

MORPHOLOGICAL VARIATION IN *ACROSIPHONIA*
ARCTA (CODIOLALES, CHLOROPHYTA) FROM
ENVIRONMENTALLY DIFFERENT HABITATS
IN NOVA SCOTIA, CANADA

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ABSTRACT. We characterized the morphological variation and algal species associations of the filamentous green alga, *Acrosiphonia arcta* (distinguishing it from its closely related sister genus *Spongomorpha*), in two contrasting environments in Nova Scotia, Canada. The habitats differed in seawater salinity and temperature (and fluctuations thereof), substratum, vertical position on the shore, wave exposure, turbidity, and diversity of macroalgae and macrofauna. *Acrosiphonia arcta* thalli exhibited distinct morphologies in the different environments. Thalli from the open-ocean Whitehead site (Atlantic coast) exhibited the typical *A. arcta* morphology of profuse, short, curved branches and rhizoids binding the filaments together to form hemispherical to spherical tufts. Thalli from the sheltered Pomquet Harbour Estuary (Gulf of St. Lawrence coast) consisted of matted clumps with extensive rhizoidal growth at the base but little branching otherwise. *Acrosiphonia arcta* was primarily associated with thick leathery and crustose (coralline) algae at Whitehead. In the Pomquet Harbour Estuary, a less stable habitat than Whitehead, sheet and filamentous algae were in greater abundance with *A. arcta* than at Whitehead. Damaged apical cells from thalli of both Pomquet and Whitehead *A. arcta* were able to regenerate new filamentous tips or to give rise to rhizoids, phenomena not previously documented for *Acrosiphonia* in North America. Morphological variation of *A. arcta* in different habitats points to its ability to respond to and persist in a wide range of abiotic (and possibly biotic) conditions, and helps to explain its seasonal dominance on the east and west coasts of North America.

Key Words: *Acrosiphonia arcta*, *Acrosiphonia spinescens*, *Acrosiphonia sonderi*, estuarine, morphological variability, Northwest Atlantic, open coastal, *Spongomorpha*

Acrosiphonia is a filamentous green alga composed of branched uniseriate filaments that tend to be bound together by hooked branchlets or by rhizoids to form ropey masses or spherical tufts. Its

thalli are seasonally abundant (spring and summer) on rocky substrata in the low to mid-intertidal zone of the exposed open coast and of relatively sheltered inlets in the northeastern Pacific (Hudson 1974; Sussmann and DeWreede 2001). In the northwestern and northeastern Atlantic, *Acrosiphonia* thalli are present in the low intertidal and upper subtidal zones of the exposed open coast and in estuarine habitats (Kornmann 1970b; Mathieson et al. 2010; Sears 1998; Taylor 1962; Villalard-Bohnsack 2003).

In southwestern British Columbia, field and molecular work has demonstrated that this seasonal alga (a gametophyte) alternates with a unicell (the sporophyte) that colonizes and overwinters in the foliose red alga *Mazzaella splendens* (Setch. & Gardner) Fredericq and in the crustose phase of *Mastocarpus papillatus* (C. Agardh) Kütz. (Sussmann and DeWreede 2001; Sussmann et al. 1999). We have little understanding of the life history of *Acrosiphonia* on the east coast of North America; alternating phases have not been elucidated in nature.

Acrosiphonia has long been difficult to separate from *Spongomorpha* (Collins 1909; Jónsson 1991; Kornmann 1965, 1970b; Scagel 1966; Wille 1900), its sister genus in phylogenetic reconstructions (Sussmann et al. 1999). The two genera were originally separated on the basis of cell length-to-width ratios (Agardh 1846), but this and other vegetative/morphological characters (e.g., cell diameters, branching patterns, and shapes of tip cells) have often been unreliable. *Spongomorpha* is absent on the northwestern coast of North America, but present on the northeastern coast (Mathieson et al. 2010; Sears 1998; Taylor 1962; Villalard-Bohnsack 2003), and has been reported from New Jersey, U.S.A., north to Baffin Island, Canada (Hillson 1977). The first objective of this study was to differentiate *Acrosiphonia* thalli in the northwestern Atlantic from *Spongomorpha* thalli.

There is also a lack of agreement on species delimitation of *Acrosiphonia*, primarily due to variability in characteristics such as cell diameters, cell length-to-width ratios, presence or absence of hooked branchlets, and branching patterns of thalli (Hudson 1974; Kornmann 1962, 1965, 1970b; Scagel 1966; Setchell and Gardner 1920; Taylor 1962). Hudson (1974) and Sussmann and DeWreede (2001) recognized two *Acrosiphonia* species, *A. arcta* (Dillwyn) Gain and *A. mertensii* Yendo, from the northeastern Pacific. *Acrosiphonia mertensii* is present only in the northeastern Pacific, whereas *A. arcta* has been documented in both the northern and southern

hemispheres, including the northwestern and northeastern Atlantic (Hudson 1974; Kjellman 1883; Kornmann 1970b; Mathieson et al. 2010; Sears 1998; Taylor 1962; van Oppen et al. 1994; van Patten 2006; Villalard-Bohnsack 2003).

Acrosiphonia arcta has been viewed both as a single, quite variable species (Burrows 1991; Hudson 1974; Kornmann 1962; Sussmann and DeWreede 2001) and conversely as a complex of closely related species (Scagel 1966; Setchell and Gardner 1920). Burrows (1991), Hudson (1974), and Kornmann (1962) united *A. spinescens* (Kütz.) Kjellm. and *A. arcta* in *A. arcta* on the basis of morphological and microscopic characters. At least for the northeastern Pacific, Hudson (1974) found the two taxa to intergrade completely for all the characteristics she observed, and culture studies demonstrated the plasticity of the alga in response to varying physical factors. Sussmann et al. (1999) were unable to separate northeastern Pacific *A. arcta* and *A. spinescens* based on rDNA ITS sequences. On the other hand, A. C. Mathieson and C. Dawes (Univ. New Hampshire, Durham, NH; pers. comm.) consider *A. arcta* and *A. spinescens* to be distinct species based on unpublished morphological and rDNA ITS sequence data from thalli from Maine, U.S.A.

According to Sears (1998), two *Acrosiphonia* species comprise the green filamentous alga in the northwestern Atlantic. In addition to *A. arcta*, Sears (1998) recognized *A. sonderi* (Kütz.) Kornmann, similar in appearance to *A. arcta*, and described by Kornmann (1962) in Helgoland, Germany. Villalard-Bohnsack (2003), on the other hand, maintained that only one well-defined entity, *A. arcta*, is represented on the east coast of North America. South and Hooper (1980) stated that they were not able to distinguish between *A. sonderi* and *A. arcta* thalli in Newfoundland, Canada. Other *Acrosiphonia* species, not reported for North America, have been identified in Japan, Germany, France, and Scandinavia (Kornmann 1962, 1970a; Miyaji 1984, 1996; Miyaji and Kurogi 1976).

Further molecular studies, involving selection of a more variable DNA sequence than ITS sequences, and applied to both Pacific and Atlantic specimens, are needed to resolve the infrageneric relationships within *Acrosiphonia*. Regardless of taxonomic uncertainties, in this study we recognize a single species, *A. arcta* (based on intergradations of all thalli for morphological and microscopic characters), occurring in considerably different environments of the northwestern Atlantic. *Acrosiphonia arcta* has several traits that are

indicative of good colonizers of unstable environments. The ability of *A. arcta* to exhibit plasticity in response to varying environmental factors, as well as its high productivity (Sussmann 2000; Sussmann and DeWreede 2005, 2007), suggest an array of strategies for the alga's survival in a wide range of environments. For this study, we hypothesized that the filamentous phase of *A. arcta* would display gross differences in morphology and algal species associations in environmentally different habitats of the northwestern Atlantic.

MATERIALS AND METHODS

We collected hemispherical to spherical, tufted green macroalgae from the low intertidal and subtidal zones in June 2007 at the sheltered estuarine system of Pomquet Harbour (45°39'N, 61°50'W) and the exposed, open coastal sites of Whitehead (45°13'N, 61°11'W) and Tor Bay Provincial Park (45°11'N, 61°21'W) in Nova Scotia, Canada. Delimitation between *Acrosiphonia* and *Spongomorpha* thalli was based on a number of dependable morphological and cytological microscopic characteristics such as the number of nuclei per cell, cell diameter, and thallus length. To determine whether cells were uninucleate or multinucleate, live specimens from the above sites were immersed in DAPI stain [0.5 mg DAPI in 100 ml distilled water; working solution of 1:9 parts stock to buffer and pH 4.1, as described by Garbary and Clarke (2001)], microwaved for 5–10 sec and viewed with an epifluorescence microscope. *Acrosiphonia* and *Spongomorpha* specimens were deposited at the herbarium of St. Francis Xavier University (STFX), Nova Scotia.

Acrosiphonia was only identified at Pomquet Harbour (between –0.1 m and +0.3 m relative to chart datum) and at Whitehead (between 0 m and +0.7 m relative to chart datum). Pomquet Harbour is a shallow lagoon system with a mean depth of about three meters. Our study site was located on a channel where the water was well mixed from tidal currents (average tidal amplitude of 0.5 m) and remained free of ice during the winter. Mean water temperature varies annually from 0 to 24°C, whereas mean salinity varies from 18‰ to about 27‰ (Bird et al. 1976; Kim et al. 2004). The lower salinity value is due to dilution by spring rain and runoff from melting snow. In the exposed Whitehead region, surface seawater temperature varies between monthly means of 0.3 and

16.4°C, whereas salinity varies between monthly means of 30.5‰ and 31.0‰ (Fisheries and Oceans Canada 2009). Figure 1 compares monthly water temperature and salinity at Pomquet Harbour and the Whitehead region.

Water temperature and salinity were recorded at the Pomquet Harbour site on 16 June 2007 and at the Whitehead site on 18 June 2007. Water temperature was measured with a mercury thermometer and salinity with a refractometer. Percentage cover of *Acrosiphonia arcta* and the associated macroalgae and macrofauna was also documented at the two sites in mid-June 2007. Twenty-meter transect lines were placed parallel to the shore in the *A. arcta* zone, and random number tables generated 25 locations for placement of 20 cm × 20 cm quadrats along the transects. Quadrats were centered on the transect line, and monofilament divided each quadrat into 100 squares.

At each site, 15 *Acrosiphonia arcta* thalli were haphazardly collected to determine reproductive status. Forty *Chondrus crispus* Stackh. blades (the prevalent foliose red alga) were collected at Whitehead and examined for the presence of '*Chlorochytrium inclusum*,' the sporophyte of *Acrosiphonia* known to colonize bladed red algae (Chihara 1969; Freeman 1899; Hudson 1974; Kjellman 1883; Kornmann 1964; Miyaji and Kurogi 1976; Printz 1926; Setchell and Gardner 1920; Sussmann and DeWreede 2002). At Pomquet Harbour, the tubular brown alga, *Scytosiphon lomentaria* (Lyngb.) Link, was collected, the search being prompted by a report of '*Chlorochytrium inclusum*' present in *Scytosiphon* collected from Pomquet Harbour in June 1974 (Bird et al. 1976). Thirty segments, 5–10 cm long, from separate thalli were cut open and flattened on a slide to check for possible colonization by '*Chlorochytrium*.'

RESULTS

Table 1 and Figure 2 illustrate and compare morphological and cytological microscopic characters of *Acrosiphonia* and *Spongomorpha*. Multinucleate thalli (Figure 2E, collected both at Pomquet and at Whitehead) belonged to the genus *Acrosiphonia*, whereas uninucleate thalli (Figure 2F, all collected at Tor Bay Provincial Park) were a species of *Spongomorpha*. Although we deemed the number of nuclei per cell the best diagnostic tool (besides molecular analysis) for distinguishing between the two genera, other characters that we used included: (1) a smaller cell diameter and

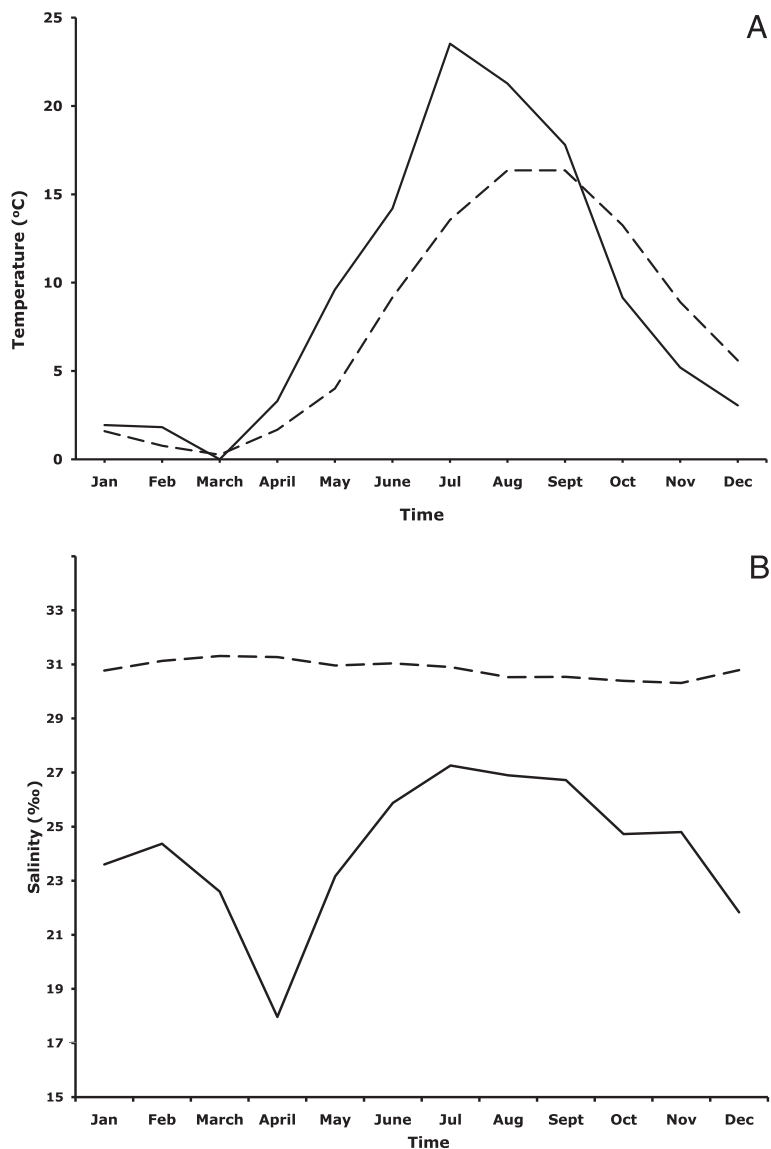


Figure 1. Water temperature and salinity in Nova Scotia in the Whitehead region during 2008 (after Fisheries and Oceans Canada 2009) and at Pomquet Harbour from August 1996 to August 1997 (after Kim et al. 2004). A. Mean monthly water temperature. B. Mean monthly salinity. Dotted lines = Whitehead; solid lines = Pomquet.

Table 1. Morphological and cytological microscopic characters for *Acrosiphonia* and *Spongomorpha* collected in 2007 in Nova Scotia at Pomquet Harbour, Whitehead, and Tor Bay Provincial Park.

Character	<i>Acrosiphonia</i>		<i>Spongomorpha</i> (Tor Bay)
	Sheltered: Pomquet	Exposed: Whitehead	
# Nuclei/cell	Multinucleate	Multinucleate	Uninucleate
# Pyrenoids/cell	35–50	35–50	5–6
Cell diameter	40–100 μm	60–120 μm	20–30 μm
Cell length: width	2–6 \times long as wide	1–4 \times long as wide	1–2 \times as long as wide
Hooked branchlets	Absent	Absent	Absent
Filament and rhizoid branching	Little branching; extensive rhizoids at base; new growth at the end of attenuated tips and broken tips	Much branching; short curved (pre-hooked or rhizoidal?) branches in upper portion; new growth at the end of attenuated tips and broken tips	Much branching; few rhizoidal branches
Fertile cells	Reproductive thalli not found	Fertile cells present, but not found in a series	Fertile cells present in series
Thallus length	5–10 cm	1–5 cm	1–1.5 cm
Thallus habit	Disorganized matted clumps; thallus loosely held together	Forms organized hemispherical to spherical tufts	Forms organized hemispherical to spherical tufts
Texture	Coarse	Coarse	Soft

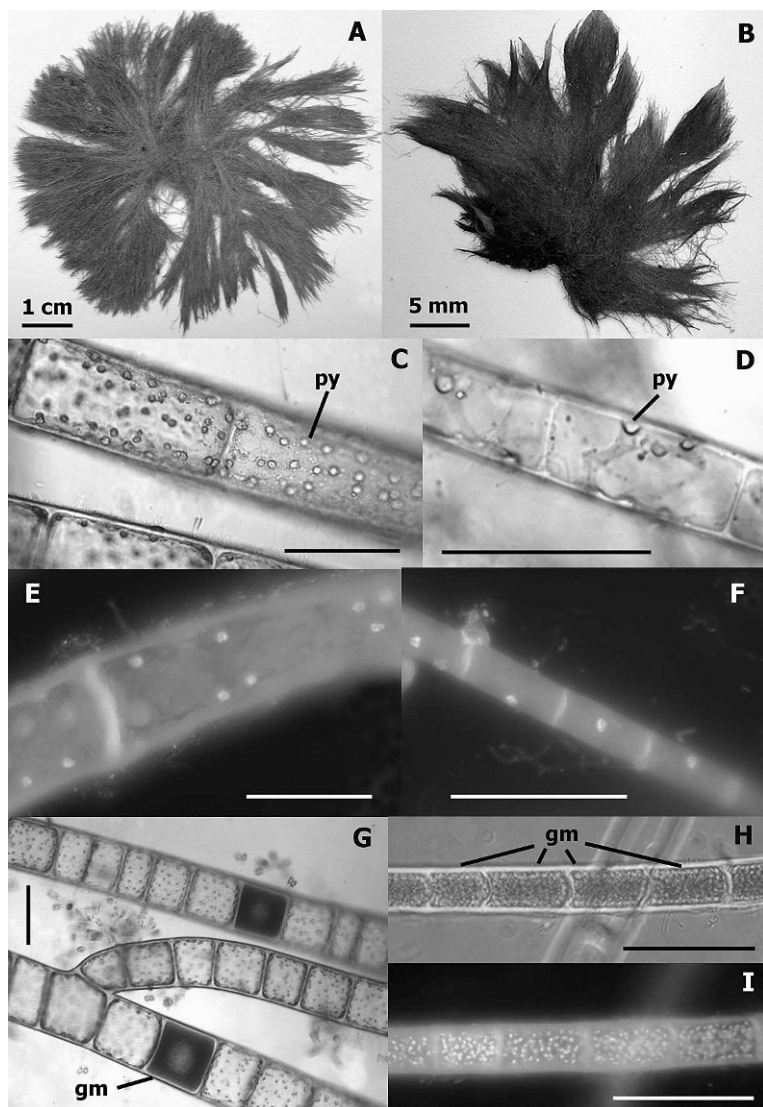


Figure 2. Morphological and cytological characters for *Acrosiphonia* and *Spongomorpha* in Nova Scotia. A. *Acrosiphonia* habit, Whitehead. B. *Spongomorpha* habit, Tor Bay Provincial Park. C. Many pyrenoids per cell, *Acrosiphonia*. D. Few pyrenoids per cell, *Spongomorpha*. E. Multinucleate *Acrosiphonia*. F. Uninucleate *Spongomorpha*. G. Single fertile cells, *Acrosiphonia*, Whitehead. H, I. Fertile cells in series, *Spongomorpha*. Scale bar = 100 μm. gm = gametangium; py = pyrenoid.

cell length-to-width ratio for *Spongomorpha* thalli; (2) smaller and softer thalli for *Spongomorpha* specimens; and (3) fewer pyrenoids per cell in *Spongomorpha* (Figure 2C, 2D). Thallus habit (Figure 2A, 2B), branching pattern, and number of fertile cells in a branch (Figure 2G–I) were not sufficient for genus identification.

Acrosiphonia thalli obtained from the two different shores exhibited wide variability in characters. The thalli were all identified as *A. arcta* based on morphological and microscopic characters. We found that the filamentous thalli intergraded for all criteria for *A. arcta* reported from the northwestern Atlantic (Sears 1998; Villalard-Bohnsack 2003) and from the northeastern Pacific (Hudson 1974; Sussmann and DeWreede 2001), as well as from Roscoff, France (Jónsson 1962), and Helgoland, Germany (Kornmann 1962): cells (1)2–4(6) times as long as wide and (40)60–100(120) μm in diameter; thalli 3–10 cm tall. Thalli from different sites differed primarily in habit and branching (Table 1; Figure 3A–D). *Acrosiphonia arcta* thalli from Pomquet Harbour were all extremely matted but loosely held together (Figure 3A), whereas those from Whitehead were tightly held together, forming distinctive hemispherical to spherical tufts typical of *A. arcta* (Figure 3B). The Whitehead thalli exhibited much more branching, in particular, with short, curved, possibly pre-hooked branchlets (Figure 3C, 3D) that were absent in the Pomquet Harbour thalli. (Hooked branchlets are distinctive for the genus, but tend to appear in older thalli.) We observed attenuated filaments in thalli from both shores (Figure 3E, 3F). New growth could be seen at the end of such attenuated tips (Figure 3F) and at the end of damaged tips (Figure 3G). Pomquet Harbour thalli produced more rhizoids at their base than did thalli from Whitehead; rhizoids could help anchor the thalli to the unstable mud substratum present at Pomquet Harbour.

Fourteen out of 15 *Acrosiphonia arcta* thalli examined from Whitehead were reproductive. In *A. arcta*, vegetative cells that were located either in side branches or in the main filament, differentiated into gametangia that changed from dark green to brown as they matured. The brown fertile cells of the Whitehead thalli were present singly (not in a series, Figure 2G). Five of the Whitehead thalli displayed empty gametangia with visible exit pores for gamete release (Figure 3H). No thalli from Pomquet Harbour were reproductive; neither brown gametangia nor empty gametangia were visible.

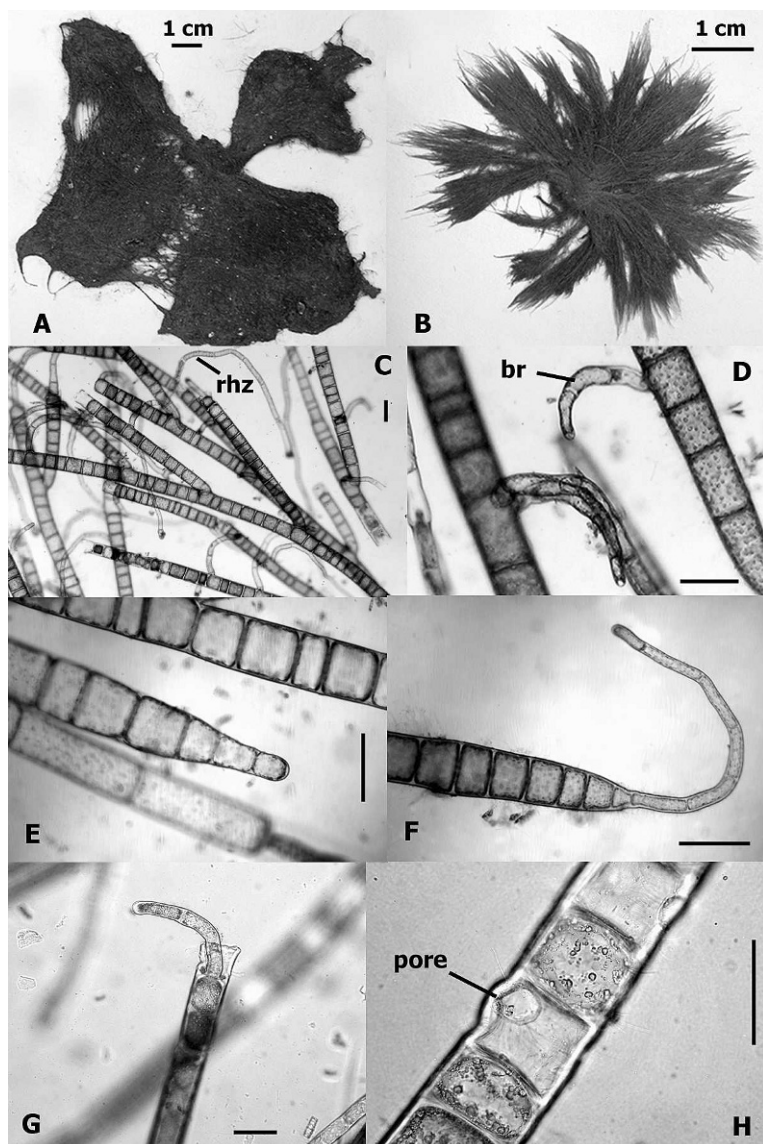


Figure 3. *Acrosiphonia arcta* from Pomquet Harbour and Whitehead, Nova Scotia. A. Matted habit, Pomquet Harbour. B. Hemispherical/spherical tufted habit, Whitehead. C, D. Short curved (pre-hooked?) branchlets (br) and rhizoid growth (rhz), Whitehead thalli. E. Attenuated filament. F. Attenuated filament with new growth. G. Regeneration of damaged filament tip. H. Empty gametangium with pore for gamete release. Scale bar = 100 μ m.

In June 2007, seawater temperature was almost 8°C higher at the sheltered Pomquet Harbour site (17.0°C) than at the exposed Whitehead site (9.5°C), whereas salinity at Pomquet (28‰) was lower by 6‰. Due to the soft, muddy substratum at Pomquet Harbour, turbidity was higher there than at the rocky shore of Whitehead. The Pomquet Harbour site also had a greater diversity of macroalgae and macrofauna, and relative abundances of species differed from those at Whitehead (Table 2). *Ulva* and *Acrosiphonia arcta* comprised the dominant green macroalgal cover (22%), *Chordaria* (3%) was the dominant brown macroalga, *Ceramium* (3%) was the dominant red macroalga, and mussels dominated (31% cover) the fauna in the shallow subtidal zone (possibly providing some stability to the mud substratum). Unlike the Whitehead site, diatoms occupied 100% cover and *Spartina alterniflora* Loisel. (cordgrass; 2%) was present. At Whitehead, the low intertidal zone occupied by *A. arcta* was dominated by coralline crusts (41%) and *Scytosiphon* (11%). Mussels were absent, and barnacles (1%) and littorinid snails (< 1%) were the only benthic macroinvertebrates present.

The 40 *Chondrus* thalli (35 vegetative, 5 tetrasporophytic) collected from the Whitehead site did not reveal any colonization by ‘*Chlorochytrium*.’ The green filamentous endophyte, *Acrochaete ramosa* (N.L. Gardner) O’Kelly, was present. We found no ‘*Chlorochytrium*’ cells in the *Scytosiphon* specimens from Pomquet Harbour, but a number of unidentified filamentous endophytes were present.

DISCUSSION

Delimitation of *Acrosiphonia* and *Spongomorpha*. It is virtually impossible to distinguish between *Acrosiphonia* and *Spongomorpha* in the field (Figure 2A, 2B). Vegetative/morphological characteristics, in isolation, have often been unreliable for separation of the two genera, probably in part due to the extreme plasticity of characters in response to temperature and light intensity (Hudson 1974; Kornmann 1965, 1970b). We found a number of northwestern Atlantic herbarium specimens at St. Francis Xavier University, Nova Scotia, that were misidentified (as *Spongomorpha* rather than *Acrosiphonia*) due to the use of morphological characteristics alone. We have found the number of nuclei per cell, first proposed by

Table 2. Percent cover of macroalgae and macrofauna in June 2007 at sites in Pomquet Harbour and Whitehead, Nova Scotia.

Taxon	Percent Cover	
	Pomquet Harbour	Whitehead
Diatoms	100.0	0.0
Chlorophyta		
<i>Acrosiphonia arcta</i>	9.7	6.0
<i>Ulva lactuca</i> L.	15.0	0.0
Phaeophyceae		
<i>Chordaria flagelliformis</i> (O.F. Müll.)		
C. Agardh	3.3	3.6
<i>Fucus vesiculosus</i> L.	0.4	0.0
<i>Scytosiphon lomentaria</i>	0.6	11.0
<i>Chorda filum</i> Stackh.	2.4	0.0
Rhodophyta		
<i>Chondrus crispus</i>	0.2	3.7
<i>Gracilaria tikvahiae</i> McLachlan	1.1	0.0
<i>Polysiphonia</i> spp.	2.2	0.0
<i>Ceramium</i> spp.	2.9	0.0
<i>Corallina officinalis</i> var. <i>chilensis</i> (Decne. in Harv.) Kütz.	0.0	6.8
Coralline crusts	0.0	41.0
Vascular Plants		
<i>Spartina alterniflora</i>	2.0	0.0
Macrofauna		
<i>Mytilus edulis</i> L.	31.2	0.0
<i>Littorina</i> spp.	0.2	0.7
<i>Asterias</i> spp.	0.3	0.0
Shrimp	0.3	0.0
<i>Carcinus maenas</i> L.	0.4	0.0
Oysters	0.4	0.0
<i>Semibalanus balanoides</i> L.	0.0	1.4
Scallops	< 0.1	0.0

Wille (1900), to be the best non-molecular diagnostic tool for the delimitation between *Acrosiphonia* and *Spongomorpha*.

None of the filamentous thalli that we collected exhibited the distinctive hooked branchlets of *Acrosiphonia* and *Spongomorpha*, although the thalli from Whitehead did display short, curved, possibly pre-hooked branchlets (Figure 3D). The absence of hooked branchlets in our collections was likely because all the

thalli collected at Tor Bay Provincial Park and at Whitehead were young specimens and/or because environmental conditions did not support the growth of hooks. Hooked branchlets are commonly found in older thalli such as those collected at Pomquet Harbour, but none of these specimens revealed hooks either. Hudson (1974) and Sussmann (2000) concluded that the presence or absence of hooks is a character that should not be given a great deal of weight in distinguishing among thalli with otherwise similar appearance. Hudson (1974) suggested that even slightly different growth conditions may determine whether or not genetically identical thalli produce hooks, and that the formation of hooks is simply sporadic.

Species delimitation in *Acrosiphonia*. Although multinucleate *Acrosiphonia* can be separated from uninucleate *Spongomorpha*, there is still a lack of agreement on species boundaries within *Acrosiphonia*. The *Acrosiphonia* thalli collected at Whitehead and at Pomquet Harbour, however, intergraded for all species criteria of *A. arcta* reported for the northwestern Atlantic (Sears 1998; Villalard-Bohnsack 2003) and the northeastern Pacific (Hudson 1974; Sussmann and DeWreede 2001), as well as at Roscoff (Jónsson 1962) and Helgoland (Kornmann 1962). Northeastern Pacific *A. arcta* thalli commonly exhibit hooked branchlets (see previous comment regarding this character), and reproductive specimens are characterized by mature gametangia in series, unlike the single fertile cells we found in thalli from Nova Scotia. The *A. arcta* thalli from Pomquet Harbour were much larger/older than those from Whitehead, and were most likely no longer reproductive since neither mature nor empty gametangia were visible. The lack of fertile and empty gametangia was commonly seen in older *A. arcta* thalli from British Columbia (Sussmann 2000). The discrepancy in the number of fertile cells in a branch for *A. arcta* specimens from the northeastern Pacific and those from the northwestern Atlantic (Whitehead thalli) brings into question the reliability of this character for *Acrosiphonia* species identification. Hudson (1974) alleged that it is a difficult criterion to use, because when *A. arcta* thalli first become fertile there are only scattered gametangia in a branch, but in culture, within one week, these subsequently lengthen to include nearly the entire thallus.

We noted the ability of damaged apical cells to regenerate new filamentous tips or rhizoids (Figure 3F, 3G) in our Nova Scotian thalli. This behavior explains the abundance of attenuated filament

tips present in specimens we collected at Whitehead and Pomquet Harbour. Although not previously documented for *Acrosiphonia* in North America, Kornmann (1962) also described this particular regenerative behavior in *A. sonderi* thalli from Helgoland, Germany. Hudson (1974) noted that damaged *A. arcta* thalli were capable of repair in culture by forming a new branch below the tip remnant, but not directly from damaged tip cells as we (and Kornmann) had observed.

***Acrosiphonia* species associations.** Bird et al. (1974) confirmed that warm estuaries such as Pomquet Harbour support a different algal composition from open coasts, and that such estuaries may harbor disjunct populations of plant and animal species related to those of more southern coasts in North America. The effects of winter ice scour, fluctuating temperatures and salinities, and unstable, muddy substratum in Pomquet Harbour may also favor more opportunistic and seasonal algal species (e.g., sheet and filamentous forms) versus late successional and perennial species (e.g., thick leathery and crustose forms). In June 2007, *Acrosiphonia arcta*, *Ulva*, *Ceramium*, *Chordaria*, and *Chorda* (all sheet and filamentous forms) were more abundant than *Gracilaria*, *Chondrus*, and *Fucus* (late successional species) at the Pomquet Harbour site, supporting this hypothesis. At Whitehead, in contrast, coralline crusts were the prevalent macroalgae, and *Chondrus* was much more abundant than at Pomquet Harbour.

Distinct *Acrosiphonia* morphologies in different environments. The *Acrosiphonia arcta* thalli displayed significantly different morphologies at the environmentally different sites, as we predicted. Hudson (1974) demonstrated that cultured *Acrosiphonia* thalli exposed to different temperatures, irradiance levels, and day lengths showed variable vegetative characteristics. It is unclear if the morphological variation we observed was due to phenotypic plasticity or to genetic differentiation. Nonetheless, we suggest that an entire suite of physical factors (temperature, salinity, irradiance, nutrients, turbidity, water flow, and substratum) of sufficiently different habitats influences this gross variation in thallus habit.

The Pomquet Harbour thalli (loosely matted-together clumps, atypical of *Acrosiphonia arcta*, young or old) resembled *Acrosiphonia* thalli from British Columbia that had grown beneath diatom mats in experimental outdoor tanks (Sussmann and DeWreede

2005). The thalli that grew in the experimental tanks were also matted together, showed little branching, and lacked the hooked branchlets that were common in thalli from the field, indicating phenotypic plasticity. Likewise, Hudson (1974) observed that *Acrosiphonia* thalli in culture very infrequently produced hooked branchlets and were often only sparsely branched. All of these environments—the outdoor experimental tanks, the cultures, and the estuary—represent habitats with low water flow relative to the open ocean. We suggest that the presence of intense branching and an organized structure is, at least in part, an indicator of relatively high-flow environments. This hypothesis is supported by Hudson's (1974) observation that *Acrosiphonia* thalli that had not previously formed hooks in culture did so when placed on a rotating shaker table.

Hudson (1974) and Kornmann (1965) also showed that increased irradiance promoted branching in thalli grown in culture. In both the experimental tanks and the Pomquet Harbour Estuary, dense diatom growth (and the high turbidity at the Pomquet Harbour site) limited the availability of light for *Acrosiphonia*. No culture studies to date have investigated the effects of temperature and salinity on branching. However, we speculate that the higher temperatures and lower salinities of Pomquet Harbour may play a role in thallus branching, whether this is due to phenotypic plasticity (contemporary response to environmental factors) or evolutionary selection by the environment.

***Acrosiphonia* life history and reproductive strategy.** Although data are limited, life history and algal reproductive strategies appear to be linked to habitat (DeWreede and Klinger 1988; Poore and Fagerström 2001; Santelices 1990). The sexual life history of *Acrosiphonia arcta* was definitively established in southwestern British Columbia: unicellular sporophytes, which alternate with the filamentous gametophytes of *A. arcta* and *A. mertensii*, colonize red algae (both blades and non-coralline crusts) and persist within their hosts over the winter. Our attempts to locate endophytic sporophytes at Whitehead and Pomquet were not successful. Since, in British Columbia, endophytes were only seen 1–3 months after the establishment of *Acrosiphonia* thalli (Sussmann and DeWreede 2001), it is possible that June was too early to detect endophyte colonization of the prevalent foliose red alga (*Chondrus crispus*) at Whitehead. Fleshy algal crusts, other potential hosts, were absent

from the region. The Pomquet Harbour site lacked abundant, attached foliose red algae and crusts. We did not detect unicells in the brown alga, *Scytosiphon*, from Pomquet Harbour. We believe that the opportunistic species, *S. lomentaria*, is not an optimal host for endophytes because its seasonality mimics that of the gametophytic *Acrosiphonia* (Sussmann and DeWreede 2005). We also question whether the endophyte identified in *Scytosiphon* from Pomquet Harbour (Bird et al. 1976) was in fact the unicellular sporophyte of *Acrosiphonia*. It is not clear if the sporophyte phase of Pomquet Harbour thalli may colonize red algae such as *Chondrus* and *Gracilaria* that have become detached and are abundant at depths of 2–3 m at our site at Pomquet Harbour (Bird et al. 1976; Schneider and Mann 1991). Sussmann and DeWreede (2005) demonstrated that '*Chlorochytrium*' was able to survive and release zoospores within detached algal blades of *Mazzaella splendens*.

There are other hypotheses to explain the life history of *Acrosiphonia* at Pomfret Harbour. Although never definitively illustrated, *Acrosiphonia*'s sporophyte phase may survive, free-living, in nature (Hudson 1974 and references therein; Sussmann and DeWreede 2005). Given the lack of optimal hosts in Pomquet Harbour, such a strategy is conceivable. Another possibility is that the unstable Pomquet Harbour environment, with fluctuating physical factors and unstable muddy bottom, may favor vegetative propagation from overwintering basal remnants over sexual reproduction. Evidence in support of such a strategy is provided by a study in which the positions of a large number (> 250) of *Acrosiphonia* thalli were mapped over two growing seasons (Sussmann and DeWreede 2007). These ideas require investigation, but they are useful in considering the variation in life history strategy that is possible for *Acrosiphonia* populations in different habitats.

ACKNOWLEDGMENTS. We thank David J. Garbary for his assistance with DAPI staining and use of the fluorescence microscope and his advice on where to find localities with filamentous green algae. We also thank Arthur C. Mathieson and Clinton Dawes for providing editorial comments on the manuscript. This work was funded by grants from the Natural Sciences and Engineering Research Council (NSERC Discovery Grant), the Canada Research Chairs program (CRC), and the Canada Foundation for Innovation (CFI) to R.A.S., and by professional

development funds from Kwantlen Polytechnic University to A.V.S.

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