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INVASIVE *FUCUS SERRATUS* (PHAEOPHYCEAE) REPLACES SHALLOW WATER KELP COMMUNITY IN SOUTHWESTERN NOVA SCOTIA

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ABSTRACT

Along the Atlantic coast of Nova Scotia, recent observations in 2020-2021 of the intertidal zone showed that the European native fucoid *Fucus serratus* was becoming more widely distributed, both geographically and ecologically. Here, we extended these observations to the shallow subtidal zone (to about 5 m below chart datum) in southwestern Nova Scotia. We used semi-quantitative and qualitative sampling via snorkeling at selected mainland and offshore island sites, observed using both transects (50 m) and spot sampling. At all sites, the expected populations of kelp species (i.e., *Laminaria digitata*, *Saccharina latissima,* and *Alaria esculenta*) were absent to rare, and extensive populations of *F. serratus* were present with > 50% cover that formed the dominant canopy species. The decline in kelp species mirrors previous accounts of kelp population collapse in St. Margaret's Bay and Lunenburg Bay in recent decades but differs in that the canopy species is *Fucus serratus* rather than red algal turfs. While ocean warming may be playing a role in regional kelp decline, significant warming did not occur in Nova Scotia until the late 1990s. We suggest that the commercial harvesting of *Chondrus crispus* by the 1970s played a key role in the replacement of shallow water kelp beds by *Fucus serratus*.

Keywords: Climate change, *Fucus serratus*, irish moss, kelp, Nova Scotia, seaweed harvesting

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INTRODUCTION

Kelp forests are declining globally (Krumhansl *et al.* 2016) with declines attributed to a variety of human induced factors including climate change and overharvesting. This decline has been noted along the Atlantic coast of Nova Scotia where an ocean warming hotspot has been implicated in the changes in community structure (Hobday and Pecl 2015, Filbee-Dexter *et al.* 2016). Here we show declines of kelp species in the southwestern corner of Nova Scotia, an area with a long history of harvesting of both *Chondrus crispus* Stackhouse (Irish moss) and *Ascophyllum nodosum* (Linnaeus) LeJolis (rockweed) (MacFarlane 1952, Pringle and Semple 1980, Vandermeulen 2013). We suggest that the overharvesting of Irish moss rather than ocean warming provided disturbance regime that facilitated kelp decline and its replacement as a canopy species by invasive *Fucus serratus* Linnaeus.

FUCOIDS AND KELP IN SOUTHWESTERN NOVA SCOTIA

Fucus serratus is native to western Europe where it is found on rocky shores from Spain to northern Norway and the White Sea (Guiry and Guiry 2026). In the British Isles and Ireland, it is a common component of intertidal shores where it can be a dominant species (e.g. Lewis 1964). The species was introduced in ship ballast to Nova Scotia in the mid-1800s from western Ireland and Scotland (Brawley *et al.* 2006). It subsequently colonized subtidal habitats around Cape Breton Island and has become widely distributed in eastern Canada with extensive populations in the southern Gulf of St. Lawrence of Nova Scotia, New Brunswick and Prince Edward Island (Johnson *et al.* 2012, Garbary *et al.* 2021). A population of *F. serratus* of unknown provenance occurs in the southwestern part of Nova Scotia in Lobster Bay. MacFarlane (1952) first noted that it occurred in "considerable quantities" in the Tusket Islands (Fig 1). Surveys and reviews in the 1970s by Edelstein *et al.* (1972), Wilson *et al.* (1979), Dale (1982), and Novaczek and McLachlan (1989) indicated a limited distribution on the mainland. Furthermore, in the 1970s a detailed survey of the low intertidal and subtidal locations on both the mainland and islands in Lobster Bay and adjacent Shelburne County showed the standard zonation pattern of a red algal zone dominated by *Chondrus crispus* leading to kelp communities in the adjacent subtidal area (Pringle and Semple 1980).

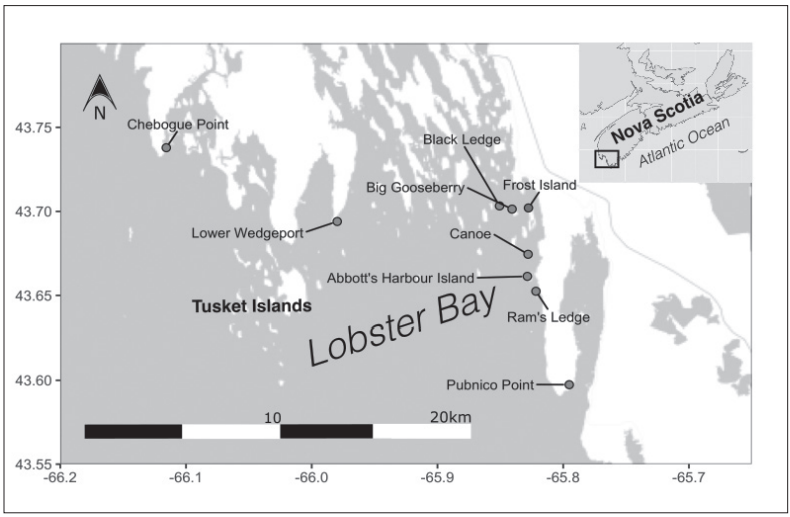


Fig 1 Map of southwestern Nova Scotia indicating sample sites in June 2021. See Table 1 for site coordinates.

A major departure from this pattern was observed by Novaczek and McLachlan (1989) and Garbary *et al.* (2021) in which *F. serratus* had become a dominant, canopy species in the low intertidal zone (Lobster Bay and Lunenburg Bay) as well as subtidally (Lunenburg Bay). Here we report on the replacement of low intertidal and shallow subtidal kelp communities in southwestern Nova Scotia by *F. serratus*.

MacFarlane (1952) surveyed kelp and fucoid algae in southwestern Nova Scotia with a focus on Yarmouth County and immediately adjacent areas in Shelburne and Digby Counties. Kelp species included *Alaria esculenta* (Linnaeus) Greville, *Laminaria digitata* (Hudson) J.V. Lamouroux, *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders (as *L. longicruris*), *Sacchoriza dermatodea* (Bachelot Pylaie) J. Agardh (as *Phyllaria*), and *Agarum clathratum* Dumortier. Importantly, *Laminaria* and *Saccharina* were described as widespread and abundant on both offshore islands and mainland sites. MacFarlane (1952) described the kelp and fucoid species in this part of the province with the phrase "in all of which the region abounds" with *F. serratus* restricted to the Tusket Islands (Fig 1). Edelstein *et al.* (1972) concluded that *F. serratus* had not spread beyond the Tusket Islands, although soon afterwards a transect at Cheboque Point in 1977 by Novaczek and McLachlan (1989, Fig Site 25 in Appendix 3) that included both the intertidal and shallow subtidal zones indicated both

Laminaria digitata and *S. latissima* (as *L. saccharina*) as common above lower low water spring tide, and these kelp species were shown as abundant. This transect showed a clear zone of *F. serratus* between the lower limit of *A. nodosum* and the low tide mark. Additional sites for *F. serratus* in Lobster Bay were added by Dale (1982) and Johnson *et al.* (2012).

Despite being observed in southwestern Nova Scotia for 70 years, there have been few accounts of the local distribution and ecology of *F. serratus* or the factors accounting for its spread. The absence of critical observations in the area is important because of the ability of *F. serratus* to become a dominant, band-forming and canopy species in habitats of *C. crispus* both in Lobster Bay and 150 km to the northeast in Lunenburg Bay, occupying 20% and 40% of the intertidal zone, respectively (Garbary *et al.* 2021). This apparent change in zonation pattern along the Atlantic coast of Nova Scotia (cf. Stephenson and Stephenson 1954a, b, Novaczek and McLachlan 1989) prompted us to undertake a snorkeling survey of low intertidal and shallow subtidal sites in Lobster Bay June 21-26, 2021 (Fig 1, Table 1).

Elsewhere, human introductions of *F. serratus* have led to the establishment of populations in Iceland and the Faroes (Coyer *et al.*

Table 1 Transect and boat survey sites for *Fucus Serratus* in Lobster Bay via snorkeling in June 2021.

Transect from shore	Coordinates	Comments
Chebogue Point	43°44.28' N; 66°6.92' W	T1: sandy with large boulders; eelgrass at 40 m T2: mainly large cobble T3: boulders, line tangled at 30 m
Lower Wedgeport	43°41.63' N; 65°58.74' W	T1: boulder field, *Codium* at 10m and 15m T2: boulder field
Pubnico Point	43°35.67' N; 65°47.91' W	T1: sandy with cobble and boulders T2: sandy with cobble and boulders T3: sandy with cobble and boulders
Snorkel surveys from boat		
Ram's Ledge (Chemin du Rocher)	43°39.15' N; 65°49.30' W	Moderately exposed shore
Abbott's Harbour Island	43°39.68' N; 65°49.71'W	Moderately exposed island
Canoe Island	43°40.47' N; 65°49.66'W	More protected island
Frost Island	43°42.12' N; 65°49.66' W	Well protected nearshore island
Black Ledge	43°42.20' N; 65°51.04' W	A tidal channel reef
Big Gooseberry Island	43°42.08' N; 65° 50.44'W	Moderately protected

2006). The report by Hooker (1811, cited by Guiry and Guiry 2027) shows that the introduction to Iceland preceded that to eastern Canada (Brawley *et al*. 2009). The species has established canopy-forming populations in the low intertidal zone along at least 100 km of shoreline in the southeastern corner of the island (Ingólfsson 2008) with limited populations on the south coast (Munda 2011). Despite the longer residence in Iceland, the ecological and geographic distribution is more limited than in eastern Canada. More recent surveys are required to determine if climate change and seaweed harvesting have impacted the distribution of *F. serratus* in Iceland.

SURVEY OF LOBSTER BAY

At three mainland sites (Chebogue Point, Lower Wedgeport and Pubnico Point), two (Lower Wedgeport) or three (other sites) 50-55 m transects were surveyed perpendicular to the shore beginning at the low water mark (about 0.7 to 1.0 m above chart datum) starting at the lower limit of a distinct zone of *A. nodosum*. Cover of *F. serratus* was recorded at 5-m intervals. The transects were 50 m apart at each site. The same observer (HV) estimated the abundance of *F. serratus* on a three-point scale (20% cover; 20-60% cover, and 60-100% cover). Maximum depth of the transects was about 2 m below chart datum. At all sites, solid substrata (boulders and large cobbles) along the transect lines had an abundance of *F. serratus* and no kelp (Table 2). Another invasive species, the green alga *Codium fragile* (Suringar) Hariot, was observed in one transect at Lower Wedgeport (Table 2). The record for *Codium* is the first for Lobster Bay and represents a range extension of about 150 km from the previously published location at Puddingpan Island (Watanabe *et al.* 2010). The low intertidal and subtidal habitats at our transect sites would have been dominated by *L. digitata* and *S. latissima* in the 1970s. The transect at Chebogue Point from 1977 by Novaczek and McLachlan (1989) had *F. serratus* forming a zone below *A. nodosum* and stopping above chart datum, and with *L. digitata* overlapping with *F. serratus* and exposed at the lowest of the spring tides. These changes in canopy dominants in the subtidal zone of Lobster Bay also were not apparent in the detailed surveys done in the mid-1970s by Haggerty and Hellenbrand (1976) and Pringle and Semple (1980).

Table 2 **Snorkel surveys indicating cover of *Fucus serratus* from 22-26 June 2021 using a transect line perpendicular to the water edge beginning at low water. Multiple transects at each site were separated by 50 m; see Table 1 for habitat details. Abbreviations: CP, Chebogue Point; WP, Lower Wedgeport; PP, Pubnico Point. Key to cover of *Fucus serratus*: 0, absent; +, about 20%; ++, 20–60%; +++, 60-100%; ND, no data.**

Location	Position (m)											
	0	5	10	15	20	25	30	35	40	45	50	55
CP1	+	+	++	++	++	++	++	++	++	+	++	0
CP2	++	++	++	++	++	++	++	++	++	++	++	0
CP3	+++	++	++	++	+++	++	+++	ND	ND	ND	ND	ND
WP1	++	++	++	+++	+++	++	+	+++	+	+++	++	++
WP2	+	+	+	+++	+++	+	++	+	+	+	+	+
PP1	0	+	+++	++	0	0	0	0	0	0	0	+
PP2	+	+++	+++	+++	+++	+++	+++	++	+	+	+	0

Offshore snorkeling surveys in shallow water at seven locations in Lobster Bay (Fig 1, Table 1) gave a similar result to the transects described above. These surveys were carried out when the tide covered the lower portion of the shore and *A. nodosum* was the canopy dominant. This gave way to *A. nodosum* with epiphytic *F. serratus,* and then to dense beds of *F. serratus* largely devoid of kelp. At about 4–5 m depth, the canopy was dominated by *L. digitata.* At Frost Island and Big Gooseberry Island the substratum changed to sand and gravel with a bed of *Zostera marina*.

HISTORICAL CHANGES TO SEAWEED COMMUNITY

It is unclear when the change in dominant canopy species occurred in Lobster Bay. The Dale (1982) and Novaczek and McLachlan (1989) accounts suggest that these changes were underway in the 1970s when they conducted their transects at Chebogue Point and Pubnico Point (as St. Ann Point). Surveys at numerous sites in Lobster Bay in the mid-1970s reporting depth limits of 30 macroalgal species do not record *F. serratus* (Pringle and Semple 1980). These authors illustrate a small band of *'Fucus'* at around chart datum (their Fig 2) that might refer to *F. serratus* or to *F. distichus* spp. *edentatus* (Bachelot Pylaie) H.T. Powell; the latter occurs at this same tidal height and was reported from Lobster Bay (MacFarlane 1952, Edelstein *et al.* 1972, Wilson *et al.* 1979). With respect to kelp, Pringle and Semple (1980) refer to these species at tidal heights of 1 m above chart datum (*L. digitata*) or even

2 m above chart datum (*S. latissima* – as *L. longicruris*) and with high densities down to -7 m and -8 m, respectively. We could not replicate these observations at any site we visited in Lobster Bay. Indeed, kelp dominance was observed beginning only at about 5 m depth.

At some sites, *F. serratus* has transformed one low canopy-forming species, *C. crispus*, into an understorey plant (Garbary *et al.* 2021), greatly reducing or replacing populations of *L. digitata* and *S. latissimma*. The cause of this change is an open question. The potential for overharvesting of *C. crispus* was initially pointed out by MacFarlane (1952) and then alluded to by Haggerty and Hellenbrand (1976). The extensive surveys of *Chondrus* beds in the low intertidal zone and shallow subtidal zone down to about -4 m (12 feet) by Haggerty and Hellenbrand (1976) in Lobster Bay and east of Cape Sable Island did not record *Fucus serratus*. Pringle and Mathieson (1987) and Vandermeulen (2013) pointed out that the commercial harvests had declined extensively by 2003 from peak harvests in 1981. Thus, the extensive bands of *F. serratus* that we observed intertidally in 2020 (Garbary *et al.* 2021), and here in 2021, have developed since the mid 1970s with the first evidence of this being the 1977 transects by Dale (1982) and Novaczek and McLachlan (1989). The shore zone where one would expect to see *C. crispus* as a canopy has been replaced by *F. serratus*. Even where we observed healthy populations of *C. crispus*, it occurred as an understory beneath *F. serratus* and *A. nodosum*, e.g., Surettes Island (Garbary *et al.* 2021). The absence of grazing patellid limpets in the northwestern Atlantic Ocean may also explain the the upward migration of invasive *F. serratus*. In western Europe, *Patella vulgata* is a major grazer on *F. serratus* and its experimental removal facilitated the upward colonization of the fucoid (Boaventura *et al.* 2002). In addition, experimental canopy removal of *A. nodosum* led to the long-term colonization by other fucoids including *F. serratus* (Jenkins *et al*. 2004); the commercial harvest of *A. nodosum* in southwestern Nova Scotia may be having a similar effect.

CLIMATE CHANGE IN SOUTHWESTERN NOVA SCOTIA

One might invoke global warming as the possible cause in kelp decline in Lobster Bay. Considerable warming has occurred since the 1960s in air temperature in Nova Scotia, although Yarmouth has

shown less temperature increase than other parts of the province, i.e., 0.6°C vs up to 1.5°C elsewhere (Garbary and Hill 2021). In addition, seashores on this part of Nova Scotia are prone to morning fog (Novaczek and McLachlan 1989) that can persist to late morning. Kelp declines elsewhere along the Atlantic coast of Nova Scotia have been attributed to increased sea surface temperature (SST) associated with an ocean warming hotspot (Hobday and Pecl 2014, Filbee-Dexter *et al.* 2016). However, the upper summer maxima of around 14°C (increase of 0.9°C in Lobster Bay and southwestern Nova Scotia (Lauzon-Guay *et al.* 2021, Scrosati and Ellrich 2020) would not restrict low intertidal or shallow subtidal kelp populations, where 15°C can maintain healthy kelp sporophytes (e.g. Andersen *et al.* 2013, Simonson *et al.* 2015) and gametophytes (Dieck 1993).

Over the last 70 y, the mean annual air temperature in Nova Scotia has risen about 1°C (Garbary and Hill 2021). This change occurred as a step-change between 1997 and 1998 (Table 3). The mean change was only 0.6°C at Yarmouth; however, the extreme annual low temperature rose almost 2.0°C and the extreme highs 1.2°C. The warmer winter temperature may facilitate colonization of the intertidal zone by *F. serratus* that had started by at least 1977 (i.e., Dale 1982, Novaczek and McLachlan 1989). Regardless, the temperature increase did not occur until at least 20 years later, and this coastline was only recognized as an ocean-warming hotspot well into the current century (Hobday and Pecl 2015, Filbee-Dexter *et al.* 2016).

The change in mean annual air temperature between 1961 and 1997 for Nova Scotia as a whole, and the Yarmouth area in particular, were not significant (Garbary and Hill 2021); indeed, the slope of the linear regressions over this period and going back to the early 1950's was typically not significant, and often negative, e.g., Table 3. Subsequent increases in air temperature of 0.7°C in mean annual air temperature as a step change in 1998 is less than the February increase of 1.4°C (i.e., from -3.4±1.6°C in 1961-1997 to -2.0±1.5°C in the 1998-2021 period; mean±s). At a mean air temperature of -2°C, *F. serratus* would be much less susceptible to freezing; hence, intertidal colonization would be more likely. The greater extent of *F. serratus* in the low intertidal zone would facilitate greater recruitment into the adjacent shallow subtidal areas where kelp communities historically existed. Overall, changing air and water temperatures in Lobster Bay are unlikely to be the direct

Table 3 Changes in metrics for air temperature 1950–2021 at Yarmouth Airport (data from Environment Canada: climate.weather.gc.ca/historical_data/search_historic_data_e.html). Note: differences between the means for early (1950-1997) and late (1998-2021) periods are significant (Student's-*t* test, P < 0.01). Linear regressions for each time-period metric generate slope (+ or –), R2, and P). Linear regressions calculated using online GraphPad calculator (www.graphpad.com/quickcalcs/linear2/); significant P-values indicated in bold.

Temperature metric	1950–1997 (°C)	1998–2021 (°C)	Temperature elevation (°C)
Annual mean	6.9±0.6 (–, 0.036, 0.196)	7.5±0.8 (+, 0.058, 0.266)	0.6
Extreme annual minimum	–17.2±2.4 (–, 0.062, 0.86)	–15.4±1.9 (+, 0.140, 0.072)	1.8
Extreme annual maximum	26.5±1.7 (+, 0.054, 0.111)	27.5±1.6 (+, 0.068, 0.217)	1.0
Mean daily minimum of coldest month	–7.8±1.5 (–, 0.139, **0.009**)	-6.6±2.0 (+, 0.067, 0.223)	1.2
Mean daily maximum of warmest month	21.0±0.9 (+, 0.111, **0.021**)	22.2±0.9 (+, 0.501, **0.0001**)	1.2

cause of kelp decline; however, such increases may have shifted the competitive interactions between kelp and *F. serratus* towards the latter species.

WHY DID THE IRISH MOSS HARVEST DECLINE?

We propose the following scenario to explain the change in community structure since the 1950s as described in various publications (e.g., MacFarlane 1952, Edelstein *et al.* 1972, Hagerty and Hellebrand 1976, Sharp and Semple 1980). In the early 1950s *F. serratus* was restricted to offshore sites in the Tusket Islands. Extensive harvesting of *C. crispus* opened both low intertidal and shallow subtidal zones in Lobster Bay, creating a favourable habitat for *F. serratus*. Overharvesting associated with rakes with narrowly spaced tines (3.5-5 mm spaced tines vs 7-12.5 mm spaced tines) removed both mature and immature fronds, and may have damaged the holdfasts to limit bed recovery (Pringle and Semple 1978, review by Vandermeulen 2013). Beginning in the late 1990s this may have been exacerbated by climate change in which

hotter summer days resulted in bleaching events as observed on the South Shore of Nova Scotia (Vandermeulen unpublished). MacFarlane (1952) described a harvest zone of *C. crispus* of about 30 ft (10 m) that was suitable for raking. Once *F. serratus* became established at a site, it became a canopy species at many sites, above the beds of *C. crispus* and hence limited the area available for raking.

POTENTIAL RISK TO ROCKWEED POPULATIONS

The reduction of landings of *C. crispus* in the 1970s based on overharvesting (Vandermeulen 2013) may have been associated with establishment of *F. serratus* (i.e., Dale 1982, Novaczek and McLachlan 1989). Subsequent changes in landings of *C. crispus* were likely driven by global changes in the market for carrageenan (Vandermeulen 2013). Our intertidal surveys in 2020 (Garbary *et al.* 2021), and subtidal surveys described here for 2021, show that *F. serratus* has now largely replaced the low intertidal and shallow subtidal (to about 5 m depth) populations of kelp, with *C. crispus* as the primary understory. The Chebogue Point transect by Novaczek and McLachlan (1989) indicated a clear demarcation of *F. serratus* and *A. nodosum*. The transect at Chebogue Point (Garbary *et al.* 2021) and shore surveys at Pubnico Point and Lower Wedgeport show that this is no longer the case, and there has been considerable upward movement of *F. serratus* into shore elevations once dominated by *A. nodosum* and *F. vesiculosus* both attached to boulders and as an epiphyte on *A. nodosum*.

The continued upward movement of *F. serratus* may be facilitated by climate warming with an increase of annual air temperature at Yarmouth post-1998 of about 0.6°C relative to 1950-1997 (Table 3). The warming trend is generally more pronounced for winter where temperature metrics for the coldest months (December through February), having increased daily minimum temperatures of 1.8°C, and with mean air temperature currently about -2 to -3°C. The stability of the temperature regime in the early period is shown by the low values for R^2 (max 0.139). In addition, four out of five metrics for the post-1998 period were not significant. These data show that the temperature increase occurred well after the decline of the *Chondrus* harvest and the likely increase in the populations of *F. serratus*. Thus, while possibly facilitated by climate change, we propose that harvesting of *C. crispus* contributed to the spread of *F. serratus* and to the decline

of this harvest industry in southwestern Nova Scotia (Vandermeulen 2013). In addition to the decline of kelp abundance in this area, our observations of the intertidal abundance of *F. serratus* in Lobster Bay (Garbary *et al*. 2021) raises the possibility that raking of *A. nodosum* near the lower margin of its zone may be facilitating the further incursion of *F. serratus* and reducing the area of intertidal zone dominated by *A. nodosum*. We consider this a potential threat to the *Ascophyllum* harvest industry. This points to the need for more government oversight of the harvest industry, and for suitable control sites that are unharvested and suitable for research by investigators unaffiliated with industry (e.g., Vandermeulen 2013, Lotze *et al*. 2019, Fass 2021, Lauzon-Guay *et al*. 2021).

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