

Multiple assessments of introduced seaweeds in the Northwest Atlantic

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Historical and recent floristic studies, rapid assessment surveys, and molecular investigations were used to evaluate the occurrence of 20 seaweeds introduced to the Northwest Atlantic, including 2 green, 4 brown, and 14 red algae. Based on floristic comparisons of Mount Desert Island and Casco Bay, ME, from the late 1800s to the early 1900s, some initial records of seaweed introductions were documented, as well as increased numbers of non-indigenous taxa. Detailed floristic studies in southern ME and NH from the mid-1960s to 2007 have revealed expansive patterns for two Asiatic taxa (*Codium fragile* subsp. *tomentosoides* and *Neosiphonia harveyi*). Rapid assessment surveys conducted between the Bay of Fundy and Long Island, NY, during four summers (2002, 2004, 2005, and 2007) revealed seven introduced species and a recent expansion of the Asiatic red alga *Grateloupia turuturu* into the Gulf of Maine. Molecular evaluations confirmed the presence of several cryptic introduced species of *Porphyra* from Asia. A synopsis of the dates of introduction, probable vectors, and sources of these 20 introduced taxa in the Northwest Atlantic is given, as well as comparisons of numbers of non-indigenous taxa from other geographies.

Keywords: cryptic *Porphyras*, F. S. Collins, introduced seaweeds, molecular evaluations, Northwest Atlantic, rapid assessment surveys.

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Introduction

Introduced species, which are also referred to as non-indigenous, non-native, or adventive, are a major problem throughout the world's oceans, altering natural communities and causing significant economic losses (Carlton, 1996, 2000; Maggs and Stegenga, 1999; Meinesz *et al.*, 1993; Thresher, 2000; Occhipinti-Ambrogi and Sheppard, 2007). Unfortunately, the numbers of introduced seaweeds are increasing worldwide, with >120 taxa currently known, some of which aggressively dominate marine habitats (Dawes and Mathieson, in press). Chapman and Carlton (1991) and Ribera and Boudouresque (1995) suggest several criteria for identifying an introduced species: it has been previously unknown in a region; there has been expansion of its geographic range after initial documentation; potential human-mediated vectors exist; the taxon is often associated with other introduced species, artificial structures, and environments; discontinuous regional and global distributions are present; and passive life history and global mechanisms for dispersion are either lacking or insufficient. We have employed many of these criteria in our present evaluation of introduced seaweeds within the Northwest Atlantic.

Pederson *et al.* (2005) emphasized that our ability to detect changes in the numbers and rates of marine introductions depended on well-documented lists of species in time and space. These should include careful records of nomenclature changes,

potential vectors, and distributional patterns. The lack of comprehensive databases on non-indigenous species has limited the critical regulatory and management activities needed to address many problems associated with such introductions (Cute, 2001). The arrival of new species often goes unnoticed or is based on serendipitous observations and reporting (Carlton, 1996; Cohen, 2000).

Here, we review the records of 20 introduced seaweeds in the Northwest Atlantic. Several methods are described, including historical documentation of voucher specimens, critical evaluation of diaries and written descriptions, field collections (including rapid assessment surveys), and molecular evaluations.

Material and methods

Historical and recent floristic studies

The most important historical collections of seaweeds in northern New England date back to the late 1800s and early 1900s, and they were made by the amateur phycologist Frank Shipley Collins, who was a bookkeeper and ticket clerk in the Malden Rubber Shoe Company, located in MA (Setchell, 1925). He collected extensively on Mount Desert Island (44°17'N 68°20'W) in Downeast, ME (Collins, 1894), the state's largest insular habitat (Rich, 1993), as well as in Casco Bay (43°40'N 70°15'W), the second largest embayment in ME (Anon., 2000). Later, Collins *et al.* (1895–1919) documented several specimens from these same two sites in Phycotheca

Boreali–Americana, the largest exsiccata of seaweeds ever published (Setchell, 1925; Taylor, 1962). Taylor (1921) and Johnson and Skutch (1928a, b, c) documented a few other records of seaweeds from Mount Desert Island, and Mathieson *et al.* (1998) compared these historical collections with more recent ones (1996) made at 28 sites around the island.

Collins' (1911) historical collections (1898–1909) from Casco Bay were concentrated on the western shoreline of Merriconeag Sound, near Potts Point (43°43'N 70°02'W), the site of the old Tufts College Marine Biological Laboratory (Mathieson *et al.*, 2008). Most of the collections were documented in his detailed diary or field notebook, which was deposited at the Jepson Herbarium of the University of California, Berkeley (UC). Aside from Collins' Casco Bay samples, a few other early collections were also made by Capt. Nicolas Pike (in 1842), John Hooper (in 1851), W. G. Farlow (in 1874 and 1876), W. A. Setchell (in 1888 and 1889), C. B. Fuller (from 1871 to 1906), and G. Dunn (1916 and 1917). Samples representing most of these early collections from Casco Bay and Mount Desert Island were evaluated from diverse herbaria: Farlow Herbarium (FH), New York Botanical Garden (NY), D. C. Eaton Algal Herbarium (YALE), University of Michigan (MICH), Jepson Herbarium of the University of California, Berkeley (UC), and Brooklyn Botanical Garden (BKL). Data from Collins' field notebook (diary), his various publications (Collins, 1900, 1902, 1903, 1906a, b, c, 1908, 1911), and other early collections (see above) were used to document historical records, which were compared with recent collections from 204 sites throughout Casco Bay (Mathieson *et al.*, 2008). The last studies were initiated in 1994 and documented by ~8400 voucher specimens that were deposited in the Albion R. Hodgdon Herbarium at the University of New Hampshire (NHA). A synopsis of introduced species from Mount Desert Island and Casco Bay was summarized, based on comparisons of historical and recent collections.

Several taxonomic references, including Taylor (1962) and Sears (2002), were employed to identify recent and historical collections of seaweeds from Mount Desert Island and Casco Bay (see Mathieson *et al.*, 1998, 2001, 2008, for detailed listings). Nomenclature primarily follows Silva *et al.* (1996) and Sears (2002), except for some recent changes resulting from molecular studies of the Ulvales (Hayden *et al.*, 2003) and Laminariales (Lane *et al.*, 2006).

The results of several detailed floristic, phenological, ecological, and molecular studies of seaweeds from NH and southern ME were used to increase our understanding of introduced seaweeds and to clarify the presence of some cryptic taxa (cf. Mathieson and Hehre, 1986; Mathieson, 1989; Mathieson and Penniman, 1991; Mathieson *et al.*, 1998, 2001, 2003, 2006; Mathieson and Dawes, 2001; Wallace *et al.*, 2004; West *et al.*, 2005). For example, Mathieson and Hehre (1986) gave a synopsis of seaweeds from 256 open coastal and estuarine sites, with representative samples of all conspicuous intertidal and subtidal species at each site being collected either monthly or seasonally for a minimum of one calendar year. Overall, the methods of collections, identification, and processing of samples were similar to those outlined by Mathieson *et al.* (2001), i.e. herbarium voucher specimens for each taxon per site were prepared, and a complete set of ~40 000 was deposited in NHA to document temporal, spatial, and biological characteristics of the region's flora.

Rapid assessment surveys

Fouling seaweed populations were evaluated at 67 sites between Downeast, ME, and Staten Island, NY, during midsummer (July–August) of 2000, 2003, 2005, and 2007 (Mathieson *et al.*, in press a). Most sites were located within harbours, ports, and marinas: 16 in ME, 5 in NH, 24 in MA, 14 in RI, 3 in CT, and 5 in NY. Eight of these 67 sites were located within national estuary programmes: Casco Bay Estuary Program (ME); New Hampshire Estuaries Program; Massachusetts Bays Program, Buzzards Bay Project (MA); Narragansett Bay Estuary Project (RI); Long Island Sound and Peconic Estuarine Programs (NY); and New York/New Jersey Estuary Program. Sampling was carried out in the intertidal and shallow subtidal zones on floating docks and associated structures (e.g. boat hulls, pilings, ropes, wires, buoys, and tires) that were permanently installed and not cleaned during the past year. Historical uses and other human-related activities were identified for each location. Sampling was limited to 1 h at each station, and typically three sites were sampled per day. Mathieson *et al.* (in press a) and Pederson *et al.* (2005) give further details of these rapid assessment surveys.

The methods of collection and identification of fouling seaweeds were similar to those outlined above, except for the short-term nature of sampling (~1 h site⁻¹), the evaluation of three collection sites per day, and the lack of scuba gear for subtidal sampling. Initial processing of samples was performed daily at various regional laboratories (the universities of Southern Maine, MA at Boston, and Dartmouth, NH, and other laboratories), and final confirmation and specimen preparation were done at the Jackson Estuarine Laboratory. Approximately 920 voucher specimens are deposited at NHA.

Cryptic *Porphyra* taxa

Molecular evaluations of rbcL and ITS-1 sequences were used to identify several cryptic or introduced *Porphyra* taxa from Long Island Sound to the Canadian Maritime Provinces (Klein *et al.*, 2003; Bray, 2006). Initially, tissue samples were ground in a mortar and pestle, then the genomic DNA was extracted using a Puregene Genomic DNA Purification kit. The ITS1-5.8S-ITS2 region was amplified using two primers, JBITS7 (Broom *et al.*, 2002) and AB28 (Steane *et al.*, 1991). The PCR reagents and amplification profiles were identical with those used by Teasdale *et al.* (2002). Before sequencing, the resulting amplicons were gel-purified to confirm their size and to decrease non-specific or contaminating products (Klein *et al.*, 2003). The PCR-amplified rbcL and ITS-1 products were evaluated with an ABI 373 Automated Sequencer located at the UNH Hubbard Center for Genome Sciences, using standard procedures outlined by Klein *et al.* (2003) and Bray (2006). Raw sequences were edited in Chromas (version 2.2, Technelysium Pty Ltd, Tewantin, Queensland, Australia). Contiguous sequence assembly and alignments were done in SeqMan II and MegAlign (version 5.08 for Windows, DNASTar, Inc., Madison, WI, USA), respectively. Searches of GenBank were conducted using Blastn via the Net Search option in MegAlign. Critical species identifications were confirmed by molecular comparisons of herbarium and recent collections (Bray, 2006), plus evaluations of GenBank accessions.

Results and discussion

Occurrence and types of introduced seaweeds

In all, 20 taxa of non-indigenous seaweeds are currently known from the Northwest Atlantic (Table 1; Figures 1 and 2), including 2 subspecies of the green alga *Codium fragile* (*atlanticum* and *tomentosoides*), 4 brown algae, and 14 red algae. Of these introduced seaweeds, 11 are probably from Asia or the Northwest Pacific: *C. fragile* subsp. *tomentosoides*, *Colpomenia peregrina*, *Melanosiphon intestinalis*, *Bonnemaisonia hamifera*, *Gracilaria vermiculophylla*, *Grateloupia turuturu*, *Neosiphonia harveyi*, *Porphyra katadae*, *Porphyra suborbiculata*, *Porphyra yezoensis* f. *yezoensis*, and *P. yezoensis* f. *narawaensis*. Eight species are probably from Europe: *C. fragile* subsp. *atlanticum*, *Fucus serratus*, *Ulonea rhizophorum*, *Dumontia contorta*, *Furcellaria lumbricalis*, *Lomentaria clavellosa*, *Lomentaria orcadensis*, and *Rhodymenia delicatula*; and one is from the Australasian region: *Antithamnion pectinatum*. Each of these introductions was either direct or secondarily from its native geography. For example, *C. peregrina*, which probably originated in the North Pacific (Jones, 1974; Farnham, 1980), was first observed on the west coast of France some time before 1906 (Blackler, 1964; Fletcher, 1987). It is now common in Europe (Mediterranean to Scandinavia), and at the Azores, the Salvage Islands, North Africa, Tanzania, Newfoundland, Nova Scotia, Australia, New Zealand, and the Solomon Islands (Abbott and Hollenberg, 1976; O'Clair and Lindstrom, 2000; Sears, 2002; Guiry and Guiry, 2007).

As shown in Table 1, the earliest records of introduced seaweeds within the Northwest Atlantic date back to the mid-1800s and early 1900s, and they include *N. harveyi* (Stonington, CT; Harvey, 1853), *F. lumbricalis* (Newfoundland; Harvey, 1853), *L. orcadensis* (MA; Farlow, 1873, 1877), *F. serratus* (Pictou, Nova Scotia; Hay and MacKay, 1887), *U. rhizophorum*, and *D. contorta* (Harpwell, ME, 1913; Casco Bay; Dunn, 1916). The status of *N. harveyi* as an introduced species was recently clarified by the molecular studies of McIvor *et al.* (2000, 2001), who found that the plant, which they designated *Polysiphonia harveyi* Bailey, originated in Japan, because this was the centre of its genetic diversity. The first published record of *D. contorta* from North America was based on Grace Dunn's (1916, 1917) doctoral studies of its development and reproductive features from the Potts Point area (43°44'N 70°02'W) of Harpswell, ME (Mathieson *et al.*, 2008). Even so, an earlier (May 1913) unpublished collection was made by A. H. Norton from Cape Elizabeth, ME (43°37'N 70°10'W), which is just south of Portland. As the brown alga *U. rhizophorum* is a specific endophyte within *D. contorta*, it no doubt arrived at the same time as its host.

As outlined in Table 1, the three most recent Northwest Atlantic introductions are *G. vermiculophylla* (~1998), *G. turuturu* (1996), and *R. delicatula* (1996). *Gracilaria vermiculophylla* and *R. delicatula* currently have rather circumscribed distributions, the former being recorded from Hog Island Bay, VA (Thomsen, 2004; Thomsen *et al.*, 2006), and the latter from southeastern MA near Woods Hole (Miller, 1997). *Grateloupia turuturu* currently extends from Long Island Sound (CT) to Boston Harbor, MA (Mathieson *et al.*, in press b). Further details of *Grateloupia*'s recent expansion into the Gulf of Maine are given below under rapid assessment surveys. In comparing the distributional patterns of the other 17 introduced species, *C. fragile* subsp. *tomentosoides* and *N. harveyi* have the broadest geographic expansions, extending from the Gulf of St Lawrence to NC and Newfoundland to GA,

respectively. *Colpomenia peregrina* and *F. lumbricalis* demonstrate the opposite pattern, being found from Newfoundland to the Canadian Maritimes and Labrador to Nova Scotia, respectively. The remaining 13 taxa tend to have intermediate geographic patterns. For example, *D. contorta* extends from Labrador to Long Island (Mathieson *et al.*, 2008), and *F. serratus* is now abundant and well-established in the Canadian Maritimes (Villalard-Bohnsack, 2002), and has been for the past few decades (D. Lyons, pers. comm.; G. W. Saunders, pers. comm.). Most of the 20 introduced Northwest Atlantic species were apparently transported by ships (i.e. ballast or hulls), shellfish, or other unknown means. For example, *N. harveyi* (Figure 2c and d) may have been introduced a second time (i.e. after 1957, cf. Table 1) with *C. fragile* subsp. *tomentosoides* (Figure 1a), because it is a common epiphyte on that host, whereas, as noted previously, the specific endophyte *U. rhizophorum* (Figure 1g) was introduced with *D. contorta*, both presumably from Europe.

Historical and recent floristic assessments

Collins (1894) recorded a single introduced species (*N. harveyi*) from Mount Desert Island, and some 100 years later, three adventive species (*M. intestinalis*, *D. contorta*, and *N. harveyi*) were found (Mathieson *et al.*, 1998). In Collins's (1911) studies of Casco Bay seaweeds, he recorded two introduced species (*D. contorta* and *N. harveyi*), whereas Mathieson *et al.* (2008) found nine [*C. fragile* subsp. *tomentosoides*, *M. intestinalis*, *U. rhizophorum*, *B. hamifera* and its "*T. intricata*" phase (cf. Chihara 1961, 1962), *D. contorta*, *L. clavellosa*, *L. orcadensis*, *N. harveyi*, and *P. yezoensis* f. *yezoensis*]. Therefore, the numbers of introduced species from Mount Desert and Casco Bay are now 3–4.5 times greater than those recorded by Collins (1894, 1911).

The collection of *D. contorta* by Collins (1911) in southern ME (i.e. Casco Bay) documents its rapid northward expansion, from its initial collection site in CT during the mid-1800s (Table 1). In discussing the invasion ecology of *N. harveyi* (as *P. harveyi*) in the British Isles, McIvor *et al.* (2001) noted that it was not yet established by the mid-19th century (Harvey, 1849). However, it is now regarded as a widespread alien in the British Isles (Maggs and Hommersand, 1993; Maggs and Stegenga, 1999), displaying many characteristics typical of algal invaders (Ribera and Boudouresque, 1995), including being eurythermal, weedy, and common as a fouling species on artificial substrata associated with boating and aquaculture activities (Maggs and Stegenga, 1999).

Based on recent floristic, ecological, and molecular studies (1965 to present) of seaweeds from southern ME and NH, 217 taxa have been recorded, including 58 green, 66 brown, and 93 red algae. Nine introduced seaweeds were the same as those recorded from Casco Bay (see above). Initial records for these nine species are as follows: *C. fragile* subsp. *tomentosoides* (1983, Babbs Cove, Appledore Island, ME, Isles Shoals; Mathieson *et al.*, 2003), *M. intestinalis* (1967, Piscataqua River, Newington, NH; ACM, unpublished), *U. rhizophorum* (at seven NH/Maine Isles of Shoals sites, five nearshore open coastal sites in NH, and three sites within the Great Bay Estuarine System; Mathieson and Hehre, 1986), *B. hamifera* (1965, Star Island, NH, Isles of Shoals; Kingsbury, 1965), and its "*T. intricata* stage" (1966, Star Island, NH, Isles of Shoals; Hehre, 1969; Hehre and Mathieson, 1970), *D. contorta* (1938, Hampton Beach, NH; Croasdale, 1941), *L. clavellosa* (1972, Dover Point; Hehre, 1972), *L. orcadensis* (1883, Rockingham County; Cole, 1883), *N. harveyi* (1900, ME

Table 1. Introduced seaweeds found within the Northwest Atlantic, modified in part from Villalard-Bohnsack (2002) and Dawes and Mathieson (in press).

Species	Date and site of first observation, plus (present known distribution)	Mode of introduction*	Probable origin†	Reference
Chlorophyta				
<i>Codium fragile</i>				
subsp. <i>atlanticum</i> (A. D. Cotton) P. C. Silva	1997, Gulf of St Lawrence (Gulf of St Lawrence)	?sf	E	Garbary <i>et al.</i> (1997); Hubbard and Garbary (2002); Silva (1955, 1957) Hubbard and Garbary (2002)
subsp. <i>tomentosoides</i> (van Goor) P. C. Silva ¹	1957, Long Island, NY (Gulf of St Lawrence to NC)	sf, sh	J	Bouck and Morgan (1957); Carlton and Scanlon (1985); Schneider and Searles (1991); Mathieson <i>et al.</i> (2003) Mathieson <i>et al.</i> (2003)
Heterokontophyta (Phaeophyceae)				
<i>Colpomenia peregrina</i> Sauvageau	1960, Canadian Maritimes (Newfoundland to Canadian Maritimes)	sf	E?	Blackler (1964) Villalard-Bohnsack (2002)
<i>Fucus serratus</i> Linnaeus	1887, Pictou, Nova Scotia (Canadian Maritimes)	b	E	Hay and MacKay (1887) Villalard-Bohnsack (2002)
<i>Melanosiphon intestinalis</i> Wynne	1970, Bay of Fundy, Nova Scotia (Labrador to Long Island Sound)	?	NWP	Edelstein <i>et al.</i> (1970); Mathieson <i>et al.</i> (in press a) Sears (2002)
<i>Ulonema rhizophorum</i> Foslie ²	?1913, Harpswell, ME (RI to Labrador)	se ²	E?	Mathieson <i>et al.</i> (2008) Sears (2002)
Rhodophyta				
<i>Antithamnion pectinatum</i> (Montagne) Brauner ex Athanasiadis & Tittley	1986, Waterford, CT (CT to ME)	b, sh	AA	Foertch <i>et al.</i> (1991) Villalard-Bohnsack (2002)
<i>Bonnemaisonia hamifera</i> Hariot (including its <i>Trailiella</i> <i>intricata</i> Batters)	1927, Woods Hole, MA (<i>T. intricata</i> , Labrador to Chesapeake Bay; <i>B. hamifera</i> , Canadian Maritimes to Long Island Sound)	?sh	E, J	Lewis and Taylor (1928); Mathieson <i>et al.</i> (2008); Mathieson <i>et al.</i> (in press a); Villalard-Bohnsack (2002) Mathieson <i>et al.</i> (in press a)
<i>Dumontia contorta</i> (S. G. Gmelin) Ruprecht	1913, Harpswell, ME (Long Island Sound to Labrador)	?	E?	Dunn (1916, 1917); Mathieson <i>et al.</i> (2008) Sears (2002)
<i>Furcellaria lumbricalis</i> (Hudson) J. V. Lamouroux	1853, Newfoundland (Nova Scotia to Labrador)	b	E	Harvey (1853) Sears (2002)
<i>Gracilaria vermiculophylla</i> (Ohmi) Papenfuss	1998 or earlier, Hog Island Bay, VA (VA)	sf	NWP	Thomsen (2004); Thomsen <i>et al.</i> (2006) Thomsen <i>et al.</i> (2006)
<i>Grateloupia turuturu</i> Yamada (initially as <i>G. doryphora</i> (Montagne) Howe) ³	1996, Narragansett Bay, RI (Waterford CT to Boston Harbor, MA)	sb	E?	Villalard-Bohnsack and Harlin (1997, 2001) Gladych <i>et al.</i> (2006); Mathieson <i>et al.</i> (in press a, b)
<i>Lomentaria clavellosa</i> (Turner) Gaillon	1963, Boston Harbor, MA (ME to Long Island Sound)	?	E	Wilce and Lee (1964); Hehre (1972); Villalard-Bohnsack (2002); Mathieson <i>et al.</i> (in press a) Sears (2002)
<i>Lomentaria orcadensis</i> (Harvey) Collins ex Taylor	1873, MA (Nova Scotia Bay of Fundy to NC)	?	?E	Farlow (1873, 1877); Schneider and Searles (1991) Schneider and Searles (1991); Sears (2002)

Continued

Table 1. Continued

Species	Date and site of first observation, plus (present known distribution)	Mode of introduction*	Probable origin†	Reference
<i>Neosiphonia harveyi</i> (J. Bailey) M-S. Kim, H. G. Choi, Guiry & G. W. Saunders ⁴ (as <i>Polysiphonia harveyi</i> J. Bailey)	1848, Stonington, CT (Newfoundland to GA)	?sh	NWP	Harvey (1853); Mathieson et al. (in press a) Mathieson et al. (in press a)
<i>Porphyra katadae</i> A. Miura	?2006, Cape Cod Canal, MA (Cape Cod Canal area)	?sh	?J,C	Bray (2006) Bray (2006)
<i>Porphyra suborbiculata</i> Kjellman (as <i>P. carolinensis</i> J. Coll & Cox)	?1960s, Beaufort, NC (Long Island Sound to FL)	?sh	NWP	Klein et al. (2003) Broom et al. (2002); Coll and Cox (1977); Dawes and Mathieson (2008); Humm (1969) Dawes and Mathieson (2008)
<i>Porphyra yezoensis</i> f. <i>yezoensis</i> Ueda ⁵	1960s, Dover Point, NH (ME to Long Island Sound)	?sf	J	West et al. (2005); Bray (2006) Bray (2006)
<i>Porphyra yezoensis</i> f. <i>narawaensis</i> A. Miura ⁶	> 1960, Long Island Sound (CT and RI)	?sf	J	Bray (2006) Bray (2006)
<i>Rhodymenia delicatula</i> P. Dangeard	1996, Woods Hole, MA (southeast MA)	?	E	Miller (1997) Sears (2002)

¹Considered to be an invasive species or an alien taxon, with deleterious effects on indigenous communities.

²Growing as a specific endophyte on *Dumontia contorta*.

³According to Gavio and Fredericq (2002), the plants that were originally recorded as *Grateloupia doryphora* should now be designated as *G. turuturu*.

⁴According to molecular studies by McIvor et al. (2001), *Neosiphonia harveyi* was introduced into the North Atlantic at least twice.

⁵*Porphyra yezoensis* f. *yezoensis* was initially identified in the Northwest Atlantic from NH, based upon molecular data (West et al., 2005).

⁶See Watson et al. (2000) and Bray (2006) in terms of farming of the U-51 strain of *P. yezoensis* f. *narawaensis* in Cobscook Bay, ME.

* Ship ballast (b), ship hulls (sh), seaweed endophyte (se), cultured shellfish (sf).

† Australasia (AA); China (C); Europe (E); Japan (J); Northwest Pacific (NWP).

and NH; Collins, 1900; and at four nearshore open coastal NH sites, plus five sites within the Great Bay Estuarine System; Newhouse, 1952; Doty and Newhouse, 1954), and *P. yezoensis* f. *yezoensis* (1960s, Dover Point; Reynolds and Mathieson, 1975; as *P. leucosticta*; Bray, 2006; West et al., 2005).

Figure 3 summarizes recent changes in *Codium* and *Neosiphonia* populations within southern ME and NH, expressed as the number of collection sites per year in various open coastal and estuarine habitats. The initial population of *Codium* at the Isles of Shoals (1983) increased to ten in 1994, and eventually reached 27 open coastal and 2 outer estuarine sites by 2005; this represents a 27-fold increase in 22 years! *Codium* tends to be found in sheltered open coastal habitats (Harris and Jones, 2005), whereas *Neosiphonia* dominates estuarine sites. In 1966, *Neosiphonia* was recorded from 16 estuarine sites, but the number increased to 43 sites in 1974, to 72 in 1977, and to 81 in 2005. A single open coastal population was recorded from 1967 to 1974; this increased to 11 in 1977, to 16 in 1983, to 18 in 1994, and to 20–22 between 1999 and 2005. Therefore, the occurrence of *Neosiphonia* increased more than sixfold between 1966 and 2005.

A comparison of occurrences for the nine introduced species based on the 256 sites studied by Mathieson and Hehre (1986) in southern ME and NH is as follows: *C. fragile* subsp. *tomentosoides* (11.3%), *M. intestinalis* (0.8%), *U. rhizophorum* (5.4%), *B. hamifera* (12.1%), and its “*T. intricata*” stage (2.7%), *D. contorta* (21.9%), *L. clavellosa* (10.2%), *L. orcadensis* (5.8%), *N. harveyi* (40.2%), and *P. yezoensis* f. *yezoensis* (0.4%). Therefore, *N. harveyi* exhibited the broadest distribution, as well as a rapid expansion (Figure 3), followed by *D. contorta*. Aside from

P. yezoensis f. *yezoensis* and *M. intestinalis*, which were only found at one and two sites, respectively, the other five species tended to have intermediate patterns of presence.

Porphyra yezoensis f. *yezoensis* was probably underestimated, because molecular confirmations were not conducted on all “*P. leucosticta*-like” specimens (Neefus et al., 2000, 2006; West et al., 2005; Bray, 2006) in NHA. *Melanosiphon intestinalis* may be occasionally abundant (i.e. 25% of 44 sites) within sandy saltmarsh habitats such as Brave Boat Harbor, York/Kittery (Mathieson et al., 2001). In comparing the values of percentage occurrence for several common native species at these same 256 sites, they exceeded both *N. harveyi* and *D. contorta*; *Cladophora sericea* (Hudson) Kützting (47.3%), *Rhizoclonium riparium* (Roth) Harvey (53.1%), *Ulva lactuca* L. (67.8%), *U. intestinalis* L. (47.7%), *U. prolifera* O. F. Müller (52.3%), *Ascophyllum nodosum* (L.) Le Jolis (59.4%), *Fucus vesiculosus* L. (62.5%), *Ceramium virgatum* Roth (46.1%), and *Chondrus crispus* Stackhouse (42.65%).

Rapid assessment surveys

Seven of the 126 total taxa recorded during the four rapid assessment surveys (Mathieson et al., in press a) were introduced (Figure 4). Four originated from Asia, either directly or secondarily (*C. fragile* subsp. *tomentosoides*, *G. turuturu*, *N. harveyi*, and *B. hamifera*, including its tetrasporophyte generation “*T. intricata*”), two from Europe (*L. clavellosa* and *L. orcadensis*), and one from the North Pacific (*M. intestinalis*). As found during previous floristic studies of NH and southern ME (Mathieson and Hehre, 1986), *N. harveyi* was the most widely distributed taxon, occurring at 47 of the 67 sites (70.1%). In contrast,

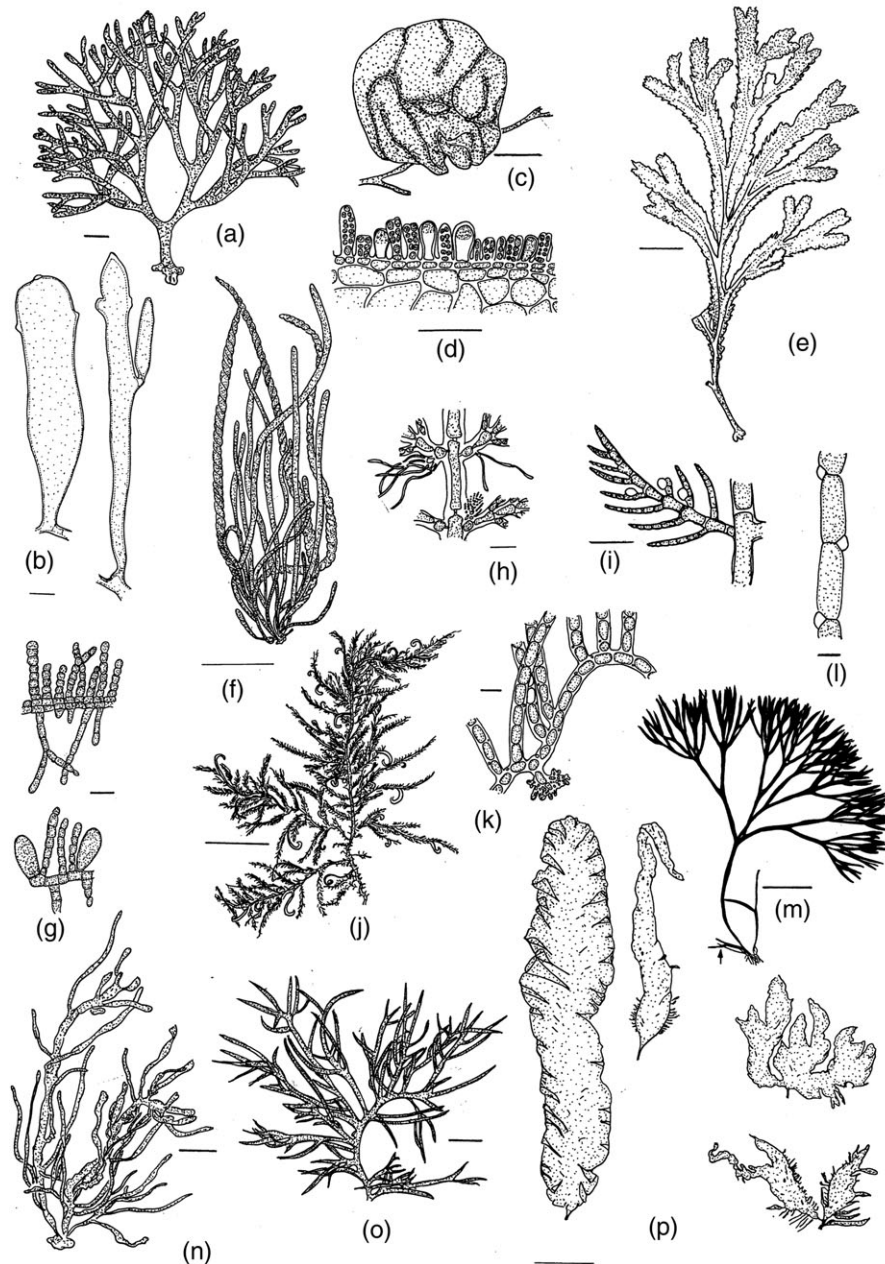


Figure 1. (a) Habit of *Codium fragile* subspecies *tomentosoides* (after Schneider and Searles, 1991), scale 200 μm ; (b) a utricle of *C. fragile* subspecies *atlanticum* on the left showing a narrow pointed tip (i.e. mucron) $<20 \mu\text{m}$, and a hair scar on its upper right, plus a utricle of subspecies *tomentosoides* on the right showing a long pointed tip (mucron) plus a subapical gametangium (after Burrows, 1991), scale 100 μm ; (c) habit of an epiphytic plant of *Colpomenia peregrina* (after Fletcher, 1987), scale 20 mm; (d) cross section of fertile thallus showing spherical paraphyses (ascocysts) and plurilocular sporangia arising from surface cells (after Fletcher, 1987), scale 20 μm ; (e) habit of portion of a small fruiting plant of *Fucus serratus* (after Taylor, 1962), scale 12 cm; (f) habit of hollow, cylindrical, and twisted thallus of *Melanosiphon intestinalis* (after Abbott and Hollenberg, 1976), scale 2 cm; (g) two transverse sections of endophytic filaments of *Ulonema rhizophorum*; the upper section shows erect filaments and rhizoids, and the lower one has unilocular sporangia (after Newton, 1931), scale 2 μm ; (h) branchlet of *Antithamnion pectinatum* with rhizoids and miniature branchlet (after Villalard-Bohnsack, 1995), scale 25 μm ; (i) branchlet of *A. pectinatum* with spherical (clear) gland cells (after Villalard-Bohnsack, 1995), scale 50 μm ; (j) habit of a bushy gametophytic specimen of *Bonnemaisonia hamifera* showing spindle-shaped hooks (after Taylor, 1962, as *Asparagopsis hamifera*), scale 1 cm; (k) "*Trailliella intricata*" stage of *B. hamifera* showing a portion of a stolon, with holdfast and the bases of several erect branches (after Taylor, 1962), scale 4 μm ; (l) close-up of the vegetative filament of "*T. intricata*" showing distinctive (i.e. clear) gland cells (after Dixon and Irvine, 1977), scale 8 μm ; (m) habit of a bushy, slender, regularly dichotomously branched frond of *Furcellaria lumbricalis*, the arrow indicating distinctive basal rhizoids that are absent in *Polyides rotundus* (after Bird and McLachlan, 1992), scale 2 cm; (n) habit of *Dumontia contorta* showing irregular branching and discoid holdfast (after Taylor, 1962, as *D. incrassata*), scale 1 cm; (o) habit of cylindrical, irregularly branched frond segment of *Gracilaria vermiculophylla* (after Guiry and Guiry, 2007), scale 1 cm; (p) morphological variability of *Grateloupia turuturu*, showing simple and divided lanceolate fronds plus irregularly cordate and proliferous fronds (after Villalard-Bohnsack and Harlin, 1997, as *G. doryphora*), scale 10 cm.

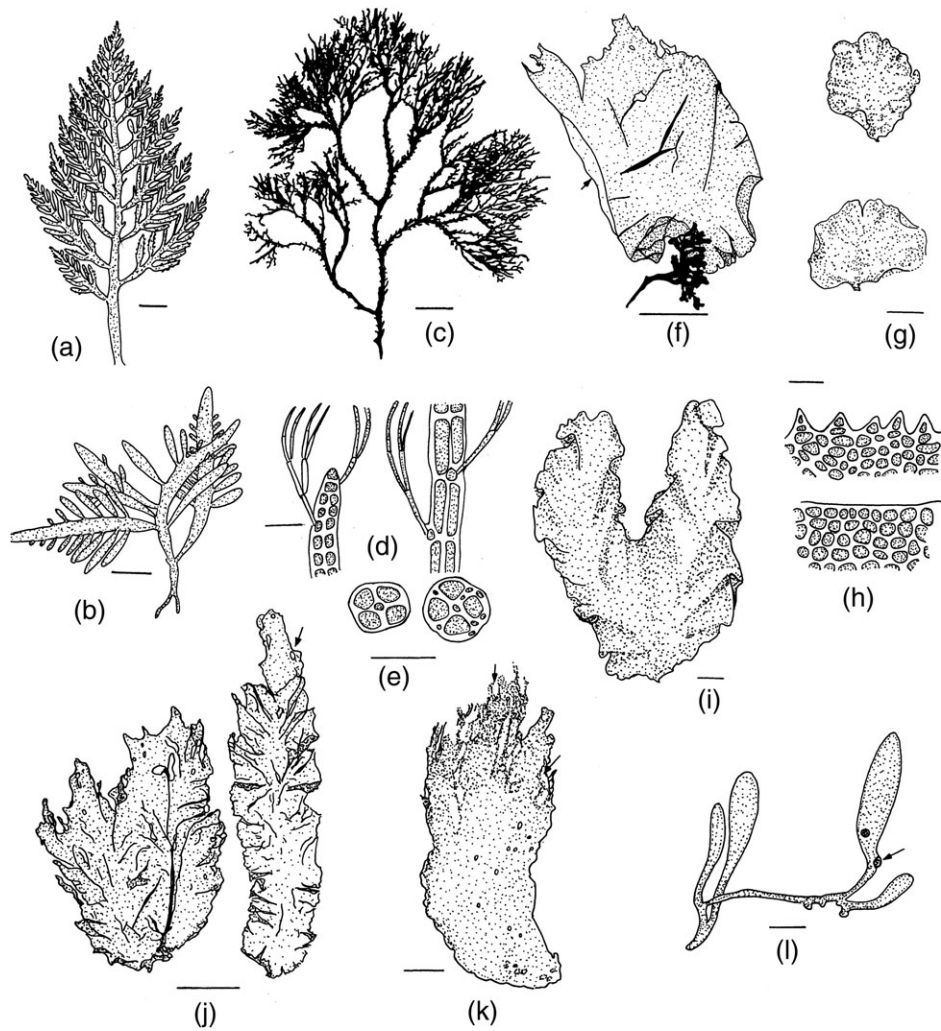


Figure 2. (a) Habit of a rough water form of *Lomentaria clavellosa* showing terete or compressed tubular fronds with a pyramidal outline (after Irvine, 1983), scale 5 mm; (b) habit of a small *Lomentaria orcadensis* with flattened axis, opposite branches, and pinnae branching 1–2 times (after Taylor, 1962), scale 7 mm; (c) habit of one main branch system of a tufted plant of *Neosiphonia harveyi* (after Taylor, 1962, as *Polysiphonia harveyi*), scale 2 mm; (d) apical and subapical portions of *N. harveyi* showing colourless trichoblasts (hairs) and four pericentral cells (after Villalard-Bohnsack, 1995), scale, 500 μm ; (e) cross sections of apical and basal portions of *N. harveyi* showing ecorcated and corticated portions of fronds and four pericentral cells (after Villalard-Bohnsack, 1995), scale, 500 μm ; (f) blade morphology of *Porphyra katadae* showing sectored male (arrow on left) and female (right) portions of thallus (after Bray, 2006), scale 5 cm; (g) habit of two small fronds of *Porphyra suborbiculata* (after Schneider and Searles, 1991, as *P. carolinensis*), scale 2 cm; (h) surface views of spiny and smooth marginal frond segments of *P. suborbiculata* (after Segawa, 1970), scale 60 μm ; (i) habit of *Porphyra rosengurttii* (after Schneider and Searles, 1991), scale 1 cm; (j) habit of two fronds of *Porphyra yezoensis* f. *narawaensis* showing morphological variability and the occurrence of white streaks (arrow) on the left specimen (after Bray, 2006), scale 5 cm; (k) habit of *P. yezoensis* f. *yezoensis* showing white streaks (arrows) and eroding terminal portions (after Chihara, 1970), scale 1 cm; (l) habit of *Rhodymenia delicatula* showing two cystocarps (arrow), peg-like attachment discs, and erect fronds originating in a slender cylindrical (horizontal) stipe (after Irvine, 1983), scale 3 mm.

C. fragile subsp. *tomentosoides* was found at 14 sites (20.9%), and *B. hamifera* (including its sporophytic stage “*T. intricata*”) and *G. turuturu* at six sites each (10.6%). *Lomentaria clavellosa*, *L. orcadensis*, and *M. intestinalis* were each found at three sites (4.5%). Overall, one or more introduced seaweeds were recorded at 46 of the 67 sites (69%). Human-mediated vectors seemed to be responsible for each introduced taxon (Chapman and Carlton, 1991; Carlton, 2001; Raven and Taylor, 2003). In particular, eutrophication (i.e. nutrient enrichment) appeared to be a major factor fostering the invasion and growth of introduced seaweeds (Lapointe et al., 2005).

In comparing the results of these rapid assessment surveys with previous floristic studies (Mathieson and Hehre, 1986; Mathieson et al., 1998, 2008), the numbers of introduced species exceeded those reported for Mount Desert (seven vs. three taxa), but they were fewer than recorded from Casco Bay and NH–southern ME (seven vs. nine taxa). Three winter/spring annuals (*U. rhizophorum*, *D. contorta*, and *P. yezoensis* f. *yezoensis*; Mathieson, 1989; Bray, 2006) were probably missed during rapid assessment surveys because sampling was in midsummer.

A pronounced northward expansion of *G. turuturu* was documented during recent (2007) rapid assessment surveys (Mathieson

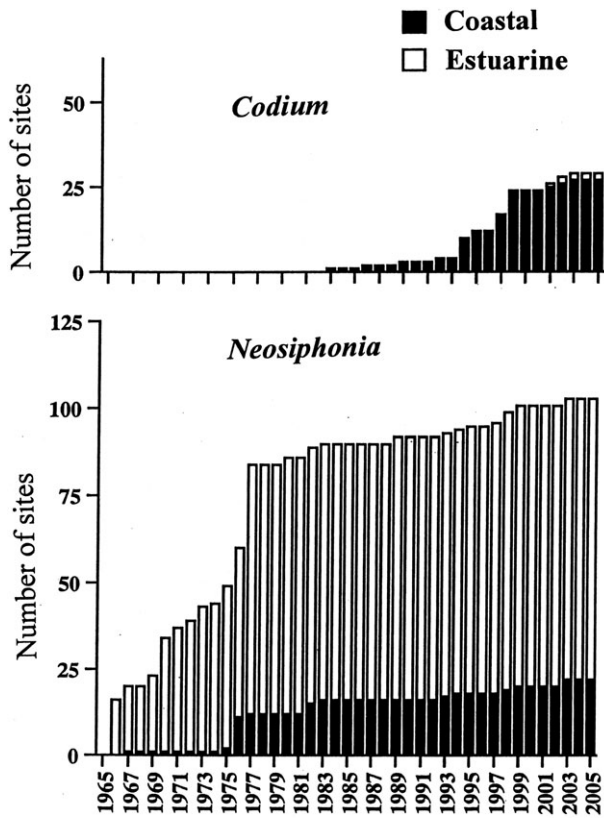


Figure 3. Annual changes of *Codium* and *Neosiphonia* populations within southern ME and NH between 1965 and 2005, expressed as the number of collection sites per year in various open coastal and estuarine habitats.

et al., in press b). In other words, the plant was initially detected in Narragansett Bay, RI, during 1994, and during the next 10 years, it expanded only into nearby Long Island Sound (CT) and to Long Island, NY, near Montauk Point (Table 1). In July 2007, we collected the plant within the Cape Cod Canal and as far north (east) as Boston, MA, which represented a northward extension of >132 km in <4 years. The plant's broad physiological tolerance (Simon *et al.*, 1999) suggest that it will be able to expand

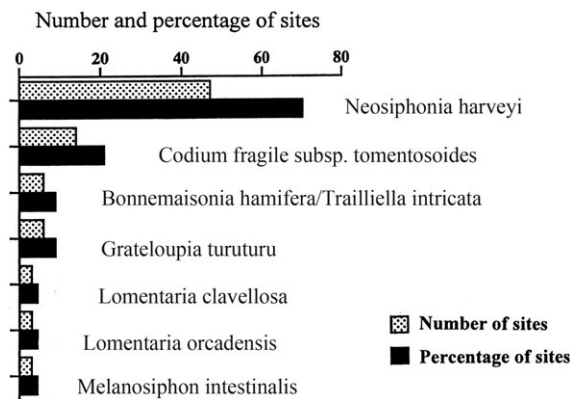


Figure 4. Percentage occurrence of seven introduced species recorded during four rapid assessment surveys (July–August 2000, 2003, 2005, and 2007) between Downeast, ME, and Staten Island, NY.

possibly as far north as the Bay of Fundy, as well as through several new global shipping corridors via the major international port of Boston (Mathieson *et al.*, in press b).

Molecular evaluation of cryptic *Porphyra* taxa

As shown in Table 1, four Asian taxa of *Porphyra* have been documented, based on detailed molecular evaluations: *P. katadae*, *P. suborbiculata*, *P. yezoensis* f. *narawaensis*, and *P. f. yezoensis*. Each may have been confused with one or more native species (Brodie *et al.*, 2007), including *P. leucosticta* Thuret in Le Jolis and *P. rosenburgii* Coll and Cox (Figure 2i). *Porphyra suborbiculata* has small fronds and marginal spines (Figure 2g and h), whereas *P. katadae* has sectored male and female blade segments (Figure 2f), like those found in *P. purpurea* (Roth) C. Agardh (Bird and McLachlan, 1992). Reproductive plants of *P. yezoensis* (Figure 2j and k) often have pale marginal or distal streaks of spermatangia in between female gametangia (Miura, 1984). Therefore, they appear similar to *P. leucosticta* (Taylor, 1962; Bird and McLachlan, 1992). *Porphyra katadae* was the most recently discovered of the four Asian taxa (Bray, 2006), whereas the others probably occurred earlier, but were not delineated until recent molecular evaluations of older herbaria samples (Neefus *et al.*, 2006). Several other previously undescribed *Porphyra* are present in the Northwest Atlantic, because they have unique *rbcl*, *SSU*, and *ITS* sequences (Bray, 2006).

As shown in Figure 5, *P. katadae* has the most circumscribed distribution, being found at just four sites near the north and south ends of the Cape Cod Canal. The two forms of *P. yezoensis* exhibit varying distributional patterns, f. *narawaensis* only occurring south of Cape Cod at seven sites (i.e. MA, RI, and CT), and f. *yezoensis* extends from mid-coastal ME to the western end of Long Island Sound. The distribution of f. *yezoensis*, which is broader than f. *narawaensis*, suggests at least two separate introductions of *P. yezoensis*. Further, because the cultivar f. *narawaensis* was developed more recently than f. *yezoensis*, the former is probably a later introduction than f. *yezoensis*. The distribution of *P. suborbiculata* extends from Long Island Sound at least to FL (Table 1), with a circumscribed presence in southern New England. Herbarium specimens of *P. yezoensis* f. *yezoensis* from Dover Point, NH, date back to the mid-1960s, when Reynolds (1971) identified it as *P. leucosticta*. In a recent molecular ecological study at the same site, West *et al.* (2005) found no *P. leucosticta*, but *P. yezoensis* f. *yezoensis* was common from January to May. It is likely that the plant has been at Dover Point for 40 or more years, but not distinguished from native species. In discussing the occurrence of *P. yezoensis* f. *yezoensis* at Dover Point, both West *et al.* (2005) and Bray (2006) ruled out the Eastport, ME, nori aquaculture operations (Levine, 1998) as a source, because the *rbcl* sequence of its U51 cultivar differed by 2 bp (Klein *et al.*, 2003), and f. *narawaensis* rather than f. *yezoensis* was at the culture site.

Concluding comments

The numbers of introduced species within the Northwest Atlantic (20 taxa) approximate those found within the Northeast Atlantic (26 taxa) and South Africa (19 taxa), but fewer have been recorded at several other sites (Inderjit *et al.*, 2006). The exception to this statement is the Mediterranean Sea, where many more taxa (80) have been recorded (Ribera and Boudouresque, 1995; Stegenga *et al.*, 1997; Maggs and Stegenga, 1999; Villalard-Bohnsack, 2002; Dawes and Mathieson, in press). Many of the introduced

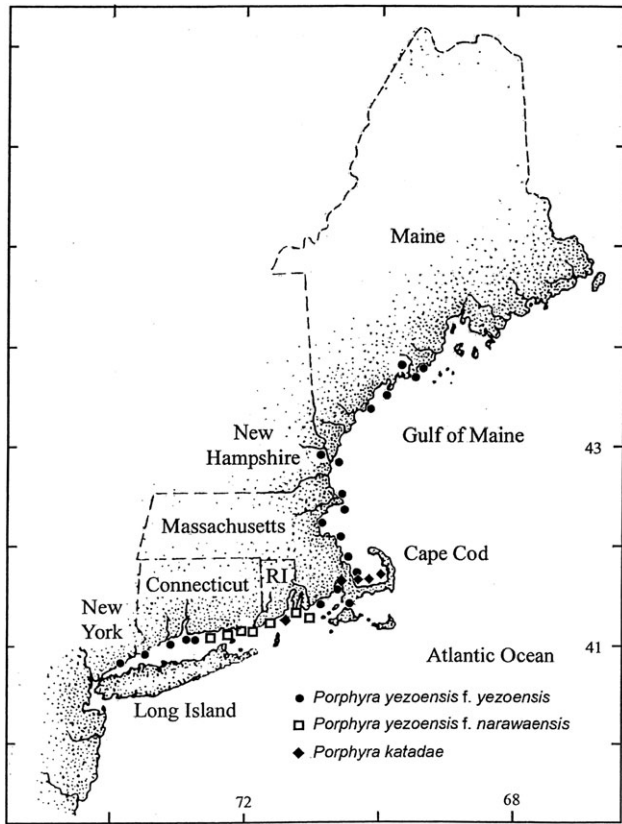


Figure 5. Distributional patterns of *Porphyra yezoensis* f. *yezoensis*, *P. yezoensis* f. *narawaensis*, and *P. katadae* in New England.

seaweeds within the Mediterranean were either introduced by Lessepsian migration through the Suez Canal (Mario *et al.*, 2004) or by importation of Pacific oyster spat into the L'Etang de Thau area of France, a hotspot of non-native macroalgae (Verlaque, 2001). In comparing several different habitats worldwide, Dawes and Mathieson (in press) note that coastal areas, with low diversity of seaweeds because of recent glaciations (e.g. the Northwest Atlantic), have high-potential niches for introduced seaweed taxa (Inderjit *et al.*, 2006). Other areas, such as FL, the Caribbean, and tropical northern Australia, support geologically old, highly diverse floras that have probably inhibited the establishment of foreign taxa. Some introduced species in the Northeast Atlantic are only maintained by repeated introductions, such as by importation of oyster spat or direct commercial farming of *Asparagopsis armata* in Ireland (Kraan and Barrington, 2005).

As noted earlier, there are many complexities involved in unravelling the occurrence and taxonomy of introduced seaweeds. For example, McIvor *et al.* (2000, 2001) found that introduced New Zealand populations of *N. harveyi* (cited as *P. harveyi* Bailey) were previously confused with a morphologically indistinguishable native sibling species, *P. strictissima* J. D. Hooker and Harvey. Therefore, the date of its introduction is difficult to determine. Another Japanese species, *P. japonica* Harvey, was also shown to be synonymous and genetically identical to *N. harveyi*, and many early Northwest Atlantic records of this plant were incorrectly identified as *P. novae-angliae* Taylor (Sears, 2002). The previously described studies of cryptic *Porphyra* also confirm many of these same complexities.

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