Temporal shifts of fouling communities in Charleston Harbor with a report of Perna viridis (Mytilidae)

Journal of the North Carolina Academy of Science, 125(2), 2009, pp. 78–84

TEMPORAL SHIFTS OF FOULING COMMUNITIES IN CHARLESTON HARBOR WITH A REPORT OF *PERNA VIRIDIS* (MYTILIDAE)

SAM CRICKENBERGER* and ERIK SOTKA

Grice Marine Laboratory and Department of Biology, College of Charleston, Charleston, SC 29412

* *Present address: Clemson University, 132 Long Hall, Clemson, SC 29634. E-mail: scricke@gmail.com*

Abstract: Since the seminal work on the succession of fouling communities by John Sutherland during the 1970s, little information on fouling communities of the southeastern United States has been published. This lack of information amounts to few opportunities to survey for the presence of non-indigenous species, which can have profound ecological and economic influences. Non-indigenous species are often transported through ship ballast water and other human mediated vectors making large ports ideal locations to monitor for non-indigenous species. In Charleston Harbor, South Carolina, one of the largest ports in the southeastern United States, we monitored settlement onto 10 cm × 10 cm fouling plates every two weeks from February 2006 to February 2007, and compared these settlement patterns with seasonal shifts in fouling communities. *Obelia* spp. hydroids were the dominant recruits during the summer, while the hydroid *Tubularia crocea* dominated the rest of the year. *T. crocea* was also abundant in adult communities along with associated corophid amphipod domiciles. Abundance of the nudibranch *Cratena pilata* and *T. crocea* closely mirrored one another in recruitment and adult communities. The non-indigenous Asian green mussel *Perna viridis*, previously undocumented in South Carolina, was found indicating the need for extended monitoring efforts.

Key Words: fouling community; recruitment; Charleston, SC; *Perna viridis*.

INTRODUCTION

Understanding the role of recruitment on community structure has a long history in marine ecology (Underwood and Fairweather 1989; Young 1990). Recruitment in most marine systems is the addition of new individuals from a dispersive larval stage that was not necessarily produced locally and therefore can have little relationship with local adult abundances (Thorson 1950; Strathmann 1987). Thus, recruitment is crucial to understanding how marine communities fluctuate through time and space. Sessile benthic communities are often used to study the influence of recruitment because of the tractability of manipulating juvenile and adult stages (Young 1987). Along the southeastern United States coastline, a relatively limited number of studies have documented the influences of recruitment on community composition in fouling communities (McDougall 1946; Caine 1987). The exception being a group of studies by John Sutherland (Sutherland and Karlson 1977; Sutherland 1978; Sutherland 1981), that provided seminal contributions to our understanding of alternative stable states and community stability.

These earlier studies are not only valuable in assessing the importance of recruitment in shaping marine communities, but additionally provide base-line data of community structure. Base-line data of community structure and compositional shifts are important in understanding influences of climate change, anthropogenic disturbances and impacts of invasive species. Coastal and estuarine systems are highly susceptible to species invasions because of their highly retentive nature and their proximity to a number of vectors for non-indigenous species (Carlton 2001). Early detection from recruitment studies in conjunction with examination of established adult communities can be useful in documenting early stages in species invasions, which is crucial to successful eradication (Williams and Grosholz 2008). Charleston Harbor presents a particularly vulnerable region to species invasions because of increasing coastal development and a larval supply from a major international shipping port (4th busiest on the east coast of the United States; AAPA 2006). Here, we examined the relationship between recruitment and adult communities in Charleston, SC and also generated a baseline dataset that can be re-evaluated during future studies.

METHODS

Fouling plates were collected bi-weekly from February 2006 to February 2007 at a marina constructed in the summer of 2005 located behind Folly Island, South Carolina (32°38′53″N, 79°57′43″W). Eight plates were collected and replaced every two weeks with the exception of lost plates (10/31/06, 11/14/06, 11/30/06) when only seven were retrieved. All plates were 10 × 10 cm (100 cm^2) panels made from gray PVC plastic and covered with 3M® no-slip tape on one side, which serves to increase rugosity and surface area, and consequently tends to increase the settlement rates of some marine species (Menge 2000). A PVC frame was used to hang plates 0.5 m below the water surface. All plates were oriented downward to reduce algal growth. Plates were returned to Grice Marine Laboratory in plastic containers with ambient seawater. The percent cover of organisms was taken from five 2.3 cm diam., circular and non-overlapping sub-samples from each plate using a dissecting scope. Species not documented in the sub-samples were noted. Identifications were made to the most resolute taxonomic group possible. During June and July plates were preserved in 10 percent formalin/seawater and percent cover was determined in August.

Seasonal changes in the adult fouling community were determined by haphazardly sampling three quadrats per month from March 2006 to February 2007 from established foulers on the marina floating dock. Fouling organisms attached to the black plastic of the dock floats were considered established foulers. A 15 × 15 cm PVC frame (225 cm^2) was used to standardize quadrat sampling. The frame was submerged one inch below the surface of the water and everything within the boundaries was collected. In order to determine site selection of each quadrat wooden planks along the dock were counted (156 total) and a random number was selected for each quadrat, which corresponded to the section of float below the plank. A wet weight was found for each animal within a quadrat and they were counted and identified to the lowest taxonomic group possible. Quadrats were not collected for June or July. All quadrats and plates were collected from the same portion of the floating dock oriented parallel to the shoreline to control for differences in species diversity with distance from shore (Sotka pers. obs.).

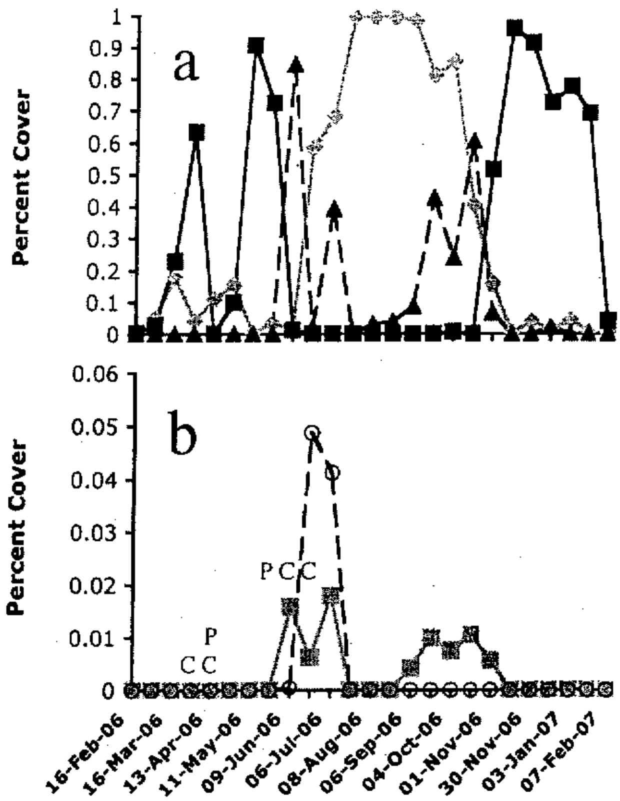

FIG. 1. a) Mean percent cover of the most abundant recruiting organisms for all five sub-samples across all eight plates. Black squares = *T. crocea*, gray diamonds = corophid amphipod domiciles, triangles = *Obelia* spp. b) Mean percent cover of the most commonly occurring recruiting organisms for all five sub-samples across all eight plates. Open circles = colonial tunicate and gray boxes = Balanid spp. spat. Letters represent mobile organisms only found on fouling plates (C = settled crab, P = pycnogonid).

RESULTS

Recruitment

The majority of recruitment was dominated by two hydroids throughout the year. *Tubularia crocea* (L. Agassiz) was the dominant hydroid recruit from November until the end of May. *Obelia* spp. were the predominant hydroid recruits during the rest of the year, but were consistently covered by corophid amphipod domiciles (Fig. 1a). Recruitment from all other species was primarily centered around two peaks with one occurring during the summer and the other in the fall (Fig. 1b). Other foulers found at only a single sampling include actinarian anthozoans, white encrusting bryozoan, and the feather duster worm *Demonax microphthalmus* (Verrill) (Table 1).

The timing of the recruitment of the eloloid nudibranch *Cratena pilata* (Gould) coincided with the peak abundance of the hydroid *T. crocea*: in particular, egg mass presence was greatest prior to the temporal end of *T. crocea* (Fig. 2a). This pattern may indicate a specialized preference for *T. crocea* for oviposition, for food, or for both. Subsequently, *T. crocea* declined in recruitment rate, however the extent that this was because of predation by *C. pilata* or other changes in the biotic or abiotic environment is unknown.

Other mobile species that recruited onto the settlement plates included an unidentified crab juvenile, an unidentified pycnogonid (Fig. 1b) and a Nereis worm (Table 1). Species richness on settlement plates was low (n = 15)..

Adult Residents

Species richness was higher than that of the fouling plates (n = 23).

Adult communities within quadrats were primarily composed of *T. crocea*, corophid amphipod domiciles, *Styela* spp. and a colonial tunicate sp. (Fig. 3a). Other adults that were commonly found include barnacles, sponges and the bivalve *Ostrea equestris* (Say) (Fig. 3b). Barnacles included *Amphibalanus eburneus* (Gould),

Table 1. Mean percent cover (P = plate) and percent of total biomass (Q = quadrat) for less abundant organisms and organisms placed within groups. A plus symbol indicates the presence of an organism on a plate that was not documented on a plate sub-sample. If a 'P' or 'Q' column is absent for a specific organism then the data was not collected. Barnacle and sponge recruitment is noted by a single plate column.

Date		Amphipods	Corophid Amphipods	Caprellid Amphipods	Actinarian Anemones		*Amphi-balanus* spp. spat	*Balanus trigonus*	*Amphi-balanus eburneus*	*Amphi-balanus amphitrite*	*Amphibalanus venustus*	*Nereis succineal falsa*		Sponge Recruits
P	Q	P	P	P	P	Q	P	Q	Q	Q	Q	P	Q	P
2 February 2006	-	0.0415	–	–	0	–	0	–	–	–	–	0	–	0
2 March 2006	3 March 2006	0.1065	–	–	0	0.0160	0	0.0000	0.1613	0	0	0	0.0012	0
16 March 2006	17 March 2006	0.1790	–	–	0	0.0118	0	0.0009	0.1485	0	0	0	0.0007	0
30 March 2006	-	0.1378	0.0875	0.1625	0	–	0	–	–	–	–	0	–	0
13 April 2006	14 April 2006	0.4105	–	–	0	0.0036	0	0.0060	0.1391	0	0	0	0.0014	0
27 April 2006	2 May 2006	0.5578	0.2856	0.2621	0	0.0044	0	0.0016	0.1050	0	0	0	0	0
11 May 2006	-	0.0200	0.0145	0.0050	0	–	0	–	–	–	–	0	–	0
25 May 2006	-	0.0555	0.0340	0.0210	0	–	0	–	–	–	–	0	–	0
9 June 2006	-	0.0256	0.0154	0.0077	+	–	0.0159	–	–	–	–	0	–	0
23 June 2006	-	0.0475	0.0325	0.0163	0	–	0.0063	–	–	–	–	+	–	0
6 July 2006	-	0.0713	0.0675	0.0038	0	–	0.0180	–	–	–	–	0	–	0
20 July 2006	-	0.0398	0.0385	0.0013	0	–	0	–	–	–	–	0	–	0
8 August 2006	9 August 2006	0.8620	0.8470	0	0	0	0	0.0052	0.0314	0	0	0	0.0005	0
23 August 06	-	0.7563	0.7563	0	0	–	0	–	–	–	–	0	–	0
6 September 2006	7 September 2006	0.3557	0.3537	0.0020	0	0	0.0043	0.0050	0.0066	0	0	0	0.0002	0
20 September 2006	-	0.3050	0.2980	0.0195	0	–	0.0100	–	–	–	–	0	–	0
4 October 2006	6 October 2006	0.5025	0.4713	0.0013	0	0	0.0075	0.0002	0.0459	0	0	0	0.0002	0
18 October 2006	-	0.3461	0.3338	0.0054	0	–	0.0105	–	–	–	–	0	–	0
1 November 2006	2 November 2006	0.0329	0.0229	0	0	0	0.0057	0.0067	0.0570	0	0	0	0.0007	0
15 November 2006	-	0.0043	0.0023	0	0	–	0	–	–	–	–	0	–	0
30 November 2006	1 December 2006	0.0029	0.0000	0	0	0	0	0.0053	0.0195	0	0	0	0.0028	0
14 December 2006	-	0.0038	0.0026	0	0	–	0	–	–	–	–	0	–	0
3 January 2007	4 January 2007	0.0319	0.0131	0.0153	0	0	0	0	0.0702	0	0.0029	0	0.0017	0
24 January 2007	-	0.1413	0.0138	0.1275	0	–	0	–	–	–	–	0	–	0
7 February 2007	8 February 2007	0.0115	0.0085	0.0031	0	0	0	0	0.0232	0.0004	0.0029	0	0.0017	0

Table 1. Extended.

Mycale sp. A	*Halichondria bowerbanki*	*Haliclona loosanoffi*	Yellow/Gray Sponge	*Amphitrite ornata*		*Demonax microphthalmus*		*Brachidontes exustus*		*Ostrea equestris*		Flatworm		White Encrusting Bryozoan	
Q	Q	Q	Q	P	Q	P	Q	P	Q	P	Q	P	Q	P	Q
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0.0027	0	0	0	0	0	0	0	0	0	0
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0	0	0	0	0	0.0015	0	0.0005	0	0.0081	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.0019	0	0	0	0	0	0
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
–	–	–	–	0	–	0	–	0.0010	–	0	–	0	–	+	–
–	–	–	–	0	–	0	–	0.0005	–	0	–	0	–	0	–
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0.0002	0	0	0.1806	0	0	+	0	0	0.0005	0	0	0	0	0	0
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0	0	0	0	0	0	0	0	0	0	0	0.0139	0	0	0	0
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0.0037	0.0000	0	0.0000	0	0	0	0	0	0	0	0.0194	0	0	0	0
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0.0166	0.0142	0.0032	0.0000	0	0	0	0	0	0	0	0.0114	0	0	0	0
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0.0069	0.0029	0	0.0000	0	0	0	0	0.0014	0	0	0.0121	0	0	0	0
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0.0018	0.0000	0	0.0000	0	0	0	0	0	0.0101	0	0.0126	0	0.0008	0	0
–	–	–	–	0	–	0	–	0	–	0	–	0	–	0	–
0.0015	0.0000	0	0.0730	0	0.0009	0	0	0	0.0006	0	0.0429	0	0.0008	0	0

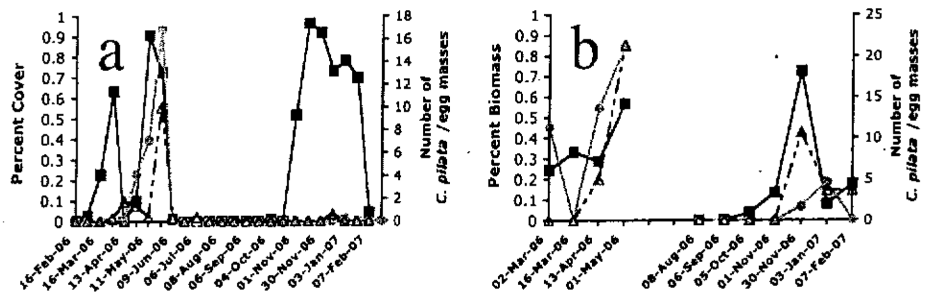

FIG. 2. Relationship between *C. pilata* and *T. crocea*. a) Mean percent cover of recruiting organisms for all five sub-samples across all eight plates and mean number of *C. pilata* and egg masses. b) Mean percent biomass for all three quadrats in adult communities and mean number of *C. pilata* and egg masses. Black squares = *T. crocea*, open triangles = *C. pilata* and gray circles = *C. pilata* egg masses.

Balanus trigonus (Darwin), *A. venustus* (Darwin) and *A. amphitrite* (Darwin) in decreasing order of abundance. Sponges included an unidentified yellow/gray sponge sp., *Halichondria bowerbanki* (Burton), *Mycale* sp. A (as in Ruppert and Fox 1985) and *Haliclona loosanoffi* (Grant) in decreasing order of abundance. The remainder of the community included unidentified actinarian anthozoans, the bivalve *Brachidontes exustus* (Linnaeus), the polychaete *Nereis succinealfalsa* (Leukart/Qautrefages), the polychaete *Amphitrite ornata* (Verrill), an unidentified flatworm and the polychaete *Demonax microphthalmus* in decreasing order of percent of total biomass.

The cyclic abundances noted on recruitment plates for *T. crocea* and *C. pilata* were also evident in resident communities (Fig. 2b). We observed heteronerid swarms (unidentified species) on 28 April 2006 although no Nereid worms were found on the following collecting date. A second heteronerid swarm was observed on 31 October 2006. Percent biomass of Nereis worms increased until the end of November and remained at similar levels through February (Table 1).

Asian Green Mussel

During this study an individual Asian green mussel, *P. viridis*, was found attached to the PVC structure holding the fouling plates in August 2006. This is the first documentation of a live *P. viridis* in South Carolina. Previously empty shells had been found on seawater intake pipes at the South Carolina Department of Natural Resources on Fort Johnson (David Knott pers. comm.), and since this documentation other live individuals and clusters of mussels have been found in South Carolina waters (David Knott pers. comm.; Barker et al. 2007).

DISCUSSION

Among some of the most common species (barnacles, colonial tunicate sp., *Obelia* spp., *T. crocea*, amphipod spp.) and a less common species (*B. exustus*), recruitment broadly mirrored adult composition (Figs. 1, 3; Table 1). Given that most of these species are generally thought to have relatively restricted larval dispersal capability, it is likely that most recruits were produced from adults that were relatively close (meters). Alternatively, the bivalve (*B. exustus*) and the Balanid barnacles generally have a larval dispersal period of days to weeks, suggesting that their sources were likely much more distant fouled substrata.

No relationship between recruits and adults was apparent among other less common foulers (actinaria

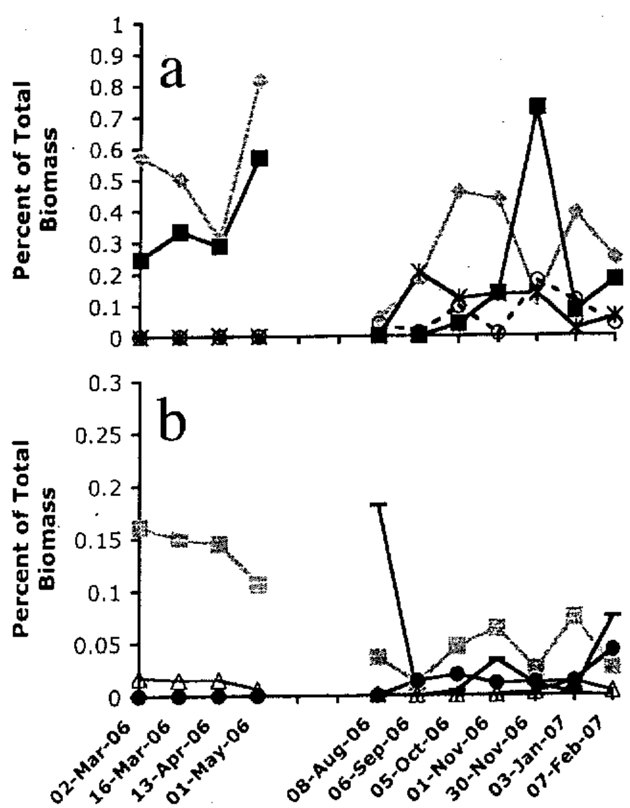

FIG. 3. a) Mean percent biomass for all three quadrats of the most abundant organisms of adult communities. Black squares = *T. crocea*, gray diamonds = corophid mud domiciles, asterisks = *Styela* spp., open circles = colonial tunicates. b) Mean percent biomass for all three quadrats of all other organisms present in adult communities. Gray boxes = Balanid spp., dashes = sponge spp., black circles = *O. equestris* and open triangles = sum of remaining species (see results).

spp., *D. microphthalmus*) (Table 1). Some common (sponges, *Styela* spp., *O. equestris*) and less common species (*A. ornata*) were never found on fouling plates and only occurred in quadrat sampling (Figs. 1, 2). White encrusting bryozoan was the only species found only on the fouling plates and not in quadrats (Table 1). The disparity between recruitment and some adult foulers may be the result of the difference in settlement substrate or low statistical power associated with low recruitment. No-slip tape used to cover the fouling plates is known to provide suitable substrate for some foulers, such as barnacles (Jarrett and Pechenik 1997; Menge 2000), but it is unclear whether other foulers are equally likely to settle.

Most mobile species (*Nereis* spp., amphipod spp., *C. pilata*, crabs) were present on both fouling plates and in quadrats. Pycnogonids were only found on fouling plates; however, we may have missed these small individuals because quadrats were not examined with a microscope. Crab species typically left areas during quadrat sampling and were therefore not recorded. Flatworms were only found in quadrats. The single *Nereis* sp. found on a fouling plate was a juvenile. *C. pilata* seemed to be mobile enough to travel between adult communities and plates and no size differences were observed. Amphipods and flatworms are known to migrate as adults and *N. succinea* are known to recruit at both larval and adult stages (Santos and Simon, 1980). It is difficult to draw meaningful comparisons of the present data with the Sutherland studies (Sutherland and Karlson 1977; Sutherland 1978; Sutherland 1981) because 1) the estuaries of Charleston, SC and Beaufort, NC differ profoundly in species composition and abiotic traits (salinity, water clarity, temperature), 2) the studies used different fouling substrata (PVC vs. wood) 3) were performed approximately 30 yr apart, and 4) no manipulations were made as they were in the Sutherland studies.

Asian Green Mussel

The previously undocumented species *Perna viridis* (Linnaeus) is indigenous to the Indo-Pacific from the Persian Gulf to the South China Sea. The first western Atlantic record of the green mussel was from the Caribbean island of Trinidad in 1990 (Agard et al. 1992). It was subsequently documented along the nearby coast of Venezuela in 1993 (Rylander et al. 1996) and in the United States, first documented in Tampa Bay, Florida, during the summer of 1999. In October of 2003 single specimens were found off of Georgia (Baker et al. 2007).

Since the first documentation of a live *P. viridis* during the course of this study, other single specimens have been found along the coast of South Carolina (see Baker et al. 2007 for review of documented locations). Based on water temperatures within the native range of *P. viridis* (11–32°C) it is unlikely that *P. viridis* will become established in Charleston, SC because of low winter temperatures. However, over the past 30 yr (1975–2007) mean winter temperatures at the docks at Grice Marine Laboratory have risen 3°C (9.5°C to 12.5°C; S.C. Department of Natural Resources, unpublished data) and similar warming trends have been documented in other estuarine waters of South Carolina (Allen et al. 2008). Given that Charleston, SC receives much of its ship traffic from tropical foreign ports (Ruiz et al. 2001) and the northward flow of the Gulf Stream, *P. viridis* in addition to other tropical species may become permanently established if this warming trend continues.

CONCLUSIONS

Little information exists on fouling communities in the southeastern United States. Information on density and recruitment can provide valuable information for future understanding of the effects of anthropogenic influences and provide current information on invasive species. As invasive species are becoming more common in coastal and estuarine habitats (Ruiz et al. 1997) monitoring efforts are crucial to gaining a fuller understanding of the impacts and dynamics of invasive species, as well as their interactions with native communities.

Acknowledgments: Funding for this research was provided by a College of Charleston Academic Year Research Award mini-grant. S.C. was supported by the NOAA Hollings Scholarship Program during this study. We would like to thank Doug Booth for allowing access to his marina, Dave Knott for his help with identification, Bill Roumillet for access to temperature data, Brently Wiles for his help in collecting, and two anonymous reviewers for helpful comments.

LITERATURE CITED

AMERICAN ASSOCIATION OF PORT AUTHORITIES (AAPA). Port Industry Statistics. Retrived from http://www.aapa-ports.org on 25 July 2008.

AGARD, J., R. KISHORE, AND B. BAYNE. 1992. *Perna viridis* (Linneaus 1758): first record of the Indo-Pacific green mussel (Mollusca: Bivalvia) in the Caribbean. Caribbean Mar. Studies 3:59–60.

ALLEN, D. M., V. OGBURN-MATTHEWS, T. BUCK, AND E. M. SMITH. 2008. Mesozooplankton responses to climate change and variability in a Southeastern U.S. estuary (1981–2003). J. Coastal Res. 55:95–110.

BAKER, P., J. S. FAJANS, W. S. ARNOLD, D. A. INGRAO, D. C. MARELLI, AND S. M. BAKER. 2007. Range and dispersal of a tropical marine invader, the asian green mussel, *Perna viridis*, in subtropical waters of the Southeastern United States. J. Shellfish Res. 26(2):345–355.

CAINE, E. A. 1987. Potential effect of floating dock communities on a South Carolina estuary. J. Exp. Mar. Biol. Ecol. 108:83–91.

CARLTON, J. T. 2001. Introduced species in US coastal waters: environmental impacts and management priorities. Arlington, Virginia: Pews Oceans Commission Report. 28 pp.

JARRETT, J. N., AND J. A. PECHENIK. 1997. Temporal variation in cyprid quality and juvenile growth capacity for an intertidal barnacle. Ecology 78:1262–1265.

McDOUGALL, K. D. 1943. Sessile marine invertebrates of Beaufort, North Carolina. A study of settlement, growth, and seasonal fluctuations among pile-dwelling organisms. Ecol. Monogr. 13:323–374.

MENGE, B. A. 2000. Recruitment vs. postrecruitment processes as determinates of barnacle population abundance. Ecol. Monogr. 70(2):265–288.

RUIZ, G. M., J. T. CARLTON, E. D. GROSHOLZ, AND A. H. HINES. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. Inter. Comp. Biol. 37(6):621–632.

RUIZ, G. M., A. W. MILLER, K. LION, B. STEVENS, A. AMWINE, COLLINETTI, AND E. WELLS. 2001. Status and trends of ballast water management in the United States. First Biennial Report of the Nat. Ballast Inform. Clearinghouse. 44 pp.

RYLANDER, K., J. PEREZ, AND J. A. GOMEZ. 1996. Status of the green mussel, Perna viridis (Linneaus 1758) (Mollusca: Mytilidae), in north-eastern Venezuela. Caribbean Mar. Studies 5:86–87.

SANTOS, S. L., AND SIMON, J. L. 1980. Marine soft-bottom community establishment following annual defaunation: larval or adulat recruitment? Mar. Ecol. Prog. Ser. 2:235–241.

STRATHMANN, M. F. 1987. Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press, Seattle. 670 pp.

SUTHERLAND, J. P. 1978. Functional Roles of Schizoporella and Styela in the Fouling Community at Beaufort, North Carolina. Ecology 59(2):257–264.

SUTHERLAND, J. P. 1981. The fouling community at Beaufort, North Carolina: a study in stability. Am. Nat. 118(4):499–519.

SUTHERLAND, J. P., AND R. H. KARLSON. 1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecol. Monogr. 47(4):425–446.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25(1):1–45.

UNDERWOOD, A. J., AND P. G. FAIRWEATHER. 1989. Supply-side ecology and benthic marine assemblages. Trends Ecol. Evol. 4(1):16–20.

WILLIAMS, S. L., AND E. D. GROSHOLZ. 2008. The invasive species challenge in estuaries and coastal environments: marrying management and science. Estuaries and Coasts 31(3):3–20.

YOUNG, C. M. 1987. Supply-side ecology. Science 235:415–416.

YOUNG, C. M. 1990. Larval ecology of marine invertebrates: a sesquicentennial history. Ophelia 32(1–2):1–45.

Received 8 September 2008