de Digby, les croûtes se trouvent seulement dans un zone étroit, à peu prés un mètre au dessus de la marée basse moyenne, entre les zones *Mastocarpus-Chondrus* et corallin. Les croûtes avaient un diamètre variable (0.01-0.5 m), et étaient ordinairement plus épaisses à la périphérie qu'au centre. L'épaisseure du périthallium changeait selon la saison, sa position dans la croûte, et la présence de tetrasporangia en développement. Les mesures faites en carats permenents ont démontré la croissance des croûtes en expansion radiale à un taux de 1.0-1.5 mm chaque année. Cette croissance prenait place du printemps jusqu'à la première partie de l'automne, et produisait une disposition de sillons qu'on peut interpréter comme anneaux de croissance. Un groupement de petites croûtes produisant une plus grande parcelle de croûte et démontrant plusieurs sillons concentriques a été décerné de temps à autre. On a découvert des tetrasporangia au long de l'année. Des tetraspores mûrs et cruciformes ont été décelés dans les filaments intercalaires du périthallium, depuis la dernière partie de novembre jusqu'à la premiere partie de mars. Apres l'émission de tetraspores, les croûtes sont devenues verdâtres excepté aux marges, et le périthallium décoloré s'est érodé de la surface de la croûte. Par la suite les filaments périthalliales se sont dégénérés. Pendant plus de trois années d'observations mensuelles à Gulliver's Cove, nous n'avons pas aperçu la germination de jeunes spores soit de *Petrocelis* ou de *Mastocarpus* sur les souches inférieures de roches deblayées, de plaques de verre, ou de cadrats permanents. Toutefois *Ulva, Porphyra, Chondrus* et d'autres macrophytes se sont établis en provenance de spores sur ces lieux.

Introduction

Petrocelis middendorffii (Rupr.) Kjellman is commonly found in the Bay of Fundy, Nova Scotia (Edelstein *et al.*, 1970; Wilson *et al.*, 1979; South, 1984) associated with

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an abundance of *Mastocarpus stellatus* (Stackh. in With.) [Guiry et al., 1984; = *Gigartina stellata* (Stackh. in With.) J. Ag.] *M. stellatus* is also very common along the Atlantic coastal waters of Nova Scotia, but *P. middendorffii* is extremely rare (Edelstein *et al.*, 1970).

West (1972) suggested that *P. middendorffii* or *Petrocelis cruenta* J. Agardh could be the tetrasporophyte of *M. stellatus,* but our early work on *M. stellatus* carpogonia (Edelstein *et al.,* 1974, as *Gigartina*) from the coastal waters of Nova Scotia and plant development in culture from carpospores (Chen *et al.,* 1974) did not indicate a linkage between these taxa in our area. Evidence, such as observed for *P. franciscana* Setchell et Gardner, (West, 1972) and *P. cruenta* (West *et al.,* 1977; Dion and Delépine, 1979), of alternation in the life history between foliose *Mastocarpus* and crustose *Petrocelis* was not seen. A number of studies have shown that heteromorphic and apomictic life histories occur in the *Mastocarpus (Gigartina)* species from the Pacific coast of Japan (Masuda *et al.,* 1987), California and Washington (West *et al.,* 1977), the Atlantic coasts of France (Dion and Delépine, 1979) the British Isles, Portugal, Spain and Denmark (Guiry and West, 1983). However, the life history of *M. stellatus* appeared to be exclusively apomictic in Nova Scotian waters (Chen *et al.,* 1974) and in Norway (Rueness, 1978). In 1981, Chen and Craigie (1981) reported on cultured *M. stellatus* plants with basal holdfasts that increased greatly in size over ten years. Analysis showed that these holdfasts contained λ-type carrageenan, the type of carrageenan found in field-collected *Petrocelis* plants and different from that produced in the apomeiotically reproducing erect fronds.

A study (Paine *et al.,* 1979) on growth and longevity of *P. middendorffii* in the coastal waters of Washington reported that this crustose red alga exhibited slow growth, a relatively great longevity and persistence. However, the report has shed little light on the mechanism(s) of persistence, but suggested that the crustose algal periphery might be less edible to molluscan grazers than the central portion, which has excellent capacity to re-establish itself. The report did not indicate that there was any evidence of linkage between *G. papillata* and *P. middendorffii* in that region. Guiry and West (1983) reported comprehensively on the linkage between *M. stellatus (G. stellata)* and *P. cruenta* which cover wide regions of the Atlantic coasts. However, they gave little information concerning *P. cruenta* in the Maritimes. Recently, Dudgeon *et al.* (1989, 1990) reported *Mastocarpus stellatus* to be a very hardy species with regard to freezing tolerance in the coastal waters of Maine. *Petrocelis* is very common in the Bay of Fundy, yet little is known regarding its morphology, growth, regeneration, colonization, seasonal variation or reproduction. We report here a long-term study of these aspects of *P. middendorffii* from the Bay of Fundy.

Materials and Methods

Field observations on a montly basis were made from October 1975 to May 1989 along the shores of the Bay of Fundy and occasionally on the Atlantic coastal waters of Nova Scotia (Fig 1). Twelve permanent quadrats were randomly established in the littoral zone at Gulliver's Cove, Digby Co., by chiselling into the rock a 1 dm square perimeter. Each quadrat was marked with fluorescent paint along the chiselled line so that the quadrats could be relocated. Quadrats were photographed and *Petrocelis* crusts and any other macroalgae counted. The elevation and position in the littoral zone of each quadrat (Fig 2) were recorded.

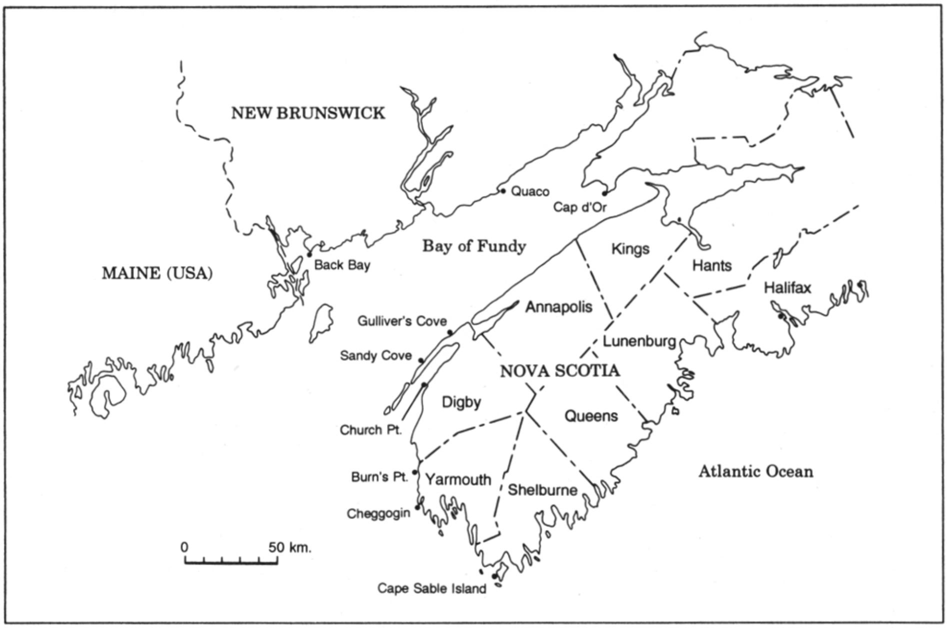

Fig 1 Study sites in the Bay of Fundy.

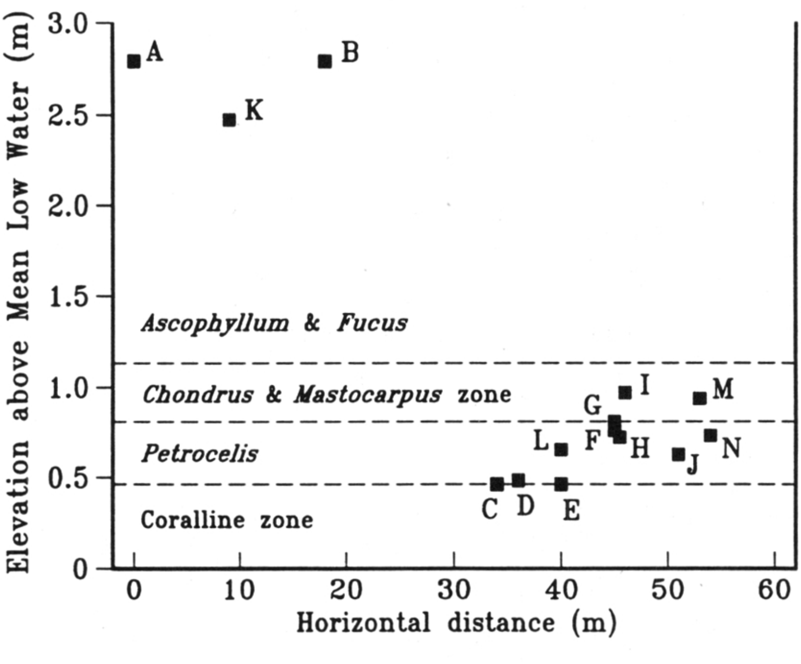

Fig 2 Distribution sample plots (quadrats) in the intertidal zone at Gulliver's Cove.

Table I Change in area of *Petrocelis* crusts as determinated in permanent quadrats at Gulliver's Cove*

	Area (cm^2)		
Quadrat**	November 1975	November 1976	January 1978
C	2.5	4.1	5.3
D	2.0	3.8	4.5
E	4.4	6.5	7.8
F	1.9	3.0	2.8*
G	4.4	7.4	9.0
H	0.9	1.7	2.5
I	2.3	3.2	5.2
J	2.4	5.2	6.2
M	8.8	8.3*	10.9
N	15.3	20.0	22.8

* Decrease in crust following spore release.
** A & B had no *Petrocelis* crusts.

One of the quadrats (H) was set up to study *Petrocelis* thallus regeneration capability over the period from 1976 to 1979. Initially, we removed approxiamtely two cm^2 (1 x 2 cm) from two locations on the crust at the margin area. At the first location both the hypothallium and perithallium were completely removed by using a surgical blade, whereas at the other one, only the perithallium was sheared off. Samples from the same study sites were taken monthly thereafter and were examined microscopically.

Monthly examinations and photographs of quadrats were made at low tide from 1975 to 1978 (Table I). For each quadrat, horizontal growth of crusts, regeneration, recolonization, population changes, reproductive maturity, animal grazing, recruitment and mortality were assessed.

Petrocelis crusts were also collected from outside the quadrats at Gulliver's Cove and from other locations in the Bay of Fundy to monitor the anatomical structure, initiation of tetrasporangia, release of tetraspores, regeneration of perithallium, and the proportion of perithallium to hypothallium. Entire small crusts were scraped from the rock to determine the developmental pattern of perithallium and hypothallium.

To observe succession and recolonization of *Petrocelis* in nature, the algal population on two boulders, one just below the *Ascophyllum* zone, the other lower, at the *Mastocarpus-Chondrus* level at Gulliver's Cove (Fig 2, K & L) were cleared of all attached plants with a kerosene flame thrower (Edelstein *et al.*, 1970) in October, 1975. Simultaneously, two sets of ground glass slides (10 each) were set up near each boulder as portable substrata for recruitment of sporelings. The boulders and slides were observed monthly for one year, and observation of the boulders continued periodically from 1977 to 1989.

To study growth rates, the *Petrocelis* crusts in each quadrat were photographed *in situ*, at one to three-month intervals over a period of thirty months beginning in September 1975. Thereafter, photographs were taken twice a year until 1989. All photographs were taken from approximately the same angle and distance from the quadrat to minimize problems of parallax. Photographs were printed to the same scale to facilitate comparison of the measurement of growth and horizontal expansion of the crusts during the observation period.

Observations

Distribution, habitat and associated species - *Petrocelis* was abundant on rocks at the collection sites in the Bay of Fundy except for the uppermost portion (beyond Quaco) of the Bay (Fig 1), where populations were sparse. The vertical distribution of *Petrocelis* varied throughout the Bay. On the New Brunswick or northwest coast, from Quaco Head westward toward St. Andrews, patches of *Petrocelis* (up to 30 cm in diameter) were common especially in the mid-intertidal zone. Crusts (>20 crusts m^{-2}) were abundant in the *Ascophyllum* zone, attached to the same rocks as the *Ascophyllum* plants, but *Petrocelis* was also well developed slightly below the *Ascophyllum* zone. However, on the Nova Scotia side of the southeastern shores of the Bay of Fundy, these crusts were found only in the low intertidal zone in various places, such as Cape d'Or, Cumberland Co.; Gulliver's Cove, Sandy Cove, Tommy Beach and Church Point, Digby Co.; Burn's Point and Chegoggin, Yarmouth Co. In these locations, patches of crusts < 1 - 50 cm in diameter were found below the *Ascophyllum* zone and growing between the *Mastocarpus-Chondrus* and *Laminaria* zones. Foliose *Mastocarpus* plants were always present wherever *Petrocelis* crusts were found. Curiously, the situation was quite different in coastal waters from Cape Sable Island (Yarmouth Co.) to Fink Cove, Halifax Co. where foliose *Mastocarpus* plants were common in the intertidal zone without any sign of crusts of *Petrocelis*.

Petrocelis was very common at Gulliver's Cove and some crusts were up to 50 cm or more in diameter. Both the small crusts and some of the large patches were usually round with very distinctive concentric grooves on the surface. We also found crusts with several sets of concentric ridges on a single large patch of crust. The shape of the crusts was usually governed by the underlying substrate to which the crusts were attached.

At Gulliver's Cove and Sandy Cove, *Petrocelis* crusts grew in a narrow zone approximately one meter above the mean low water mark (Fig 2), usually between the *Mastocarpus-Chondrus* and coralline zones. The crusts were sometimes found below and adjacent to the *Ascophyllum* zone but not above it (Fig 2, A & B have no *Petrocelis* crusts). These crusts usually grew together with the morphologically similar crusts of *Hildenbrandia rubra* (Sommerf.) Menegh. During the spring season both appeared reddish-brown in colour and were firmly attached to the rock-substrate. However, they could be distinguished macroscopically later in the year, when the *Petrocelis* crusts became thicker, darker and showed concentric zones; such zones were absent in the *Hildenbrandia* crusts, which remained thin and became a lighter reddish brown.

Examination of randomly collected samples of the crusts indicated that these species grew intermixed down to the coralline zone, and furthermore, that *Hildenbrandia* occurred largely at the upper edge of the mid-intertidal zone and gradually diminished towards the lower intertidal zone (*Laminaria* zone). *Petrocelis* crusts (5-10 cm in diameter) were abundant (< 20 crusts m^{-2}) in the *Mastocarpus-Chondrus* zone, but most abundant (> 20 crusts m^{-2}) below the *Mastocarpus-Chondrus* zone on vertical boulders facing the open water. However, below the *Laminaria* zone (in the infralittoral fringe) these crusts disappeared.

At most of our collection sites in the Bay of Fundy, *Petrocelis* crusts competed for space with other crustose algae, such as *Ralfsia fungiformis* (Gunner) Setchell et Gardner, *Peyssonnelia rosenvingii* Schm. in Rosenv. and especially coralline red algae. The last were often found to overlap with *Petrocelis*. At the low water level among the *Alaria* and *Agarum*, large boulders were occasionally found to be covered with extensive patches of smooth, dark reddish-brown *Peyssonnelia* crusts.

Animals such as limpets and marine snails were common throughout the year on the surface of *Petrocelis* crusts, except in January, when they were noticeably rare.

Seasonal aspects - Many changes in the colour of *Petrocelis crusts* were observed throughout the year. In general, the colour was dark reddish-brown for both *Mastocarpus* and *Petrocelis,* but darkest and richest in December when the illumination was lowest and growth was reduced. Anatomical observation showed tetrasporangia were abundant in this month. In late January some greenish spots appeared on the surface of the crusts, in some cases expanding over the whole surface except the peripheral area. By March, the surface colour of many crusts has gradually returned to light brown and reddish-brown. Observations confirmed that tetraspores had been released from the filaments during this period. Deterioration of tissue during and after release of tetraspores might have contributed to the change in colour of the crust surface. From April to August many portions of the *Petrocelis* crust appeared somewhat yellowish, particularly in the central zones. This colour change may have also been related to the amount of light received.

Anatomy and physical characteristics - The crustose thallus of *P. middendorffii* consists of a basal, compact layer of multicellular hypothallium bearing an upper layer of relatively loose erect perithallial filaments. The hypothallium is initially established as a radially filamentous layer which expands horizontally to increase the size of the crust and forms upward-growing loosely coalescent filaments to develop the upper hypothallium and perithallium. The thickness of the cursts can vary from 0.49 to 1.75 mm.

The hypothallial layer consisted of irregularly shaped cells that had long cross links to laterally adjacent cells by pit connections. This tissue sometimes also had a very compact lower stratum of cells loosely connected to the upper portion of the layer. The range in thickness of the hypothallium was 0.24 - 1.00 mm. The perithallial layer consisted of rectangular cells (5-10 x 11-25 μm) in loosely cohesive erect filaments. Generally, the cells of the perithallium were linked only by primary pit connections, with an occasional lateral secondary pit connection in the lower portion close to the hypothallium. Perithallial filaments were branched dichotomously, usually in the upper third of the tissue layer; however, dichotomies occasionally occured quite close to the hypothallium. In some areas of the perithallium, the cells were more irregular and compact, and had more secondary pit connections which apparently caused the distortion in shape. The thickness of the perithallial layer varied from 0.25 - 0.91 mm.

The thickness of the hypothallium and the perithallium appears to depend upon the season, position on the crust, stage in reproduction, growth and age. For example, at the crust margin the hypothallium normally is slightly thicker than the perithallium; however, in early spring the perithallium was thicker. In addition, during the period of the formation of tetrasporangia and before tetraspore release, the thickness of the perithallium increased significantly. Samples of young crusts of *Petrocelis* showed that the marginal areas were always thicker than the central region.

The mean thickness of crusts examined was thinner in May than in August; this might be a result of the intercalary perithallium growing more rapidly during the summer. The ratio of hypothallium to perithallium thickness varied from 0.54 to 1.5, in monthly samples collected from quadrats from April to December. This variability might be explained by the factors influencing the thickness of the crust mentioned above. As well, samples from the extreme outer zone of *Petrocelis* crusts showed a variety of growth patterns. In some cases they had a well-developed hypothallium with short perithallial filaments and very actively growing apical cells. There were also some long perithallial filaments and sometimes apparently a single layer of large irregular hypothallial cells. These growth patterns might indicate that the crust had begun to expand horizontally.

A small green *Codiolum*-type alga, ("*C. petrocelidis*"), was commonly found growing between the filaments of the perithallial layer of *Petrocelis,* especially near the margins. Only a few young *Codiolum* plants were found in the hypothallial layers. This endophytic alga did not seem to affect the development of *Petrocelis* crusts.

Tetrasporocytes were found monthly throughout the year, occurring irregularly in small patches on the crusts. Mature divided sporangia, 40-50 x 20-30 µm in diameter, were found only from late November to February; the mature spores were arranged cruciately in the sporangia and were ready for discharge. Discharged tetraspores measured approximately 20-30 µm in diameter. There was generally a single intercalary tetrasporangium per filament of perithallium. However, in a few exceptional cases there appeared to be more than one developing sporangium per filament, arranged in a series as Wilce & Maggs (1989) described for *Haemecharia hennedyi* comb. nov.

The location of tetrasporangia on perithallial filaments can vary, sometimes being very near the apex, sometimes close to the hypothallium. Following release of tetraspores, patches on the surface of crusts (except near the edges) turned greenish and later eroded. This phenomenon was prevalent in early March; thereafter, the crusts gradually recovered their original reddish-brown colour. By April, the number of tetrasporangia in the samples had decreased dramatically and they were observed only occasionally after April. In general, our observations were in agreement with those of Polanshek and West (1975, 1977) on crusts of *P. franciscana.*

Recruitment and regeneration - At the two quadrats (Fig 2, K & L) set up in Gulliver's Cove to study colonization and succession, populations of *Petrocelis* and other algae eventually re-established themselves. However, the manner in which this occurred in each of the two sites appeared to be different. Monthly observations during the first year showed no signs of *Petrocelis* crusts on the boulder (K) in the *Ascophyllum* zone. However, *Fucus vesiculosus L., Ascophyllum nodosum (L.) Le Jol, M. stellatus, (G. stellata), C. crispus, H. rubra* and encrusting corallines had regenerated there. Interestingly, on the boulder (L) located at the *Mastocarpus-Chondrus* level, *Petrocelis* crusts were found developing mainly along cracks in the rock. There were also a few seasonal plants such as *Porphyra miniata, Ulva lactuca, Polysiphonia urceolata* and *Petalonia fascia.* On neither of these boulders nor the glass slides did we see any young sporeling crusts of *Petrocelis, M.* stellatus, *C. crispus,* or *Fucus* spp. However, some marine animals including snails and limpets were found.

During the periodic observations from 1977 to 1989, we found crusts of *Corallina officinalis* and *H. rubra,* growing on both of the boulders along with *Fucus evanescens C. Ag., C. crispus* and other macrophytes. On the boulder in the *Mastocarpus-Chondrus* zone, the crusts of *Petrocelis* found initially along the cracks of the rock, gradually expanded in size. There were also two young *M. stellatus* plants developing along the cracks in this rock. Three possible explanations for this are: germination from tetraspores of *Petrocelis;* germination from the carpospores of *M. stellatus;* and vegetative regeneration from parts of holdfasts that may have survived. However, the glass slides set up near the boulders to collect germinating plants showed no crustose algae had colonized there after one year. Some annual plants such as *Porphyra, Polysiphonia,* and unidentified green and brown algal sporelings were found on the slides. This parallel recolonization experiment suggests that it is unlikely that the reappearance of crusts and young *Mastocarpus* plants along the rock cracks resulted from germination of spores.

Our regeneration studies were carried out on a fixed quadrat from June to October 1976. During this period there was little indication of regeneration after both hypothallium and perithallium of the crusts had been removed from the substrate. After 36 months some regeneration was noted, presumably from microscopic residual tissue. By contrast, in the crusts where only the perithallium was removed, some regneration of perithallial filaments occurred after two months. In cases where parts of the hypothallium were damaged as the perithallium was scraped away, the crust became yellowish and began to degenerate.

Horizontal growth - Table I shows the growth of individual crusts measured in each quadrat (except A & B) from 1975 to 1978. Overall, the crusts exhibited slow expansion (Table I). Some of these crusts however, decreased in area due to erosion of a certain portion of the crusts. In these cases, some marine animals on the crusts of *Petrocelis* were observed.

In one of the quadrats in the horizontal expansion study there were four small crusts which we observed for long-term growth. The individual crusts grew very slowly, widening in radius at a rate of 1-1.5 mm a^{-1}. Fig 3 represents diagrammatically the

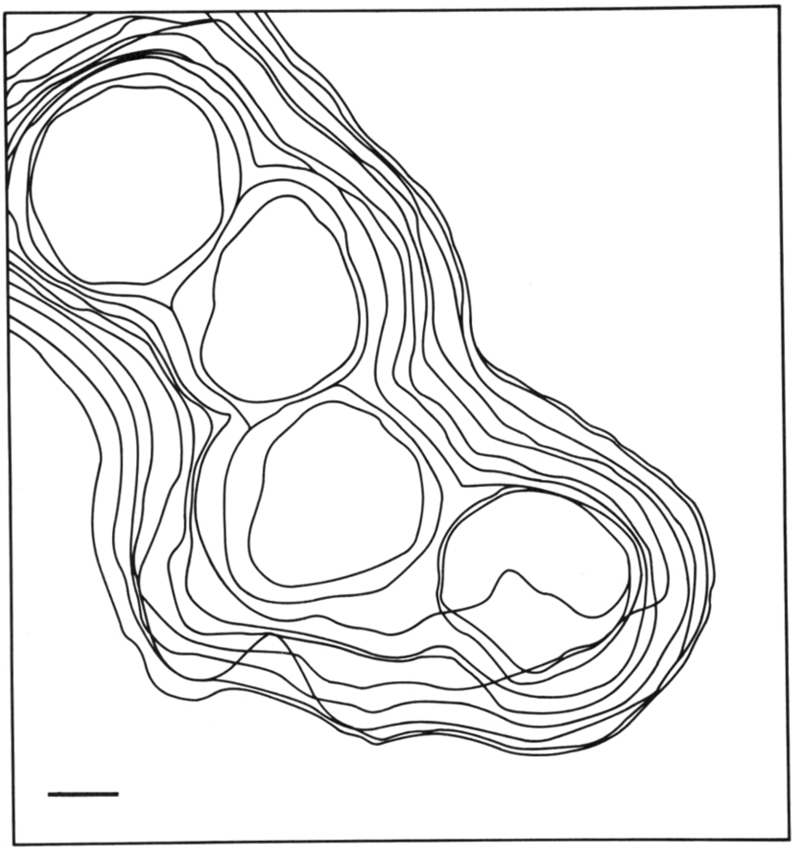

Fig 3 A diagrammatic representation of the horizontal expansion of four crusts during a 12 year period. Each line represents yearly expansion.

horizontal expansion of the crusts during a 12-year period. Successive area expansions were drawn from photographs and these drawings were superimposed showing how both the area and the shape of the crusts changed with time (as in *Chondrus crispus* holdfasts, Taylor *et al.,* 1981). The diagram shows that some overlapping and merging of crusts took place.

The observations recorded for each quadrat in the horizontal expansion study indicated that there were some tetrasporangia and changes in colour of crusts. Most of the crusts that were selected initially were small individuals, but after a few years they began to merge with one another (Fig 3). During this period, there was no indication of new *Petrocelis* sporelings or new crusts. However, some annual algae were observed in these quadrats.

Discussion

Our observations show that *P. middendorffii* is a perennial plant with an extremely slow horizontal expansion (Table I), capable of attaining great age and size under favourable environmental conditions. The regeneration studies in which crust tissue was partially removed indicate that these crusts have an excellent capacity to regenerate to their original form from portions of filaments retained in the rock matrix. They are surprisingly capable of recovering within two months after damage to the perithallial filaments. In other cases where both perithallial and hypothallial filaments were damaged, they may take years to recover. This evident persistence suggests that the population of crusts once established may remain on a substrate so long as the substrate exists. However, growth of *Petrocelis* crusts was restricted by competition for space with other crustose algae on the substrate. The regeneration investigation shed little light on recruitment of original crusts, in spite of the abundance of tetraspores of *Petrocelis* and carpospores of *Mastocarpus* in this area. Nor was there any evidence of sporeling recolonization *in situ* on the glass slides, on the cleaned rock surfaces or on the permanent quadrats. One possible explanation is that because of the apparent vulnerability of the released spores to the severe environmental stresses in the study area, germination was unable to occur. Overgrazing by a large population of animals may have also contributed to the lack of recruitment or re-establishment of sporeling by *Petrocelis* during the course of this study. Further laboratory study might lead to better understanding of the germination capability of tetraspores of *Petrocelis* and carpospores of *Mastocarpus (Gigartina).*

Our observations suggest that overall size of the crust is not necessarily an indication of age. In some cases, large patches of crusts of *Petrocelis* observed in nature appear to be the result of many small crusts merging with one another as shown in Fig 3. Throughout the collection sites, single large crusts were often found to have several intersecting sets of concentric zones. This suggests that several small crusts had merged to form a large single patch of crust. Figure 3 shows the growth of four small individual crusts, which changed their shape and size from year to year until they finally merged as indicated by four sets of concentric grooves on one large patch.

We agree with the previous report (Paine *et al.* 1979) that regeneration of damaged central portions of the crusts results in slow expansive growth. However, we disagree with their explanation that the cause of this damage was by grazing molluscs which find the central perithallial tissue to be more palatable than the peripheral portions of the crust. Our observations show that damage to the perithallial tissue is a natural part of the reproductive process. Investigation of seasonal colour changes on the surface of the crusts led to the observation that the release of tetraspores weakens perithallial tissue causing portions of the tissue to erode. Severe environmental conditions, such as sub-zero air temperatures at low tide during the reproductive season may exacerbate this damage to the perithallial tissue.

Measurements of thallus thickness and ratio of the length of perithallial to hypothallial filaments were relatively uniform among very small crusts collected from October to early December, just before the tetraspores were discharged but the samples collected randomly from December to September showed great variation. The seasonal variation in thickness of crusts might also be related to the development of reproductive structures. Localized erosion of perithallial filaments after release of tetraspores caused changes to both the overall thickness and ratio of thickness between the two layers. The concentric zones in the crusts would further contribute to this localized variability. It appears that both the variation of thickness and ratio of the length of perithallium to hypothallium depend upon season, the reproductive period of the crust, the location on the crust where the measurement is taken, and especially, whether or not tetraspores have been discharged. Thus, the overall thickness of crust and the ratio of the hypothallium to the perithallium may not be useful characteristics to distinguish taxa. Table II summarizes the morphological characteristics of northeast Pacific *P. middendorffii / P. franciscana, P. cruenta* from Ireland and *P. middendorffii* in the Bay of Fundy. It is apparent that the anatomical features of these crustose algae show great variability, making the crusts indistinguishable on morphological grounds. We feel that further comparative culture and cytological studies among strains from typical localities throughout the know ranges are needed in order to use these characteristics to clarify and distinguish the different types of crusts. It is possible that analysis of nucleotide sequence data, may also be used as a taxonomic tool.

The life history studies of *Mastocarpus (Gigartina)* species from various regions (West, 1972; Polanshek and West 1975; West *et al.,* 1978; Dion and Delépine, 1979;

Table II Summary of morphological characteristics of *Petrocelis* crusts from various locations.

Species:	*P. middendorffii** *P. franciscana*	*P. cruenta**	*P. middendorffii*
	Location		
Characteristics	North Pacific	Waterford, Ireland	Bay of Fundy
Perithallium (thickness)	200-900 μm	400 μm	250-1000 μm
Hypothallium	50-175 μm	300-400 μm	150-540 μm
Crust (total thickness)	0.25-1.1 mm	0.7-0.8 mm	0.5 mm-1.3 mm
Tetrasporangia	17-30 x 25-35 μm		20-30 x 30-40 μm
Tetraspore diameter	14.6-16 μm	13 μm	12-20 μm
Rectangular cell of the perithallium	3-4 x 8-14 μm		5-10 μm x 11-20 μm
A phase of	*Mastocarpus papillatus*	*M. stallatus*	?

* West *et al.* 1977.

Masuda and Kurogi, 1981; Guiry and West 1983; Masuda *et al.,* 1987) indicate that *Petrocelis* is the tetrasporic phase of *Mastocarpus* (formerly a subgenus of *Gigartina*). West *et al.* (1978) demonstrated that *P. middendorffii* in Pacific coastal waters is the tetrasporic phase of *G. papillata (M. papillatus),* a species which has not been reported in the coastal waters of Nova Scotia. Obviously, the so-called *P. middendorffii* in this region is different from the Pacific coastal plant. Moreover, from our field observations in the Bay of Fundy, there is no positive evidence to suggest that *P. middendorffii* alternates with *M. stellatus,* despite the fact that the latter is commonly found in association with *Petrocelis* in the Bay of Fundy. It is also interesting to note that *M. stellatus* is abundant in the Atlantic coastal waters of Nova Scotia where no *Petrocelis* was found during this study. Whether or not *M. stellatus (G. stellata)*, which is reported as the gametophytic phase of *P. cruenta* of northeastern Atlantic coastal waters (West *et al.,* 1977), is an alternate generation of "*P. middendorffii*" in Nova Scotia coastal waters has to await further study for clarification. At present, we are unable to demonstrate unambiguously a linkage between local *Mastocarpus* and *Petrocelis.*

We were unsuccessful in observing the recruitment of *Petrocelis* in nature. In the cleared natural substrate monitored from 1975-1978, the glass slides set up *in situ* for one year, and the twelve permanent quadrats observed over nearly 14 years, there was no evidence of sporeling germination or colonization. We saw neither the tetraspores of *Petrocelis,* nor the carpospores of *M. stellatus* germinating on these substrates, although some macrophytic algae did re-establish themselves on the burned boulders and the permanent quadrats after several years. We did observe some crusts of *Petrocelis* developing along cracked areas in these boulders which probably indicates that these *Petrocelis* crusts may have regenerated from those portions of the tissue retained in the rock metrix after animals grazed (Paine *et al.,* 1979); or perhaps the natural degeneration of cells from the filamentous portion of the crusts left isolated groups of cells on the boulders from which the new crusts regenerated. It may also be that these crusts in the deeper cracks had not been completely removed, or perhaps the rough surface in the deeper cracks had trapped the released spores thus allowing vegetative regeneration of new populations of *Petrocelis.* We have no conclusive evidence to show that patches of *Petrocelis* along the sides of rock cracks were the result of germination of the carpospores of *M. stellatus.* Only once, during the period of our studies, did we detect some small crusts in the vicinity of these denuded boulders, which had also formed on a few other boulders which we suspect may have developed from spores. They may also have developed from small amounts of tissue remaining after animal grazing. Further studies on the viability and germination of the tetraspores from *Petrocelis* are needed in order to develop a comprehensive understanding of the question of linkage between *P. middendorffii* and *M. stellatus.*

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