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REVIEW

Species composition and geographic distribution of invertebrates in fouling communities along the east coast of the USA: a regional perspective

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ABSTRACT: In recognition of increasing coastal development, warming seas, species invasions, and numerous systematic revisions, we have reviewed the fouling community literature to update the species composition and geographic distributions exhibited by this fauna along the east coast of the USA. We found 1443 records for 317 species. The Bryozoa were the most prevalent phylum in terms of numbers of records and species, but 2 invasive ascidians were the most frequently reported species. Among all species, 9.1% of the fauna have been reported to be invasive. Most species were represented by only 1 to 3 records, suggesting that this fauna has been underrepresented in the literature. The number of species estimated per state peaked in Florida, North Carolina, and Massachusetts, where provincial faunas overlap. Although Cape Cod in Massachusetts and Cape Hatteras in North Carolina represent putative faunal boundaries along the east coast, 63% of the fouling organisms have distributional limits which extend well beyond one or both of these capes. A large proportion of this fauna is widely distributed from New England to the South Atlantic Bight, yet 22 northern species and 96 southern species have restricted distributions. Analysis of community-level studies also revealed regional differences, especially between New England and southern states. These patterns are indicative of latitudinal variation and the transitional nature of this fauna. Given the strong representation of subtropical/tropical species and the prospects for continued warming of the ocean, we anticipate more species invasions and northward extensions of warm-water species along much of the east coast.

KEY WORDS: Species composition · Invasions · Range extensions · Systematic revisions

INTRODUCTION

In recent years, we have begun to recognize significant mesoscale patterns in the structure of species assemblages in the sea (e.g. Kritzer & Sale 2006, Witman & Roy 2009). This emerging perspective began largely with metapopulation and macroecological studies in terrestrial systems. Some believe the application of the metapopulation concept to marine systems represents 'the most important milestone of marine ecology in more than 50 years' (Roughgarden 2006). Previously, many ecological studies in the sea were conducted only at local spatial scales. For example, we note our own community studies from 35 yr ago (Osman 1977, Sutherland & Karlson 1977, Karlson 1978). More recently, community ecologists emphasize using both local and much broader spatio-temporal scales (Cornell & Lawton 1992, Ricklefs &

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Schluter 1993) in order to address broad-scale patterns and the dispersal processes linking local communities with the regional species pool.

Here we focus on the assemblage of invertebrate species comprising marine fouling communities along the east coast of the USA. These organisms occur on artificial substrates and are typically widespread. Early studies of this fauna were mostly conducted at a few sites (e.g. Woods Hole, Massachusetts and Beaufort, North Carolina) and many of these were focused only on the more abundant species. Consequently, there were many gaps in our knowledge of the distribution and abundance patterns of this fauna. In more recent years, a broader range of study sites and increased sampling effort for selected taxa has improved the quality of this information.

Currently, this fauna is changing due to a number of factors. Worldwide coastal development is increasing the available substrate (Bulleri & Chapman 2010). Global climate changes are warming the temperate waters on both the east and west coast of the USA and altering distribution and abundance patterns (e.g. Stachowicz et al. 2002, Jones et al. 2009, Sorte et al. 2010, Sorte & Stachowicz 2011). These changes, along with shipping-related activities (direct transport on ship hulls, release of ballast water) and hitchhiking with oyster introductions, contribute to a growing number of species invasions (e.g. Ruiz et al. 1999, 2000, Winston 2009). In recognition of the above changes and recent advances in the taxonomic nomenclature used to describe this fauna, we perceived the need to review the literature and update the current status of fouling communities along the east coast. Here we take a regional perspective in this endeavor.

Along the east coast, temperature variation is highly seasonal, especially at mid-latitudes. At the extreme, annual water temperatures vary by approximately 30°C in North Carolina (Sutherland & Karlson 1977, Coles & Musick 2000). Larval recruitment and the abundance of many species there vary seasonally (e.g. *Ectopleura crocea* flourishes in the spring and fall while *Pennaria disticha* does so in the summer; Sutherland & Karlson 1977). Other species (e.g. *Hydractinia* sp. and *Xestospongia halichondrioides*) recruit slowly and are long-lived (Karlson 1978). Much further south in the Florida Keys, seasonal variation in temperature is less extreme (21 to 31°C) and the warm water in the winter favors more long-lived invertebrates such as corals (Soto et al. 2011). To the north at Woods Hole, Massachusetts, water temperatures are lower, ranging from near zero to 24°C (Osman 1977, Nixon et al. 2004) and larval recruitment is highly seasonal (Osman 1977, 1978). Thus, temperature along this coast is an important environmental parameter influencing larval recruitment and abundance patterns in fouling communities (see Engle & Summers 1999 for an analysis linking temperature and latitudinal variation in largely infaunal, estuarine benthic communities from Florida to Massachusetts).

In their analysis of 295 sites, Engle & Summers (1999) emphasized temperature, but also highlighted variation in the salinity regimes experienced by estuarine benthic invertebrates. We include this information here because it nicely covers the salinity regimes experienced by inshore fouling species along the east coast. The full range of variation included marine, polyhaline (18 to 35), high and low mesohaline (12 to 18 and 5 to 12, respectively), oligohaline (0.5 to 5), and tidal freshwater (0 to 0.5) locations, but most of the variation in the benthic fauna was attributed to the simple distinction between low (<12) and high salinities (>12). South of latitude 35° N, predominantly high salinity locations were located from Florida to southern North Carolina south of Pimlico Sound. Engle & Summers (1999) report mean salinities of 23.5 to 27.5 for these southern locations. Rainfall during hurricanes is a major source of freshwater to these environments (see Sutherland & Karlson 1977). Northward riverine influences on salinity increase in Pimlico Sound and the Chesapeake Bay (mean salinity: 22.4 ppt), where a full range of salinity regimes occur (Engle & Summer 1999). The lowest mean salinity was reported for estuarine locations between Cape May, New Jersey, and Cape Cod, Massachusetts (15.4).

The coastal waters between Cape Cod in Massachusetts and Cape Hatteras in North Carolina have long been known as transitional between the stable, cold water to the north and the stable, warm water to the south (Cerame-Vivas & Gray 1966, Gosner 1971, Engle & Summers 1999). The water circulation from Labrador to the Florida Keys is dynamic, variable, and quite unusual because of the proximity of polar and subtropical water along this coast (Longhurst 2007). In the winter, the North Wall of the Gulf Stream is only about 300 km from the pack ice of the Gulf of St. Lawrence. However, the strength and location of westerly winds in the winter are strongly driven by the North Atlantic Oscillation (NAO), and these winds influence the displacement of the Gulf Stream offshore, and the strength of the equatorward flow of the Labrador Current (Longhurst 2007). Mean flows vary substantially along the east coast as follows: at Newfoundland, the total southward transport of the Labrador Current over the shelf and slope is 0.8 and 5.7 Sverdrups, respectively (Longhurst 2007). The total transport over the shelf drops predictably to 0.4 Sverdrups off Cape Cod, 0.2 Sverdrups off New Jersey, and 0.03 Sverdrups off Cape Hatteras (Loder et al. 1998). The much larger Gulf Stream transport increases northward from 30 Sverdrups in the Straits of Florida to 63 Sverdrups off Cape Hatteras and 150 Sverdrups off the Newfoundland shelf (Richardson & Knauss 1971, Hogg 1992).

There are several distinguishing features in the coastal oceanography of waters north and south of Cape Hatteras. North of Cape Hatteras, a meandering southward coastal flow over the shelf is characteristic throughout the year (Longhurst 2007). Stratification of shelf waters is complicated by the direction of sustained winds and the influence of tidal streams. Sustained northerlies result in stratification, but sustained southerlies destratify the water. Sustained longshore winds, especially north of Cape Cod, result in upwelling and generally colder water than south of Cape Cod. 'In the Middle Atlantic Bight, tidal fronts parallel the coast and separate an inner neritic from an outer open shelf zone' (Longhurst 2007). South of Cape Hatteras in the South Atlantic Bight, water circulation is less well characterized by mean flows than are shelf flows to the north (Boicourt et al. 1998). Water stratification generally depends on the prevalent wind direction in the spring (Longhurst 2007). The plume of light water from the Chesapeake Bay moves southward, but varies in extent between being close to shore or spread over the entire shelf. It is separated from slope water by a coastal front over the shallow shelf. In general, this water 'is permanently stratified except when disrupted by energetic frontal eddies' bringing slope water from the Gulf Stream across the shelf (Longhurst 2007) or when mixing occurs at the end of the summer with the onset of cooler weather. These frontal eddies are a dominant feature of shelf circulation in the South Atlantic Bight (Boicourt et al. 1998).

These major oceanographic differences between the Northeast Shelf and the South Atlantic Bight are likely to control species distributions along the east coast. North of Cape Hatteras, the opposing Labrador Current and the Gulf Stream produce a gradual north to south change in water temperatures, except for the more abrupt shift to cold water at Cape Cod and the Gulf of Maine. South of Cape Hatteras, oceanographic conditions would appear to favor more unpredictable episodic events influencing larval transport, but the shift from a temperate to a tropical climate must also be considered. For example, *Mytilus edulis* is well known in fouling communities in New England and the Mid-Atlantic Bight, but occasional recruitment onto substrates south of Cape Hatteras extends its distribution into the South Atlantic Bight (Wells & Gray 1960). Ruppert & Fox (1988) noted that mussels south of North Carolina are typically 'small stunted individuals' and these usually die due to high summer temperatures. In fact, Jones et al. (2009) recently concluded that the thermal limit of this species is, indeed, in the vicinity of Cape Hatteras and it 'is shifting poleward in a manner indicative of global warming'. Comparable shifts may also occur among warm-water species as they reach their cold tolerance limits.

The invertebrates of the northwest Atlantic coast have traditionally been divided into the American Atlantic Boreal Region from Cape Cod to the coast of Labrador and the American Atlantic Temperate Region from Cape Cod to southern Florida. Gosner (1971) noted that there are few endemic species in this latter region and that the tropical Atlantic 'is faunistically the most important contributor to the temperate region'. Within this region, Cape Hatteras has also been recognized as a faunal boundary between the Virginian Province to the north and the Carolinian Province to the south (Cerame-Vivas & Gray 1966, Gosner 1971).

More recently, Longhurst (2007) used an oceanographic perspective emphasizing the physical forcing of water motion and stratification over the continental shelf to partition the Northwest Atlantic Shelves Province from Labrador to the Florida Keys into 4 'compartments': (1) Newfoundland shelf, (2) Gulf of St. Lawrence, (3) Northeast shelf and Gulf of Maine from Cabot Strait (between Newfoundland and Nova Scotia) to Cape Hatteras, and (4) South Atlantic Bight from Cape Hatteras to the Florida Keys. In so doing, the invertebrate fauna along the east coast of the USA is simply divided at Cape Hatteras.

METHODS

It is important to note that we have confined our analyses to studies of invertebrates that reported attachment to or fouling of man-made artificial structures (including experimental substrates) or that reported species present on such structures. This epifaunal invertebrate community also occurs on many natural substrates such as rocks, macroalgae, seagrasses, and other invertebrates. We have not included studies of those substrates and thus the species included in this study are a subset of the epifaunal invertebrates found along the coast. We began our review by searching the published literature through 2009 for reports of invertebrate species occurring in fouling communities along the east coast of the USA. We used the Thomson Reuters Science Citation Index Expanded database and various keyword combinations with 'fouling' and the names of individual states for this search. A single record for each species in a publication included the genus and species, the state(s) where each study was conducted, and notes on distributional range, systematics, and substrate type. We restricted this analysis to sessile invertebrates (e.g. sponges, hydroids, anthozoans, tube-dwelling annelids, barnacles, entoprocts, bryozoans, ascidians), and a few semi-sessile species such as some bivalves reported by a few authors. It has been estimated that these fouling community organisms comprise approximately 2% of the entire invertebrate fauna (Woods Hole Oceanographic Institution 1952). This rough approximation emphasizes the point that only a small percentage of invertebrates occur in fouling communities. However, much more systematic research is needed to yield better estimates of the total number of species. Mora et al. (2011) recently estimated that 92% of all animal species in the ocean have yet to be described.

Some of our earliest records are from faunal surveys conducted in the vicinity of Woods Hole, Massachusetts (e.g. Verrill & Smith 1874, Nutting 1901, Hargitt 1908, Osburn 1910, Sumner et al. 1911, 1913). More recent records come from other faunal surveys, ecological studies, systematic publications, and invertebrate keys on selected taxa. We report our sources in Tables 1 & 2 in the main text and in Tables S1 & S2 in the supplement at www.int-res.com/articles/suppl/m458p255_supp.pdf. We attempted to include records from all the ecological studies conducted from Florida to Maine. These ecological sources include all of the published studies cited in Woods Hole Oceanographic Institution (1952), thus covering the early literature well.

Over the years, numerous changes in the taxonomic nomenclature covering this fauna have made it necessary for us to establish a temporal baseline with currently accepted names matched with the published genus and species in our records. To accomplish this, we consulted several primary resources. Firstly, we used the World Register of Marine Species (WORMS, www.marinespecies.org). This website provided currently accepted names for most species along with some recent name changes and distributional information. It also is linked to other systematic websites (e.g. Integrated Taxonomic Information System [ITIS], www.itis.gov) and to distributional data on the Ocean Biogeographic Information System (OBIS, www.iobis.org). For many tropical species, we cross-checked these names with the recent comprehensive work on species in the Gulf of Mexico (Felder & Camp 2009). Secondly, we consulted systematic publications and invertebrate keys covering our geographic area of interest (e.g. Smith 1964, Weiss 1995, Pollock 1998, Martinez 2010) or the specific taxa covered in our survey (e.g. Fraser 1944, Van Name 1945, de Laubenfels 1949, Wells et al. 1960, Maturo & Schopf 1968, Cairns et al. 2002, Winston 2005). This latter group includes some studies from other geographic locations (e.g. Brazil, Costa Rica, and Panama), but these also cover systematic revisions involving some east coast species. Thirdly, we consulted several individuals with considerable experience with selected taxa in order to include some recent systematic revisions or to resolve some particularly problematical taxa (see Acknowledgements). All these resources allowed us to infer northern and southern distributional limits for each species and to estimate the number of fouling species in each state based on the assumption that each species occupied all states over the range between these limits.

To test for any spatial or temporal community-level variation, we conducted similarity and nonmetric multidimensional scaling analyses (Primer 6: ANOSIM, MDS). These analyses used species presence/absence data generated from species lists for each of the studies. The Bray-Curtis dissimilarity index was used to quantify differences in species composition among studies and regions. Studies were initially classified by state and date of publication, and were further separated by period of publication and between native and invasive species. Period designations were based on publication date as Early (1948 or earlier), Mid (1949 to 1982), and Recent (1983 to 2009). These temporal divisions were nominally 1950 and 1980, but adjusted slightly to be within large gaps in the times between studies. For studies that included data from multiple states, we created a separate species list for each state. These analyses were limited to studies covering at least 3 phyla. This was done to emphasize the community-level studies in the literature and to reduce possible biases that might result from inclusion of studies focused on a single species or phylum. As Massachusetts spanned the biogeographic barrier of Cape Cod and North Carolina spanned the barrier of Cape Hatteras, we classified studies in those states as North and South of their respective barrier. Finally, states were assigned to 7 broader biogeographic regions: (1) Maine, New

Hampshire, and northern Massachusetts designated as Northern New England, (2) southern Massachusetts, Rhode Island, and Connecticut as Southern New England, (3) New York, New Jersey, Delaware, and Maryland as Northern Mid-Atlantic, (4) Virginia and northern North Carolina as Southern Mid-Atlantic, (5) southern North Carolina as North Carolina, (6) South Carolina and Georgia as the South Atlantic Bight, and (7) Florida. This pooling allowed increased replication for each region and reduced biases resulting from the disproportionate number of studies conducted in the different states.

RESULTS

Our survey of 105 publications on east coast invertebrates in fouling communities yielded 1443 records for 317 species (see complete set of these records in Table S2 in the supplement at www.int-res.com/articles/suppl/m458p255_supp.pdf). An ordered ranking based on the number of records per phylum is as follows: Bryozoa (402), Cnidaria (308), Chordata (300), Arthropoda (140), Mollusca (97), Annelida (94), Porifera (87), and Entoprocta (15). A similar ranking based on the number of species recorded per phylum is: Bryozoa (95), Cnidaria (69), Chordata (47), Annelida (32), Arthropoda (25), Mollusca (24), Porifera (22), and Entoprocta (3). Clearly bryozoans, cnidarians, and chordates have been well represented in these fouling communities. In Table 1, we specifically identify a total of 51 species and 2 species complexes that were the most frequently reported in each phylum. There were 3 to 43 reports per species in this selection, but most of these species were reported in at least 10 publications. In contrast, most species in our survey were represented by only 1 (121), 2 (55), or 3 (41) records (Fig. 1).

Table 1. The most frequently reported invertebrate species in each of 8 phyla. Current name, date (yr-mm-dd) of entry or last change at the World Register of Marine Species (WORMS), the original reported name if different from current name, number of reports (No.), and east coast distribution from WORMS/OBIS/NAS are provided. Ranges are given by states and in wide (W), intermediate (I), and narrow (N) categories (see Results for summary of overall patterns). Footnotes provide supplemental systematic and distributional sources. No distributional information is provided for multi-species complexes

Species	No.	East coast distribution
Porifera		
Clathria prolifera (Ellis & Solander); 2009-04-12; *Microciona prolifera*	20	Maine to Florida (W)
Halichondria bowerbanki Burton; 2007-09-07	14	Maine to Florida (W)
Chalinula loosanoffi (Hartman); 2007-11-26; *Haliclona loosanoffi*	7	Maine to South Carolina (W)
Mycale americana van Soest; 2007-07-19; *M. cecilia*, *M. microsigmatosa*	7	North Carolina to Florida (N)
Halichondria panicea (Pallas); 2010-03-18	6	Maine to Florida (W)
Cnidaria		
Ectopleura crocea (Agassiz); 2009-07-07; *Tubularia crocea, Parypha crocea*	24	Maine to Florida (W)
Pennaria disticha (Goldfuss); 2004-12-21; *Halocordyle disticha*, *P. tiarella*	20	Maine to Florida (W)[n,p,q]
Obelia dichotoma (Linnaeus); 2004-12-21; *O. articulata, O. commissuralis, O. pyriformis*[r]	15	Maine to Florida (W)
Eudendrium carneum Clarke; 2004-12-21	14	Maine to Florida (W)
Diadumene leucolena (Verrill); 2009-09-14; *Sargatia leucolena*	12	Maine to North Carolina (W)
Halopteris tenella (Verrill); 2008-09-05; *Schizotricha tenella*	11	Maine to Florida (W)
Annelida		
Hydroides dianthus (Verrill); 2008-11-04; *H. hexagona, H. hexagonis, H. hexagonus, Serpula dianthus*	29	Maine to Florida[g] (W)
Sabellaria vulgaris Verrill; 2008-03-26	9	Maine to Florida (W)
Parasabella microphthalma (Verrill); 2010-10-09; *Demonax microphthalma, Sabella microphthalma*	8	Massachusetts[n] to Florida (W)
Branchiomma nigromaculata (Baird); 2010-10-05	4	Florida[n] (N)
Spirorbis borealis Daudin; 2008-03-26	4	Maine to New York (I)
Arthropoda		
Amphibalanus eburneus (Gould); 2010-10-22; *Balanus eburneus*	33	Maine to Florida (W)[i,n]
Amphibalanus improvisus (Darwin); 2010-10-22; *Balanus improvisus*	18	Maine to Florida (W)[i,n]
Balanus amphitrite species complex[a,f–h]	14	
Amphibalanus venustus (Darwin); 2010-10-22; *Balanus amphitrite, Balanus amphitrite niveus*[h]	12	Massachusetts to Florida (W)[a,h,i,n]
Semibalanus balanoides (Linnaeus); 2004-12-21; *Balanus balanoides*	11	Maine to New Jersey (I)
Balanus trigonus Darwin; 2004-12-21	7	North Carolina[l] to Florida (N)[a,g]

Table 1 (continued)

Species	No.	East coast distribution
Mollusca		
Mytilus edulis Linnaeus; 2004-12-21	22	Maine[s] to Georgia (W)
Crassostrea virginica (Gmelin); 2004-12-21; *Ostrea virginica*	15	Maine to Florida (W)
Anomia simplex D'Orbigny; 2010-03-31; *A. glabra*	11	Maine to Florida (W)
Ostrea equestris Say; 2010-07-09; *Ostreola equestris*	9	Virginia[n] to Florida (I)
Ischadium recurvum (Rafinesque); 2005-05-20; *Brachidontes recurvus*, *Mytilus hamatus*	5	Massachusetts to Florida (W)
Entoprocta		
Pedicellina cernua (Pallas); 2004-12-21	8	Maine to Florida (W)
Barentsia major Hincks; 2007-09-05	4	Maine to Connecticut (I)[o]
Barentsia laxa Kirkpatrick; 2007-09-05	3	Maine to Florida (W)[k]
Bryozoa		
Bugula neritina (Linnaeus); 2004-12-21	25	Massachusetts to Florida (W)[c,d,e]
Bugula turrita (Desor); 2005-05-30	24	Maine to Florida (W)
Bowerbankia gracilis Leidy; 2004-12-21; *Vesicularia gracilis*	22	Maine to Florida (W)
Cryptosula pallasiana (Moll); 2004-12-21; *Lepralia pallasiana*	20	Maine to Florida (W)
Schizoporella errata species complex[d]; *S. unicornis*	19	
Bugula simplex Hincks; 2004-12-21; *B. flabellata*[d]	15	Maine to Florida (W)[j]
Conopeum tenuissimum (Canu); 2010-03-22; *C. tenuissem, C. tenuissium, Electra crustulenta, Membranipora crustulenta*[d]	15	Maine to Florida (W)[d]
Schizoporella variabilis (Leidy); *S. errata, S. unicornis, Escharella variabilis*[d]	15	Maine to North Carolina (W)[d]
Anguinella palmata van Beneden; 2004-12-21	13	Massachusetts[d] to Florida (W)
Membranipora tenuis Desor; 2004-12-21; *Acanthodesia tenuis*[t]	12	Maine to Florida (W)[n,t]
Bugula stolonifera Ryland; 2004-12-21	11	New Hampshire[j] to Florida (W)[d]
Electra pilosa (Linnaeus); 2004-12-21; *Membranipora pilosa*	10	Maine to North Carolina (W)[d,k]
Chordata		
Molgula manhattensis (De Kay); 2004-12-21	43	Maine to Florida (W)[b]
Botryllus schlosseri (Pallas); 2004-12-21; *B. gouldii*	41	Maine to Florida (W)[a]
Ciona intestinalis (Linnaeus); 2010-10-12; *C. tenella*	19	Maine to North Carolina (W)[u]
Styela plicata (Lesueur); 2004-12-21	19	North Carolina to Florida (N)
Perophora viridis Verrill; 2004-12-21	16	Massachusetts to Florida (W)
Botrylloides violaceus Oka; 2009-07-20; *B. diegensis*	15	Maine to Virginia (I)[a]
Diplosoma listerianum (Milne-Edwards); 2010-06-25; *D. macdonaldi*	13	Maine to Florida (W)[a]
Didemnum candidum Savigny; 2005-02-24; *D. lutarium*[m]	12	Maine to Florida (W)
Ascidia interrupta Heller; 2004-12-21; *Phallusia hygomiana*[m]	10	North Carolina to Florida (N)
Styela canopus (Savigny); 2004-12-21; *Cynthia partita, Styela partita*	10	Maine to Florida (W)[a]
Styela clava (Herdman); 2009-05-02	10	Maine to New York (I)[a]

[a] Nonindigenous to the east coast (NAS, nas.er.usgs.gov); [b]Nonindigenous from Virginia to Florida (NAS), native distribution subject to debate (WORMS, www.marinespecies.org); [c]Nonindigenous to New England (Altman & Whitlatch 2007); [d]Winston & Hayward (2012); [e]Cryptic species group (McGovern & Hellberg 2003); [f]Ruiz et al. (2000); [g]McCann et al. (2007); [h]Zullo (1964, 1966, 1979); [i]Cosmopolitan and cryptogenic (Farrapeira 2010); [j]Winston (1977); [k]Maturo (1968); [l]Williams et al. (1984); [m]McDougall (1943); [n]Felder & Camp (2009); [o]Hutchins (1945); [p]Fraser 1944; [q]Winston (2009); [r]Kelmo & Attrill (2003); [s]Harris & Tyrrell (2001); [t]Maturo (1957); [u]Plough (1978)

The invertebrate species in our survey range from those with very broad to those with more restricted latitudinal distributions along the east coast (see 'Methods' regarding the multiple resources used to determine these ranges). Among frequently reported species, a large majority (75%) are widely distributed from New England to the South Atlantic Bight (designated as wide in Table 1). Among all species in our survey, there are 145 widely distributed species representing nearly half of the species total; 87 species are distributed from Maine to Florida and an additional 58 species have limits reaching as far north as Massachusetts and as far south as North Carolina. More restricted latitudinal distributions occur among 118 species, a group comprised of 22 northern species in the Gulf of Maine and/or in Massachusetts and 96 southern species occurring in the range from North Carolina to Florida (designated as narrow in Table 1). There are no reports of species in these fouling communities which are restricted to the middle range of states from Rhode Island to Virginia. On the other hand, 21 southern species and

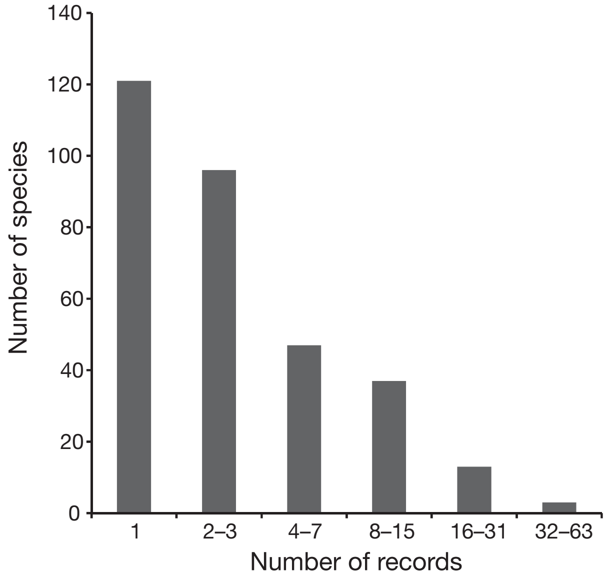

Fig. 1. Distribution of species across frequency classes representing the number of records

33 northern species extend partially into this mid-Atlantic region (designated as intermediate in Table 1). The most frequently reported among these species are *Botrylloides violaceus*, *Ostrea equestris*, *Semibalanus balanoides*, *Spirorbis borealis*, and *Styela clava*.

Assuming that each species can occur in each state between its northern and southern limits along the east coast, the number of species per state ranges between 161 species in Maine and New Hampshire and 228 species in Florida (Fig. 2). The proportion of widely distributed species in each state varies between 50% in Florida and 88% in Maryland and Delaware. Narrowly distributed species, restricted to the warmer waters south of Virginia, reach a maximum proportion of 42% in Florida. Although many of these southern species also occur elsewhere in tropical and subtropical seas, 41 species occur only in Florida along the east coast.

North of Florida, the total number of species peaks again in North Carolina and Massachusetts (Fig. 2). These peaks occur with changes in the distributions of both widely and narrowly distributed species. The number of widely distributed species remains the same from Massachusetts to North Carolina, but drops by 21% north of Massachusetts and by 22% south of North Carolina. In Massachusetts, 145 widely distributed species co-occur with 21 northern, narrowly distributed species and 33 additional northern species with ranges extending into Long Island Sound or along the mid-Atlantic Bight. In North Carolina, 51 southern, narrowly distributed species reach their northern limit, occurring along with 145 widely distributed species.

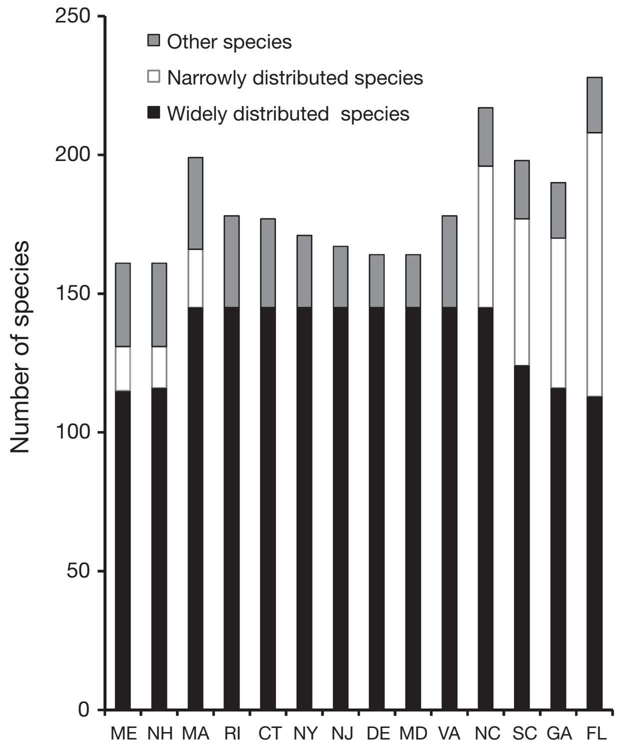

Fig. 2. Number of species in the fouling communities of each state along the east coast. Each species is assumed to occur in all states between the northern and southern limits. Widely distributed species occur at least as far north as Massachusetts and as far south as North Carolina. Narrowly distributed species are restricted from Maine to Massachusetts or from North Carolina to Florida. Other species with intermediate distributions are also indicated. ME: Maine; NH: New Hempshire; MA: Massachusetts; RI: Rhode Island; CT: Connecticut; NY: New York; NJ: New Jersey; DE: Delaware; MD: Maryland; VA: Virginia; NC: North Carolina; SC: South Carolina; GA: Georgia; FL: Florida

Among the 317 fouling community species in our study, 29 species have been reported to be nonindigenous to the east coast (McCann et al. 2007, Nonindigenous Aquatic Species [NAS], nas.er.usgs.gov). Among the frequently reported species identified in Table 1, those designated as nonindigenous include barnacles (*Amphibalanus venustus*, *Balanus trigonus*, and the *Balanus amphitrite* species complex for reports where we could not attribute them to currently recognized species), 1 bryozoan (*Bugula neritina*), and several ascidians (*Botrylloides violaceus*, *Botryllus schlosseri*, *Diplosoma listerianum*, *Molgula manhattensis*, *Styela canopus*, and *S. clava*). Among the less frequently reported species, there are 4 cnidarian, 1 annelid, 3 barnacle, 2 molluscan, 7 bryozoan, and 3 ascidian species (Table 2). Among all 29 species, 12 are widely distributed (as defined above) and 7 are narrowly distributed southern species occurring only in the South Atlantic Bight.

In the community-level analyses, there was consistent latitudinal variation among studies, regardless of whether the data were analyzed as a whole or by time period (Early, Mid, or Recent) or species group (native or invasive). For all studies including 3 or more phyla, the MDS plot depicts a clearly evident trend of increasing dissimilarity from Florida to northern New England (Fig. 3). Similarly, the MDS plot for Recent studies illustrates this general latitudinal trend (Fig. 4C). There were fewer studies in the Early and Mid time periods, but some degree of regional clumping and latitudinal variation is evident in the MDS plots (Fig. 4A,B). Finally, separate evaluation of native and invasive species revealed latitudinal variation, especially between the northern fauna in New England and the southern fauna in South Carolina, Georgia, and Florida (Fig. 5). Significant differences in faunal composition were evident among regional groupings for native species (ANOSIM Global $R = 0.436$, $p = 0.001$, Fig. 5A) and for invasive species (ANOSIM Global $R = 0.554$, $p = 0.001$, Fig. 5B).

DISCUSSION

The most frequently reported species in our survey were 2 ascidians, *Botryllus schlosseri* and *Molgula*

Table 2. Less frequently reported, nonindigenous invertebrate species in east coast fouling communities. Current name, date (yr-mm-dd) of entry or last change at the World Register of Marine Species (WORMS), the original reported name if different from current name, number of reports (No.), and east coast distribution from WORMS/OBIS/NAS are provided. Ranges are given by states and in wide (W), intermediate (I), and narrow (N) categories. Footnotes provide supplemental systematic and distributional sources

Species	No.	East coast distribution
Cnidaria		
Diadumene lineata (Verrill); 2009-12-22; *Aiptasiamorpha luciae, Haliplanella luciae*	7	Massachusetts to Florida (W)[a]
Cordylophora caspia (Pallas); 2004-12-21	2	Maine to Florida (W)[a]
Garveia franciscana (Torrey); 2004-12-21	2	Maine to Florida (W)[a,c]
Moerisia lyonsi Boulenger; 2004-12-21	2	Delaware to South Carolina (I)[a,i–l]
Annelida		
Ficopomatus enigmaticus (Fauvel); 2008-11-04	1	Virginia to Florida (I)[a,b]
Arthropoda		
Megabalanus tintinnabulum (Linnaeus); 2004-12-21; *Balanus tintinnabulum, M. antillensis* [g]	7	Massachusetts to Florida (W)[a]
Amphibalanus amphitrite (Darwin); 2009-10-06; *Balanus amphitrite*	1	Massachusetts to Florida (W)[a,e,f]
Amphibalanus reticulatus (Utinomi); 2009-10-06; *Balanus reticulatus*	1	Florida (N)[a,d]
Mollusca		
Mytilopsis leucophaeata (Conrad); 2005-05-20; *Congeria leucopheata*	2	New York to Florida (I)[a,c]
Perna viridis (Linnaeus); 2008-10-01	1	South Carolina to Florida (N)[a]
Bryozoa		
Membranipora membranacea (Linnaeus); 2004-12-21	6	Maine to Florida (W)[a]
Victorella pavida Saville Kent; 2004-12-21	4	New York[h] to Florida (I)[a]
Celleporaria pilaefera (Canu & Bassler); 1997-12-03	1	Florida (N)[d]
Electra bengalensis (Stoliczka); 2010-04-27	1	Florida (N)[d]
Hippoporina indica Madhavan Pillai; 2010-04-27	1	Virginia to Florida (I)[d]
Sinoflustra annae (Osburn); 2009-05-18	1	Florida (N)[d]
Sundanella sibogae (Harmer); 2009-05-18	1	North Carolina to Florida (N)[a,c,d]
Chordata		
Ascidiella aspersa (Müller); 2004-12-21	8	Maine to North Carolina (W)[a]
Ecteinascidia turbinata Herdman; 2004-12-21	3	Virginia to Florida (I)[a,b]
Didemnum vexillum Kott; 2009-11-28; *D. vestum*	2	Maine to New York (I)[a]

[a]Nonindigenous to the east coast (NAS, nas.er.usgs.gov); [b]Nonindigenous to the Chesapeake Bay (Ruiz et al. 2000); [c]Felder & Camp (2009); [d]McCann et al. (2007); [e]Zullo (1979); [f]Cosmopolitan and cryptogenic (Farrapeira 2010); [g]Henry & McLaughlin (1986); [h]Winston & Hayward (2012); [i]Calder & Burrell (1967); [j]Calder (1971); [k]Sandifer et al. (1974); [l]Purcell et al. (1999)

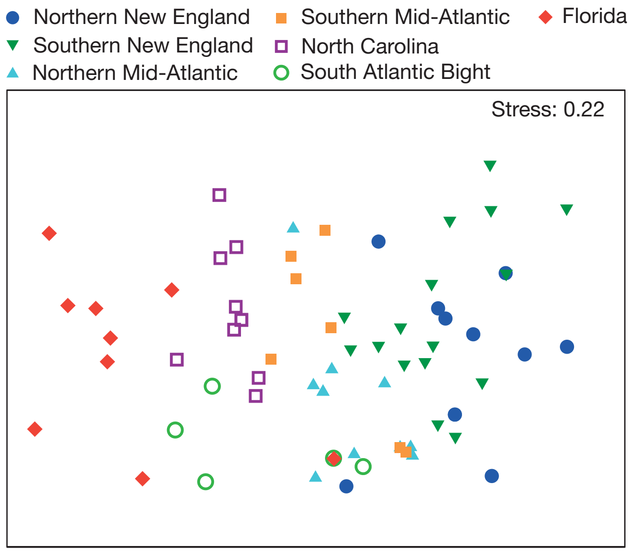

Fig. 3. MDS plot of Bray-Curtis dissimilarities in species composition among sites. All studies include 3 or more phyla. Each point represents a single study or each state for studies reporting on multiple states. Sites are designated within 7 regions along the east coast (see 'Methods' for more detail)

manhattensis, with 41 and 43 reports, respectively (Table 1), dating back to early studies in Massachusetts (Verrill & Smith 1874). Ascidians such as these are widespread and well known for their ability to numerically dominate fouling communities in different geographic regions (e.g. Scheer 1945, Sutherland & Karlson 1977, Dijkstra et al. 2007a,b). Both species are also invasive along some or all of the east coast (Table 1). Twenty-nine invasive species represented 9.1% of all species in the survey and between 6.8% (Maine and New Hampshire) and 10.7% (Virginia) of the species estimated for each state. The Chordata, as

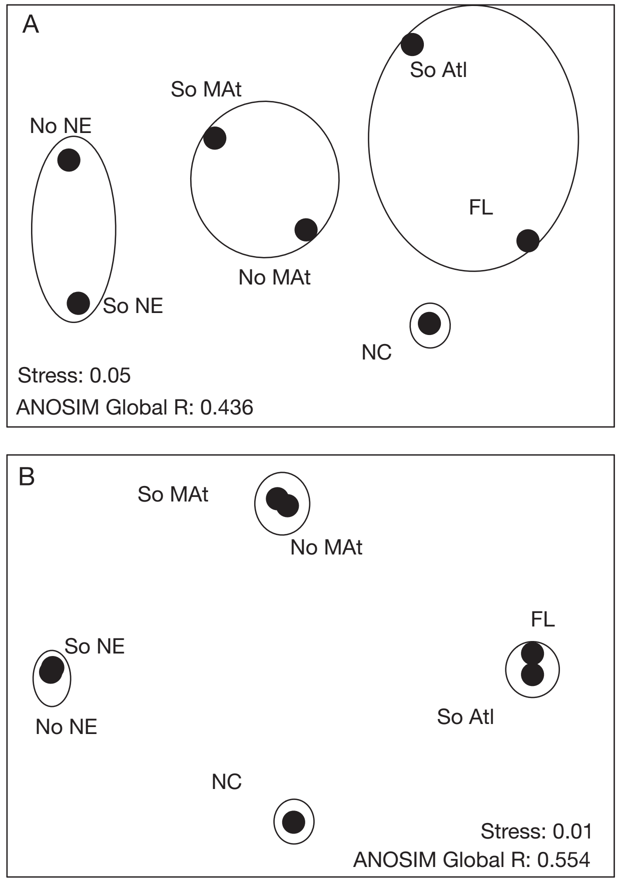

Fig. 5. MDS plots of Bray-Curtis dissimilarities among the 7 regions for species classified as (A) native or (B) invasive. The ellipses link regions with greater than 70% similarity. Note the latitudinal variation among regions (see 'Methods' for more detail). Regions: Northern New England (No NE), Southern New England (So NE), Northern Mid-Atlantic (No MAt), Southern Mid-Atlantic (So MAt), North Carolina (NC), South Atlantic Bight (So Atl) and Florida (FL)

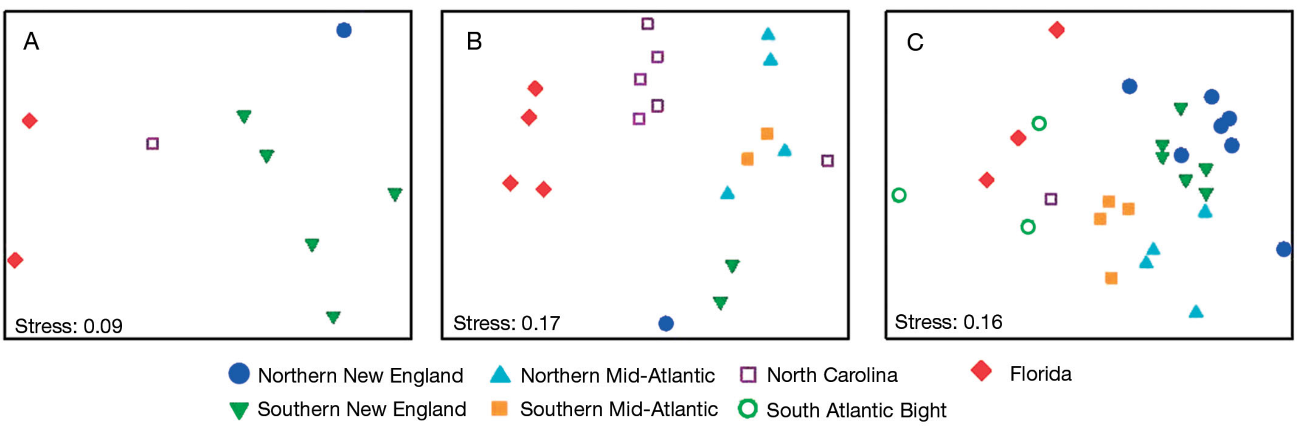

Fig. 4. MDS plots of studies classified by period of publication. Periods are (A) Early (1948 or earlier), (B) Mid (1949 to 1982), and (C) Recent (1983 to 2009). Methods as in Fig. 3

represented by ascidians in these fouling records, were the third most frequently reported phylum in terms of numbers of records. The Bryozoa and Cnidaria were the most frequently reported phyla, representing 49% of all reports and 52% of all species.

One striking feature of these frequency data is the large number of species reported in the literature only 1 to 3 times (here designated as rare species). These species represent 68% of the 317 species (Fig. 1). This probably indicates undersampling of the regional pool of species suggesting that additional sampling effort and more comprehensive surveys would add many additional species to those comprising fouling communities. Typically, many ecological studies use analytical methods requiring one to focus on the most abundant species, so very rare species are often not reported (e.g. Sutherland & Karlson 1977, Karlson 1978). Nevertheless, rare species are a common component of most fouling community studies. Here they represent 70% of 253 species reported in 55 community studies. Although it is possible that misidentifications have erroneously inflated the proportion of rare species in this literature survey, it is unlikely that most of these species were misidentified.

The distribution of species can be viewed on multiple spatial scales representing, for example, several localities, states, regions, and entire coastlines. Above, we have summarized distributional patterns by noting that most frequently reported species are widely distributed, occurring from New England to the South Atlantic Bight, and many of these range all the way from Maine to Florida. This pattern indicates that Cape Cod and Cape Hatteras do not represent distributional boundaries for many species (46% of the fauna in this case). An additional group of 33 northern species and 21 southern species extend beyond one of these capes reaching a distributional limit in the mid-Atlantic region. Thus, 63% of the fauna have distributional ranges extending beyond these putative boundaries.

On the other hand, this fouling community fauna does include species which are not known to extend south of Cape Cod or north of Cape Hatteras. Twenty-two northern species range to the south only as far as Massachusetts, while 96 southern species occur only from North Carolina to Florida. The Bryozoa and Chordata are well represented among the reported species in these 2 regions (61%). Recent systematic revisions of the Bryozoa north of Cape Hatteras confirm that the boreal region north of Cape Cod is more diverse than that occurring in the temperate water between the capes (Winston & Hayward 2012). We found 7 bryozoan species constituting 32% of the fouling community species restricted to these boreal waters. Across the entire east coast, 30% of the species in this community are bryozoans.

There are 2 major distributional patterns exhibited by species restricted to the South Atlantic Bight. Fifty species occur over the full range from North Carolina to Florida, while 41 are known only for Florida. The former group is comprised of warm-water species occurring no farther north than Hatteras Harbor (Wells et al. 1964) or the offshore hard-bottom of Onslow Bay (Williams et al. 1984). Several tropical species, including the corals *Siderastrea siderea* (Ellis & Solander) and *Solenastrea hyades* (Dana) (see Macintyre & Pilkey 1969), other sessile taxa, the echinoid *Diadema antillarum*, and multiple fish species, are also known to occur in Onlsow Bay (M. Hooper pers. comm.). For these species, the distributional break at Cape Hatteras is consistent with the oceanographic conditions emphasized by Longhurst (2007). The latter group in Florida is dominated by 19 bryozoan species. Some of these species are new to Florida waters as a result of species invasions (Table 2, see McCann et al. 2007) and, possibly, range extensions from tropical waters (Winston 2009). Further northward movement in the future, at least to Cape Hatteras, would appear to be likely.

In our analysis of community-level studies, we found additional support for regional differences in fouling communities (Figs. 3, 4 & 5). In large part, the regions separate into New England, Mid-Atlantic, North Carolina, and South Carolina to Florida. Such latitudinal variation is evident here and in other recent analyses of benthic invertebrates along the east coast (Engle & Summers 1999, Cook & Auster 2007, Hale 2010). These patterns appear not to change with more recent species invasions. Even though the distribution of more southern species such as *Ecteinascidia turbinata* and *Symplegma viride* have shifted northward, many of the species that have invaded northern regions (e.g. *Botrylloides violaceus, Styela clava, Didemnum vexillum*) in the past 40 yr are not found in southern regions. Yet, these same southern regions have been invaded by different species during the same time period (e.g. *Celleporaria pilaefera, Electra bengalensis, Sinoflustra annae*).

Thus the fouling community along the east coast of the USA is a composite assembly of mostly widespread species tolerant of a wide range of water temperatures, cold-water boreal species, and tropical species with varying degrees of cold-tolerance. This view is mostly consistent with Gosner (1971), with his references to the transitional nature of the invertebrate fauna along the east coast and the strong contribution made by tropical species to the fauna of the American Atlantic Temperate Region. Currently, many boreal and tropical species appear to be limited by either Cape Cod or Cape Hatteras, but oceanographic conditions (mean flows and variability associated with the NAO, prevailing winds, storms, etc.) can facilitate range extensions around these physical obstructions (see Introduction). Given that oceanographers have begun to consider the dynamics of variable flow (as opposed to focusing primarily on mean flows) in coastal waters (see Introduction), we should anticipate learning more in the future about how distributional limits of fouling and non-fouling species are dictated by physical processes. In addition, physiological studies on the influence of temperature on reproduction, growth, and mortality (e.g. Jones et al. 2009) will be useful, especially as the seas continue to warm. The future is likely to include more species invasions and northward extensions of warm-water species along much of the east coast.

In fact, one of us (R. W. Osman) has examined unpublished evidence from ongoing recruitment and other experimental studies in New England (Long Island Sound), the mid-Atlantic (Chesapeake Bay and a Virginia coastal bay), and Florida (Indian River Lagoon). As we have found in the literature, there are species that are common and abundant in all of these regions (e.g. *Amphibalanus improvisus* and *Molgula manhattensis*) but others that are present and abundant in only 1 region (e.g. *Styela clava* in Long Island Sound, *Membranipora chesapeakensis* in Chesapeake Bay, and *Megabalanus cocopoma* in Indian River Lagoon). In addition, many of the invasive species seen in Long Island Sound are not found in the Indian River Lagoon (e.g. *Botrylloides violaceus, Styela clava, Didemnum vexillum, Membranipora membranacea,* and *Clavelina lepadiformis*; see Reinhardt et al. 2010), although other species of these same genera are. The maintenance of similar regional patterns over time (Fig. 4) and with both resident and invasive species (Fig. 5) suggests that even with an increasing potential of northern movement of southern species, latitudinal differences in environmental conditions continue to influence distributional patterns. These patterns remain despite the likely human assistance, both in terms of increased and faster shipping (hull fouling and ballast water) and increasing man-made structures along the coast, but, most importantly, in areas with little natural habitat.

In conclusion, we note that the currently accepted nomenclature differed from earlier usage by the authors in our survey for 127 of the 317 species. Most of these differences are due to systematic revisions by taxonomic specialists, but a few misidentifications and misspellings are also in the record. We attempted to correct these latter 2 cases where possible. The largest number of differences were among the Bryozoa (41 of 95 species) and the largest proportion of differences among the Porifera (55% of 22 species). Some notable recent changes among the frequently reported species include the sponge *Clathria prolifera*, previously *Microciona prolifera*, the hydroids *Ectopleura crocea*, previously *Tubularia crocea*, and *Obelia dichotoma*, and multiple barnacle species *Amphibalanus* spp. (Tables 1 & 2). Such a large number of changes behooves ecologists to follow the systematic literature closer than has been the case in the past. This is especially true as molecular evidence supports species distinctions among morphologically similar forms. For example, McGovern & Hellberg (2003) reported 2 cryptic species occurring north and south of Cape Hatteras within what we call *Bugula neritina* (Winston & Hayward 2012). As cryptic speciation is predicted to be widespread among colonial invertebrates (Hughes 2005), we should expect more such examples of cryptic species in the future.

In the course of undergoing this survey, it became apparent that some taxa still require more attention. As examples, we note 2 species common in North Carolina which play a key ecological role in the dynamics of fouling communities in the presence of intense grazing by the echinoid *Arbacia punctulata*. One is the conspicuous bright orange sponge *Xestospongia halichondrioides* (misspelled as *X. halichondroides* in Karlson 1978). This sponge is known to occur from the Gulf of Mexico to North Carolina (Wells 1969, Ruppert & Fox 1988). However, *Xestospongia halichondrioides* is not a valid name and the spicules from museum specimens do not match the putative holotype slide for *Petrosia halichondrioides* as suggested by Wells et al. (1960) (see Acknowledgements). On the other hand, the spicules are similar to those of *Pseudospongosorites suberitoides*. It is recommended that fresh material from the southeastern USA be analyzed to resolve this systematic problem.

The second species in need of attention is *Hydractinia* sp., an encrusting hydroid common in the fouling communities of Virginia and North Carolina (McDougall 1943, Calder & Brehmer 1967, Calder 1971, Sutherland & Karlson 1977, Karlson 1978). All of these studies reported this hydroid to be *Hydrac-*

tinia echinata. Based on molecular evidence from specimens collected on shells occupied by hermit crabs, Buss & Yund (1989) identified *H. symbiolongicarpus*, *H. symbiopollicaris*, and *H. polyclina* as part of a sibling species complex of western Atlantic *Hydractinia* that 'are distinct from *H. echinata*'. Cairns et al. (2002) stated that this group of species still needs more molecular analysis to resolve taxonomic problems. Some continue to recognize *H. echinata* in the eastern Atlantic and the Gulf of Mexico (Felder & Camp 2009). Others indicate *H. echinata* occurs in the northwestern Atlantic, but only as far south as Long Island Sound (C. Cunningham pers. comm.). Based on extensive molecular evidence, Miglietta et al. (2009) confirm 'deep divergence' between the *Hydractinia* in the Gulf of Mexico and in the Northwest Atlantic. Yet the debate over species designations in Europe, the Gulf of Mexico, and the Northwest Atlantic still leaves our reports from Virginia and North Carolina fouling communities in question. Given the likelihood of future changes in distributions, the taxonomic status of this temperate warm-water species needs resolution.

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