

Long-term epifaunal community assessment in estuarine waters of New Jersey

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Article begins on next page

1 **LONG-TERM EPIFAUNAL COMMUNITY ASSESSMENT IN ESTUARINE WATERS**
2 **OF NEW JERSEY**

3
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13 **Abstract:** *Epifaunal communities in estuarine waters of Great Bay and Barnegat Bay, New*
14 *Jersey were investigated to assess differences among time periods, soak durations, locations and*
15 *plate surfaces over a ten-year period of time. Polyvinyl chloride settlement plates were deployed*
16 *at five sampling stations in Great Bay and Barnegat Bay, New Jersey with two collections*
17 *annually from 2006 to 2015. Community composition, taxa richness, and plate percent cover*
18 *were examined among plate surfaces, locations, years, and soak durations. Analysis of the 17*
19 *present taxa revealed variable composition of the epifaunal community, with the cheilostome*
20 *bryozoan Membranipora sp. and, secondarily, the red alga Polysiphonia sp. dominating. In*
21 *years when plate percent cover was low, the golden star tunicate Botryllus schlosseri dominated.*
22 *Analysis of response variables across all taxa revealed that taxa richness and plate percent*
23 *cover were higher on the top surfaces of the plates in most years. Taxa richness and plate*
24 *percent cover were also higher with longer soak durations. Percent cover varied by location in*
25 *the study area for select individual taxa, as did plate surface cover in select years. No taxa*
26 *exhibited significant differences in percent cover based on soak duration. Multivariate analyses*
27 *indicated that distinct epifaunal communities developed in different: a) geographic locations, b)*
28 *years, and c) plate surfaces for some years. Comparisons with historic data show that about half*
29 *of the taxa common across all time periods were introduced. Almost all of the taxa present*
30 *historically, but not present currently, were native. One of the two new taxa not present*
31 *historically was introduced. This study furthers our understanding of the spatial and temporal*
32 *aspects of the epifaunal community in New Jersey over a protracted period of time and adds to*
33 *the national and global databases of case studies on epifaunal recruitment and settlement.*

34
35 **Keywords:** Epifaunal community; temporal; spatial; Great Bay; Barnegat Bay; long term
36

37 **INTRODUCTION**

38
39 Epifaunal community composition has been the subject of intense research over the years
40 (Loveland and Shafto 1984, Railkin 2004) and thus the literature on these communities on the
41 east coast of the United States is quite extensive. As such, we know that the flora and fauna
42 comprising eastern United States epifaunal communities consist of a diverse assemblage of
43 species (Woods Hole Oceanographic Institution 1952, Loveland and Shafto 1984) including
44 algae, barnacles, bryozoans, hydrozoans, molluscs, polychaetes, sponges and tunicates, and that
45 these are the principle components in most communities.
46

47 The composition and abundance of adult epifaunal organisms are often highly variable in
48 space and time (Raimondi 1990, Railkin 2004, Holthuis et al. 2015). In settling plate studies,
49 Raimondi (1990), Railkin (2004), and Holthuis et al. (2015) noted a number of factors that
50 contribute to variability in settlement including the number of competent propagules, the number
51 of settlers at a site, the type of settlement surface, and the occurrence of conspecifics.
52 Recruitment in turn varies with settlement or post-settlement mortality, as well as with
53 immigration and emigration of mobile forms. Post-settlement processes, notably competition
54 and predation, can have far greater effects on the population dynamics of the fouling community
55 than settlement variability (Menge 1991). Due to all these factors, spatial and temporal variation
56 of settling plate colonization remains a major focus of epifaunal community studies.

57
58 Much work has historically been done in the Barnegat Bay estuarine system in New
59 Jersey to investigate epifaunal community composition and understand spatial and temporal
60 variation. Young and Frame (1976) and Evans (1977) studied the effects of thermal discharges
61 on epibenthic organisms in Barnegat Bay. Shafto (1974) collected monthly data on the structure
62 of communities from October 1971 to October 1972. Hoagland et al. (1978), Hoagland and
63 Crockett (1979a, 1979b), Hoagland and Turner (1980), and Hoagland (1982) examined the
64 dynamics of epifaunal communities throughout the bay and its tributaries. Loveland and Shafto
65 (1984) compiled information from these sources to create a set of baseline data on historic
66 abundance and composition of the epifaunal communities in Barnegat Bay.

67
68 No known recent studies have been conducted in the estuarine waters of the New Jersey
69 coast to assess spatial and temporal variation in the epifaunal community. We aimed to address
70 this gap by assessing epifaunal communities in estuarine waters of Great Bay and Barnegat Bay,
71 New Jersey over an extended period. Specifically, we assessed taxa composition, taxa richness,
72 and plate percent cover of the epifaunal community at five estuarine locations across ten
73 consecutive years. The goals of this study were to evaluate differences among locations, plate
74 surfaces (top vs. bottom), soak durations, and annual changes over time. We then compared
75 results from our study with historic community composition data (Loveland and Shafto 1984).
76 The importance of long-term studies at this scale and with these characteristics has been noted
77 (Lucy 2006, Madin et al. 2009). This contribution is important as it evaluates spatial and
78 temporal aspects of the epifaunal community in New Jersey over a protracted period of time,
79 places our results in historical context, and adds to the national and global databases of case
80 studies on epifaunal recruitment and settlement.

81 82 **METHODS**

83 84 *Study area*

85 This study consisted of five sampling stations in the Great Bay and Barnegat Bay estuarine
86 systems in New Jersey during the summer and fall seasons (Figure 1). These sites were
87 originally chosen to document fouling of dataloggers used in the bays for monitoring water
88 quality conditions in the Jacques Cousteau National Estuarine Research Reserve (JCNERR)
89 program.

90
91 Great Bay is a circular-shaped, coastal plain estuary in southern New Jersey having a
92 surface area of 41.6 km² (Figure 1). All of the waters of Great Bay are within the boundaries of

93 the JCNERR. Water temperature ranges from ~0-30°C, and salinity from ~10-32 ppt (Kennish et
94 al. 2004). It is a well-mixed system characterized by strong tidal currents in the lower bay with
95 peak velocities exceeding 2 m s⁻¹.

96
97 Barnegat Bay is a eutrophic coastal lagoon that forms a long, narrow, and irregular tidal
98 basin extending north-south for nearly 70 km along the central New Jersey coastline (Figure 1)
99 (Fertig et al. 2014). Little Egg Harbor, in the southern part of Barnegat Bay, is within the
100 JCNERR. Ranging from 2 to 6 km in width and 1 to 6 m in depth, Barnegat Bay has a volume of
101 ~3.5 x 10⁸ m³ and a wet surface area of ~280 km² (Kennish and Lutz 1984). Water temperature
102 ranges from -1.5-30°C, and salinity from ~10-32 ppt. Characterized by semidiurnal tides with a
103 tidal range of <0.5-1.5 m, the estuary is well-mixed by winds and currents. Current velocities are
104 typically <0.5-1.5 m s⁻¹. Both Great Bay and Barnegat Bay support diverse benthic invertebrate
105 communities (Kennish 2001, Kennish et al. 2004).

106 107 *Settlement plates*

108 Samples of the epifaunal community were collected annually over a ten-year period (2006-2015)
109 using PVC settlement plates attached to metal racks. PVC settlement plates measuring 25.4 cm
110 x 25.4 cm were used from 2006 to 2013; smaller PVC settlement plates measuring 20.3 cm x
111 20.3 cm were used in 2014 and 2015. No significant differences were found in means of plate
112 percent cover (F = 0.13, p = 0.72) or richness (F = 1.63, p = 0.20) when comparing results from
113 the two different plate sizes, thus we analyzed the data from the two different sized settlement
114 plates together. The plates were attached to the four corners of a metal frame measuring 86.4 cm
115 x 86.4 cm x 45.7 cm and submerged at the sampling stations such that each plate was positioned
116 horizontally in the water column ~0.5 m off the bottom (Figure 2).

117
118 The settlement plates were deployed once and collected twice each year. The set of four
119 plates was submerged in the spring (May or early June). Two of the four plates were removed in
120 the summer (July, August, or September). The remaining two plates were removed in the fall
121 (October or November). Thus, we have two soak durations: short (2-4 months) and long (5-6
122 months). Panels were removed from opposite corners of the frame on each sampling date so as
123 to not bias one side of the frame or the other (e.g., in a case where one side of the frame may
124 have been closer to a bulkhead or partially shaded by a dock or other overhead structure). All
125 recovered plates were immediately placed in heavy duty zip-lock bags containing ethanol and
126 labels specifying the station ID, date, and plate number. The plates were stored in ice within a
127 cooler for transport back to the Rutgers University Marine Field Station (RUMFS) in Tuckerton,
128 New Jersey for analysis. At RUMFS, the zip-locks containing plates were placed in 38.5-L
129 drums of ethanol for storage prior to analysis. The settlement plates were subsequently analyzed
130 in the laboratory by visual observation, with all epifaunal organisms identified and their percent
131 areal cover recorded. The plates were carefully inspected for alteration and damage.

132
133 Not all stations were sampled throughout the ten-year period because of unusual events
134 (e.g., damage to docks and other structures during coastal storms) and the loss of access to
135 marine sampling stations. For example, in October 2012, docks at the Green Street and
136 Dutchman's stations were destroyed by Superstorm Sandy. In 2014, sampling at the Dutchman's
137 station was reactivated after dock repairs were completed. Sampling at the Green Street station
138 was not reactivated because of severe structural damage.

139

140 **Data analysis**

141 We analyzed relationships between response variables (taxa richness and plate percent cover)
142 and explanatory variables (spatial and temporal) both across all taxa and for each taxon
143 individually (only percent cover was assessed individually). We used generalized linear mixed
144 models (PROC GLIMMIX in SAS version 9.4, SAS Institute, Cary, NC) with a Bonferroni
145 correction to examine the effects of the explanatory variables on each of the untransformed
146 response variables, both across taxa and for each of the taxa individually. The design for the
147 models included VC as the covariance structure. Year, soak duration, plate surface, and location
148 were included as fixed effects and plate number was used as a random factor with intercept and
149 slope over year, and slope over plate surface as random effects. The richness model also
150 included slope over soak duration as a random effect. Individual taxa models also included slope
151 over location, year, soak duration, and plate number as random effects. For all models, we
152 included interaction effects for year and plate surface. No significant soak duration and plate
153 surface interactions were found across all taxa or for individual taxa; thus, we removed this
154 interaction effect from the study models. Post hoc Tukey-Kramer tests were performed for
155 multiple comparisons in all models. Denominator degrees of freedom were computed using the
156 KENWARDROGER option.

157

158 We tested for spatial autocorrelation separately for the response variables and found
159 none; thus, we did not include this in the models. The missing and imbalanced data interfered
160 with the testing for temporal autocorrelation (i.e., repeated measures). Using a CS covariance
161 structure, we found low covariates for plate percent cover (0.01) and richness (0.2). Thus, we
162 concluded that either there is little autocorrelation or, if it exists, we do not have the data to test
163 for it. Thus, we did not include this form of autocorrelation in any of the models.

164

165 The Bonferroni correction compensates for increased Type I error by testing each
166 individual hypothesis at a significance level of α/m , where $\alpha = 0.05$ and m is the number of
167 hypotheses. In the case of this study, $m = 2$, therefore significant differences were determined in
168 this study at $\alpha = 0.025$ after applying the Bonferroni correction. Individual taxa models use
169 $\alpha = 0.05$. Taxa with few data points often could not compute; these were noted in the results in
170 Table 1.

171

172 We used non-metric multidimensional scaling (NMDS) to show variation within or
173 among locations and plate surfaces and across years based on percent cover of epifaunal taxa.
174 With plot as the sampling unit, we ran NMDS analyses (BiodiversityR library, R version 3.11)
175 using Sorensen (Bray-Curtis) dissimilarity matrices of untransformed percent cover interval data
176 for all taxa occurring in more than one plot. Short and long soak durations were analyzed
177 separately. One taxa, *Gracilaria* sp., proved to be an outlier in the long soak duration ordination
178 and its presence made it hard to discern the patterns of the rest of the taxa. Thus, the long soak
179 duration figures were redrawn after *Gracilaria* sp. was removed from the ordination. We then
180 analyzed differences in taxa composition among factors (locations, plate surfaces, and years)
181 using repeated measures nonparametric multivariate analysis of variance, with plot nested within
182 location. The repeated measures analysis employed Adonis (Vegan library, R version 3.11) to
183 test differences over time and interactions with time (i.e., the repeated measure), and
184 nested.npmanova (BiodiversityR library, R version 3.11) to test the main effect of location or

185 plate surface. This analysis also used Sorensen (Bray-Curtis) dissimilarity matrices of
186 untransformed percent cover data, through 999 permutations. Because the repeated measures
187 analysis identified interactions between plate surface and year, we also used Adonis to test the
188 effect of plate surface for years individually.

189
190 Composition of the epifaunal community was compared during three time periods: 1971-
191 1972, 1982, and 2006-2015 (current study) to look at change and constancy of the community
192 over time in Barnegat Bay and its surroundings (Loveland and Shafto 1984). Study design
193 varied somewhat in terms of location, sample abundance, and substrate across the three periods.
194 Samples from October 1971 - October 1972 were collected monthly at nine sites in Barnegat Bay
195 from wooden panels (Shafto 1974). Samples from June - August 1982 were collected from
196 nineteen sites in Barnegat Bay and its tributaries using wooden panels, aluminum racks, and
197 cement blocks (Hoagland 1982). Samples in our current study were collected at five sites in
198 Great Bay and Barnegat Bay using PVC settlement plates.

200 RESULTS

201 *Patterns in current taxa abundance*

203 Seventeen taxa were found on the sampling plates between 2006 and 2015. The dominant sessile
204 taxa based on the frequency sampled (i.e., number of times they were found in 264 samples,
205 noted in parentheses) were: the cheilostome bryozoan *Membranipora* sp. (166), tube-building
206 serpulid polychaete *Hydroides dianthus* (140), acorn barnacle *Balanus* sp. (116), unidentified
207 macroalgae (94), golden star tunicate *Botryllus schlosseri* (71), sea grape tunicate *Molgula*
208 *manhattensis* (57), and red alga *Polysiphonia* sp. (50) (Table 1). The remaining taxa were found
209 in fewer than 15% of the samples and included such organisms as the creeping bryozoan
210 *Bowerbankia gracilis* (39), the slipper limpet *Crepidula fornicata* (33), sponges (27), *Gracilaria*
211 sp. (11), orange sheath tunicate *Botrylloides violaceus* (10), sea anemone (10), gastropods (4),
212 hydrozoans (3), polychaete worms (1), and *Crassostrea virginica* (1) (Table 1). Based on
213 information from the National Exotic Marine and Estuarine Species Information System
214 (NEMESIS) database (Fofonoff et al. 2018), the most abundant taxa found in our samples
215 (*Membranipora* sp.) was introduced to North Atlantic waters. In addition, some *Balanus*
216 species, *Polysiphonia* sp., some hydrozoans, *Gracilaria* sp., *B. schlosseri* and *B. violaceus* were
217 also introduced. Thus, non-native taxa made a considerable contribution to richness and plate
218 percent cover in our samples.

220 *Spatial and temporal variation across taxa*

221 Results from the generalized linear mixed-effects model analyses, with taxa richness and plate
222 percent cover as response variables, showed that the variable effects of soak duration were
223 significant across all taxa (Table 1). Richness was significantly higher with longer soak
224 durations (3.87 ± 0.22) than shorter (3.09 ± 0.18), and plate percent cover was also significantly
225 higher with longer soak durations ($78.10 \pm 4.35\%$) compared with shorter ($64.13 \pm 3.24\%$) (Table
226 2).

227
228 Spatially, richness was highest at First Bridge Marina (4.16 ± 0.49) and lowest at
229 Dutchman's (2.72 ± 0.29), and plate percent cover was also highest at First Bridge Marina
230 ($76.98 \pm 10.09\%$) and lowest at Dutchman's ($57.19 \pm 5.05\%$) (Table 2). Results for location were

231 not significant. We found significant differences in both taxa richness and plate percent cover
232 among the interaction of plate surfaces and years with taxa richness and plate percent cover
233 higher on the top surfaces of the plates in all years except 2008 and 2010, with the additional
234 exception of 2006 for just richness, and 2013 for just plate percent cover.

235

236 ***Spatial and temporal variation for individual taxa***

237 No taxa exhibited significant differences in average percent cover based on soak duration (Table
238 1). *Gracilaria* sp., *Molgula manhattensis*, and *Polysiphonia* sp. exhibited significant differences
239 in average percent cover of plate surface (Table 1), with higher values on the top surfaces for all
240 taxa except *Gracilaria* sp. Several taxa varied significantly in average percent cover by location.
241 These are: *Balanus* sp. (highest at Dutchman's), *H. dianthus* (Dutchman's), *Membranipora* sp.
242 (RUMFS), *Polysiphonia* sp. (Seaside Park Yacht Club), and unidentified macroalgae (Green
243 Street).

244

245 *Balanus* sp., *B. violaceus*, *B. schlosseri*, *C. fornicata*, *H. dianthus*, *Membranipora* sp.,
246 and unidentified macroalgae exhibited significant differences in average percent cover of plate
247 surfaces among years. *Balanus* sp. had higher average percent cover values on the bottoms of
248 plates for all years except 2006, 2007, 2008, and 2011. *B. schlosseri* had higher average percent
249 cover values on the tops of plates for all years except 2007 and 2008. *C. fornicata* had higher
250 average percent cover values on the tops of plates for all years except 2008, 2009, 2011, 2012,
251 and 2014. *H. dianthus* had higher average percent cover values on the bottoms of plates for all
252 years except 2006, 2007, and 2015. *Membranipora* sp. had higher average percent cover values
253 on the tops of plates for all years except 2008, 2009, and 2010. Unidentified macroalgae had
254 higher average percent cover values on the bottoms of plates for all years except 2006, 2009,
255 2010, and 2013. *B. violaceus* had higher average percent cover on the top surfaces of the plates
256 for all years on record.

257

258 ***Spatial and temporal variation in community composition***

259 Distinct epifaunal assemblages developed in different geographic locations ($F=4.08$, $p=0.02$)
260 during the short soak durations of 2006-2015, driven in large part by the First Bridge Marina site
261 as shown in the NMDS analysis (Figure 3). Additionally, there exists an effect of year ($F=6.00$,
262 $p=0.001$; Figure 4) in structuring epifaunal communities. The main effect of plate surface
263 interacted with year ($F=1.96$, $p=0.002$), indicating distinct assemblages were present among the
264 plate surfaces in some years for short soak durations. For individual years, the epifaunal
265 community composition differed among plate surfaces during the short soak duration of 2015
266 ($F=5.28$, $p=0.002$) and more weakly in the years 2007 ($F=4.61$, $p=0.055$) and 2012 ($F=6.14$,
267 $p=0.078$).

268

269 Similar results were found for long soak durations for years 2006, 2007, 2008, 2012, and
270 2014 (missing data restricted the dataset to only these years). Distinct assemblages developed at
271 different geographic locations ($F=10.39$, $p=0.010$) during the long soak durations. Additionally,
272 there exists a significant effect of year ($F=4.28$, $p=0.001$) in structuring epifaunal communities.
273 The main effect of plate surface interacted with year ($F=1.76$, $p=0.025$), indicating distinct
274 assemblages were present among the plate surfaces in some years for long soak durations. For
275 individual years, the epifaunal community composition differed among plate surfaces during the
276 long soak durations of 2007 ($F=7.78$, $p=0.008$) and 2012 ($F=4.95$, $p=0.016$).

277
278 For short soak duration ordinations, *Gracilaria* sp. was well separated from the other
279 clustered taxa indicating a clear dissimilarity (Figures 3 and 4). Additionally, for short soak
280 durations, *Polysiphonia* sp. was also well separated from both *Gracilaria* sp. and the remaining
281 taxa (Figures 3 and 4). For long soak duration ordinations *Gracilaria* sp. was so well separated
282 from the other clustered taxa that we redrew the figures after removing *Gracilaria* sp from the
283 ordination (Figures 5 and 6). In the redrawn figures, *Polysiphonia* sp. was well separated from
284 the clustered taxa, as were *C. fornicata*, *B. schlosseri*, and sponges.

285
286 ***Community composition change over time***
287 Thirty-eight taxa were recorded from samples taken in 1971-72, 47 from 1982, and seventeen
288 from 2006-2015 (Table 3). Six specific taxa were common across all three time periods:
289 *Balanus* sp., *B. schlosseri*, *B. gracilis*, *Gracilaria* sp., *H. dianthus*, and *M. manhattensis*. Current
290 samples included the broad categories of gastropods, hydrozoans, polychaete worms, sea
291 anemones, sponges, and unidentified macroalgae which may also overlap with records in the
292 more specific historical samples. Of the six specific taxa common across all time periods, half
293 were introduced (some *Balanus* sp., *B. schlosseri*, *Gracilaria* sp.) (Fofonoff et al. 2018).
294 *Corophium* sp., *Doridella obscura*, *Haliplanella luciae*. *Ilyanassa obsoleta*, *Mitrella lunata*,
295 *Mytilus edulis*, *Nereis succinea*, *Polydora ligni*, and *Sabellaria vulgaris* were all present
296 historically but absent in recent collections. All but one of these (*H. luciae*) were native to the
297 area (Fofonoff et al. 2018), though several taxa were cryptogenic (*Corophium* sp., *N. succinea*,
298 and *P. ligni*) meaning taxa that lack clear evidence of introduction and that lack clear records of
299 their distribution. *B. violaceus* and *C. virginica* were found in recent collections but had not
300 been seen historically. *B. violaceus* was introduced (Fofonoff et al. 2018).

301 302 DISCUSSION

303
304 A major goal of this paper was to investigate the spatial and temporal variation in epifaunal
305 communities of New Jersey estuarine waters. A secondary goal was to compare current results
306 against historic data from the area. Analysis of longitudinal epifaunal community data from the
307 study area revealed important patterns in community composition, taxa richness and plate
308 percent cover. Longitudinal comparisons across decades provided insights about change in the
309 epifaunal community and contributions of invasive species to historic and current species
310 composition.

311
312 Shafto (1974), Hoagland (1982), and Loveland and Shafto (1984) documented the
313 epifaunal community of Barnegat Bay and its surrounding area many decades ago. Their
314 collective work provides an opportunity to look at change and constancy in the epifaunal
315 community over time in this estuarine area of New Jersey. Overall, taxa richness seems to have
316 declined, though sampling designs were different across studies (e.g., varying numbers of
317 sampling sites, regional extent and different substrate) which may contribute to the differences
318 observed. Several taxa were common across all time periods. A few of these, *Balanus* sp. and
319 *H. dianthus*, were most dominant and abundant historically (Loveland and Shafto 1984), a result
320 we found in our study as well. About half of the taxa common across all time periods were
321 introduced. Almost all of the taxa present historically, but not present currently, were native.
322 One of the two new taxa not present historically was introduced. Concerns were raised by

323 Loveland and Shafto in 1984 over establishment of non-native taxa in Barnegat Bay and
324 surroundings. It appears their concerns have been realized.

325

326 Analysis of current longitudinal epifaunal community data revealed important patterns in
327 taxa abundance. Notably, *Membranipora* sp. was the most dominant epifaunal organism among
328 sampling stations, having the highest percent cover of the plates in four of the 10 years of study.
329 It was also the most dominant epifaunal organism among soak durations and years of sampling.
330 Most of the seventeen taxa identified in this study are common in estuaries of the Mid-Atlantic
331 region of the United States (Fofonoff et al. 2018). Although there were similarities in the
332 dominant fauna of the epifaunal community among sampling stations and years, variability in
333 local hydrodynamics, reproduction, settlement cues, predator-prey interactions, and post-
334 settlement competition and mortality likely negated constancy of recruitment among the
335 sampling stations.

336

337 Analysis of current longitudinal epifaunal data also revealed important differences in taxa
338 richness and plate percent cover among relevant factors of this study. Notably, taxa richness and
339 plate percent cover were higher on the top surfaces of the plates in most years. This is consistent
340 with Miller and Etter (2008) and Rius et al. (2010) who found that well-lit surfaces favored the
341 development of algal-dominated fouling communities. Multivariate analyses also indicated that
342 distinct epifaunal assemblages developed on each of the plate surfaces in some years for both
343 short and long soak durations. Physical factors such as the composition and texture of the
344 settlement surface may be important. For example, surface roughness has been shown to affect
345 epifaunal colonizers on hard substrates (Sweat and Johnson 2013). Organisms may exhibit a
346 preference for upper surfaces to avoid the suspended mud and detritus often abundant on the
347 lower surfaces of substrate (Loveland and Shafto 1984). Post-settlement processes such as
348 competition might also be involved.

349

350 Despite higher taxa richness and plate percent cover on the top surfaces of the plates in
351 most years, several taxa, notably *Balanus* sp. and *H. dianthus*, displayed a significant preference
352 for the bottom surfaces of the plates. These taxa were also among the dominant taxa which
353 settled more frequently on the lower surfaces of panels historically in the same area (Loveland
354 and Shafto 1984). This behavior was assumed to be due to the photonegativity of the larvae,
355 attribution to the same species, and avoidance of interspecific competition for surface area
356 (Loveland and Shafto 1984). Other factors, such as attraction to microflora, bacteria, and
357 substratum chemicals, were also considered possible reasons for the settling patterns observed
358 (Loveland and Shafto 1984).

359

360 Multivariate analyses revealed that distinct epifaunal assemblages developed each year
361 for both short and long soak durations. Statistically significant year-to-year differences in plate
362 percent cover were also found for *Balanus* sp., *B. schlosseri*, *C. fornicata*, *H. dianthus*,
363 *Membranipora* sp., *M. manhattensis*, and unidentified macroalgae, depending on plate surface.
364 The vagaries of environmental conditions in Great Bay and Barnegat Bay (Kennish, 2001,
365 Kennish et al. 2004) are major drivers of change in structuring epifaunal communities,
366 particularly along shallow water areas. Historically, on a shorter time scale, Shafto (1974)
367 noticed that dominant taxa experienced fluctuations in settling rates during the summer months
368 which she attributed to high water temperatures and salinity. Due to the design of this study, we

369 were not able to investigate the individual factors responsible for the results discovered.

370
371 Mean taxa richness and plate percent cover were highest in 2010, 2011, 2012, 2014, and
372 2015 when encrusting bryozoans, serpulid polychaetes, and barnacles were abundant. They were
373 lowest in 2013 when tunicates (i.e., *B. schlosseri*) were more abundant. The low taxa richness
374 and plate percent cover in 2013 may be the result of Hurricane Sandy, which directly impacted
375 the area in the fall of 2012, though the results may also be due to poor reproduction, settlement,
376 or recruitment of epifaunal taxa relative to the other years of sampling. It may also reflect the
377 effects of negative interspecific interactions of the epifaunal taxa on the PVC plates, with *B.*
378 *schlosseri* activity limiting the coverage of other competitive species, or possibly even excluding
379 some forms. Historically, Loveland and Shafto (1984) also found that, when present, *B.*
380 *schlosseri* completely covered and smothered other organisms and had a controlling influence on
381 the community.

382
383 Multivariate analyses indicated that distinct epifaunal assemblages developed at different
384 locations both for short and long soak durations. Additionally, *Balanus* sp., *H. dianthus*,
385 *Membranipora* sp., *Polysiphonia* sp., sponges, and unidentified macroalgae had statistically
386 significant differences in average percent cover by location. These characteristics describing
387 location as an influence on epifaunal assemblages were also reported for many other estuaries
388 (Railkin 2004, Wahl 2009, Dürr and Thomason 2010) and marine environments (Whomersley
389 and Picken 2003) in addition to historic Barnegat Bay (Loveland and Shafto 1984). Berntsson
390 and Jonsson (2003) also showed that the composition and abundance of sessile organisms on
391 settlement plates after exposure for a one-month period varied considerably among sampling
392 sites. All of our sampling stations are located in shallow sheltered areas, although they differ in
393 environmental characteristics. These findings reflect the effects of large variation in larval
394 settlement and colonization of hard surfaces within estuarine habitats (Wahl 1989).

395
396 Overall, the epifaunal communities varied considerably in the Great Bay and Barnegat
397 Bay estuarine systems both spatially and temporally. Our multivariate analyses support the
398 conclusions that distinct assemblages developed in different locations of the study area, among
399 different years, and for different plate surfaces in some years for both short and long soak
400 durations. Historically, temporal and spatial complexity of the fouling community in Barnegat
401 Bay was controlled to a large degree by the dynamics of the larvae whose settling appeared to be
402 responsive to illumination and to mud and detritus accumulation on substratum surfaces
403 (Loveland and Shafto 1984). Historical seasonal patterns of reproduction, settlement, and
404 predator-prey interactions, and seasonal cycles of environmental parameters, such as water
405 temperature and photoperiod, strongly influenced that composition of the Barnegat Bay
406 community (Loveland and Shafto 1984). Similarly, the compositions of epifaunal communities
407 in other estuaries have been shown to vary spatially and temporally at different scales with fluxes
408 in larval settlement, recruitment, and post-recruitment processes (Connell 1985, Koehl 2007,
409 Dürr and Thomason 2010, Ruis et al. 2010, Holthuis et al. 2015). A study of a New England
410 intertidal rocky habitat found that post-settlement competition and predation explained 50-78%
411 of the sessile invertebrate abundance, while recruitment explained less than 11% (Menge 1991).
412 The relative contributions of recruitment vs. post-recruitment processes to adult population
413 structure are not well understood for many epifaunal communities (Menge 2000). Likewise,
414 habitat selectivity at settlement (Underwood and Keough 2001, Ruis et al. 2010) and predation

415 and competition (Richmond and Seed 1991), often determine adult distribution patterns of sessile
416 and sedentary species. Additionally, anthropogenic factors can play a major role in the
417 development of epifaunal communities. Hence, spatial and temporal variation of settlement plate
418 colonization remains a major focus of marine epifaunal community studies.

419
420 A number of future studies may derive from this work. To accurately determine the
421 relationship between epifaunal community structure in the Great Bay and Barnegat Bay estuarine
422 systems in New Jersey, more data are needed on hydrodynamics, local sea-level rise, and other
423 effects influencing recruitment and settlement. The distribution of epifaunal organisms, their
424 reproductive strategies, larval and spore responses to physical and chemical conditions,
425 settlement cues to conspecifics, and variations in recruitment fluxes are important factors
426 controlling the structure of adult epifaunal assemblages in the estuarine system. Temporal
427 differences in hydrodynamics are a primary control of larval delivery to estuarine hard surfaces,
428 but they can also dislodge recent colonizers from these substrates, thereby altering the
429 composition and structure of the epifaunal communities through time. Therefore, a study
430 directly linking epifaunal assemblages to hydrodynamics and associated controlling factors over
431 a protracted time frame would be useful.

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434
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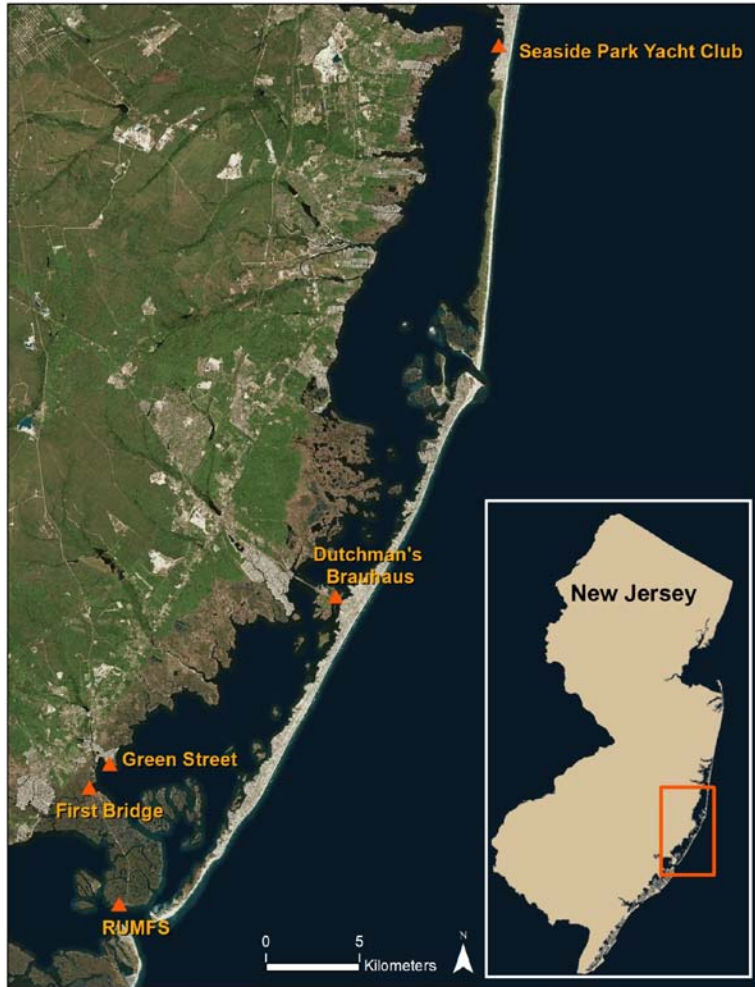
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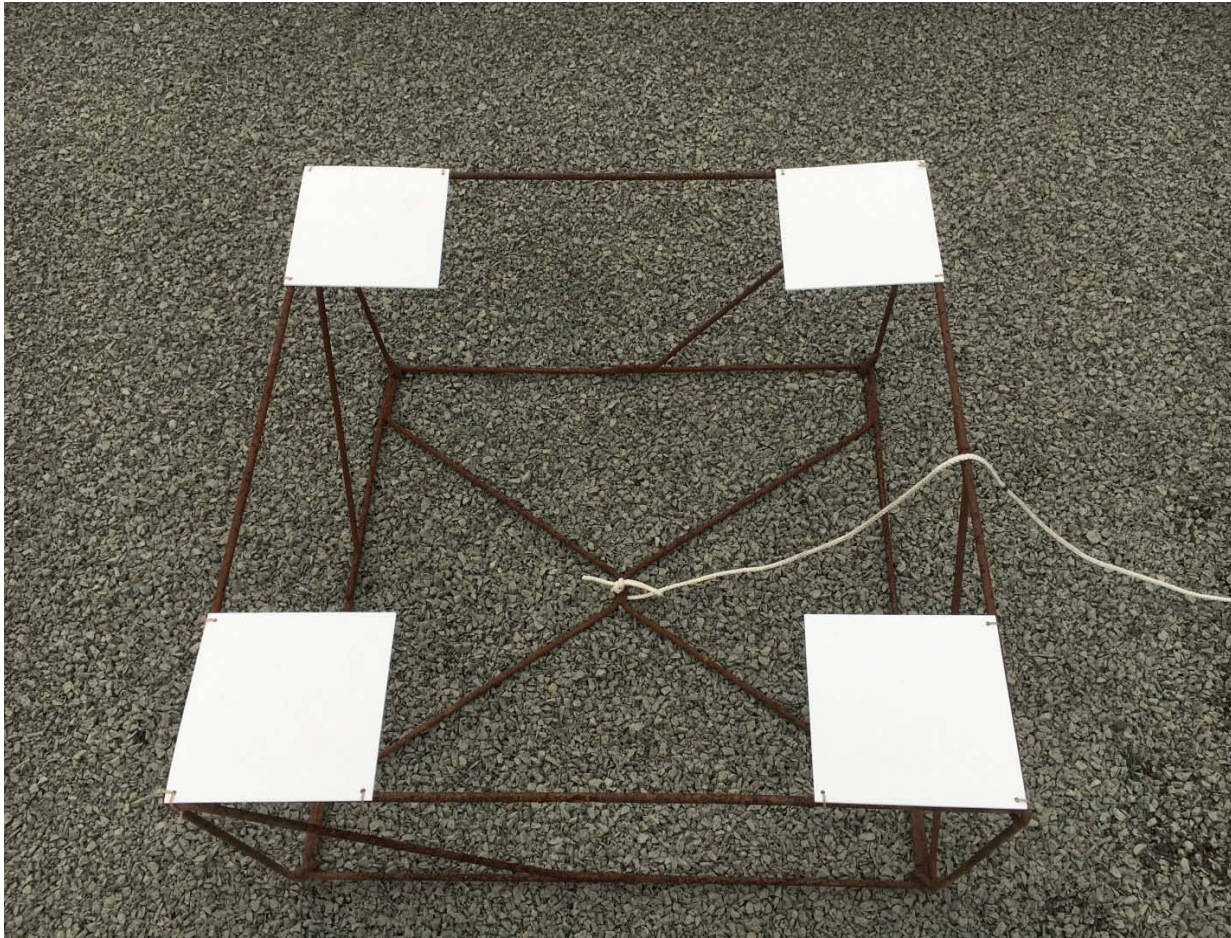
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564 Figure 1. Epifaunal community sampling stations in the Great Bay and Barnegat Bay estuarine systems used in this study.

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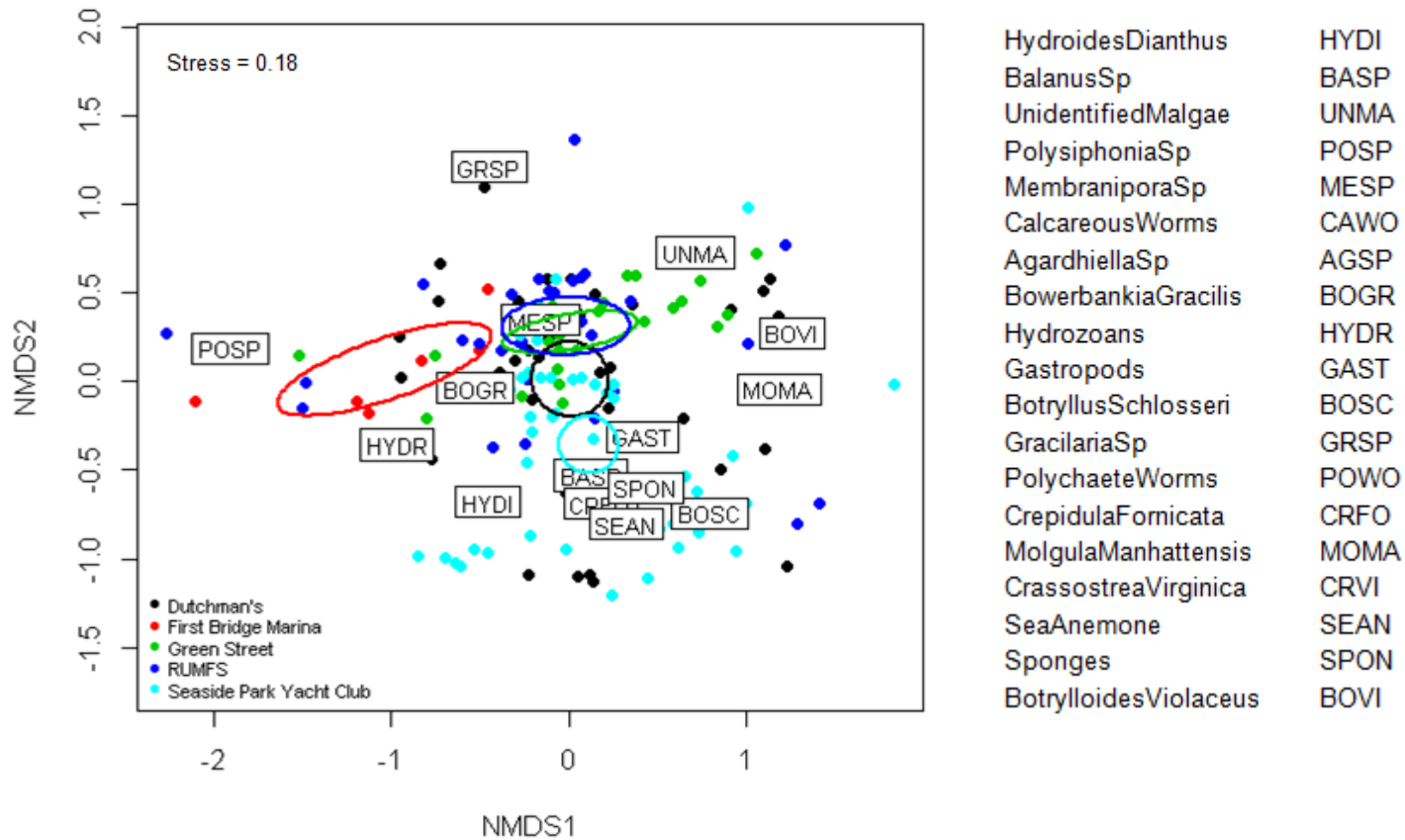


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569 Figure 2. Epifaunal community sampling plates and rack deployed at all stations in the study area.

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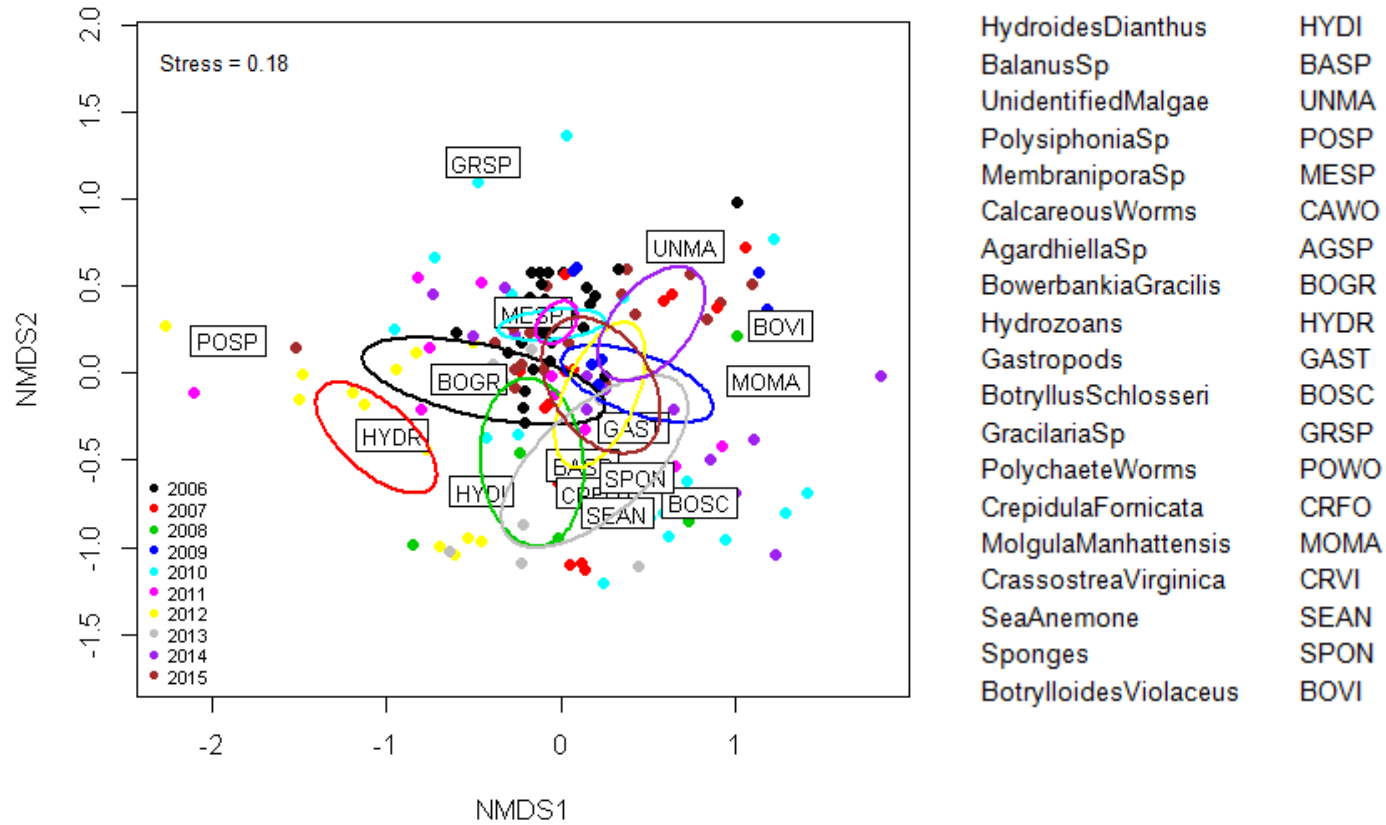
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573 Figure 3. Non-metric multidimensional scaling (NMDS) showing 176 field plots sampled in the Great Bay and Barnegat Bay estuarine

574 systems during short soak durations of 2006 to 2015, grouped by location.

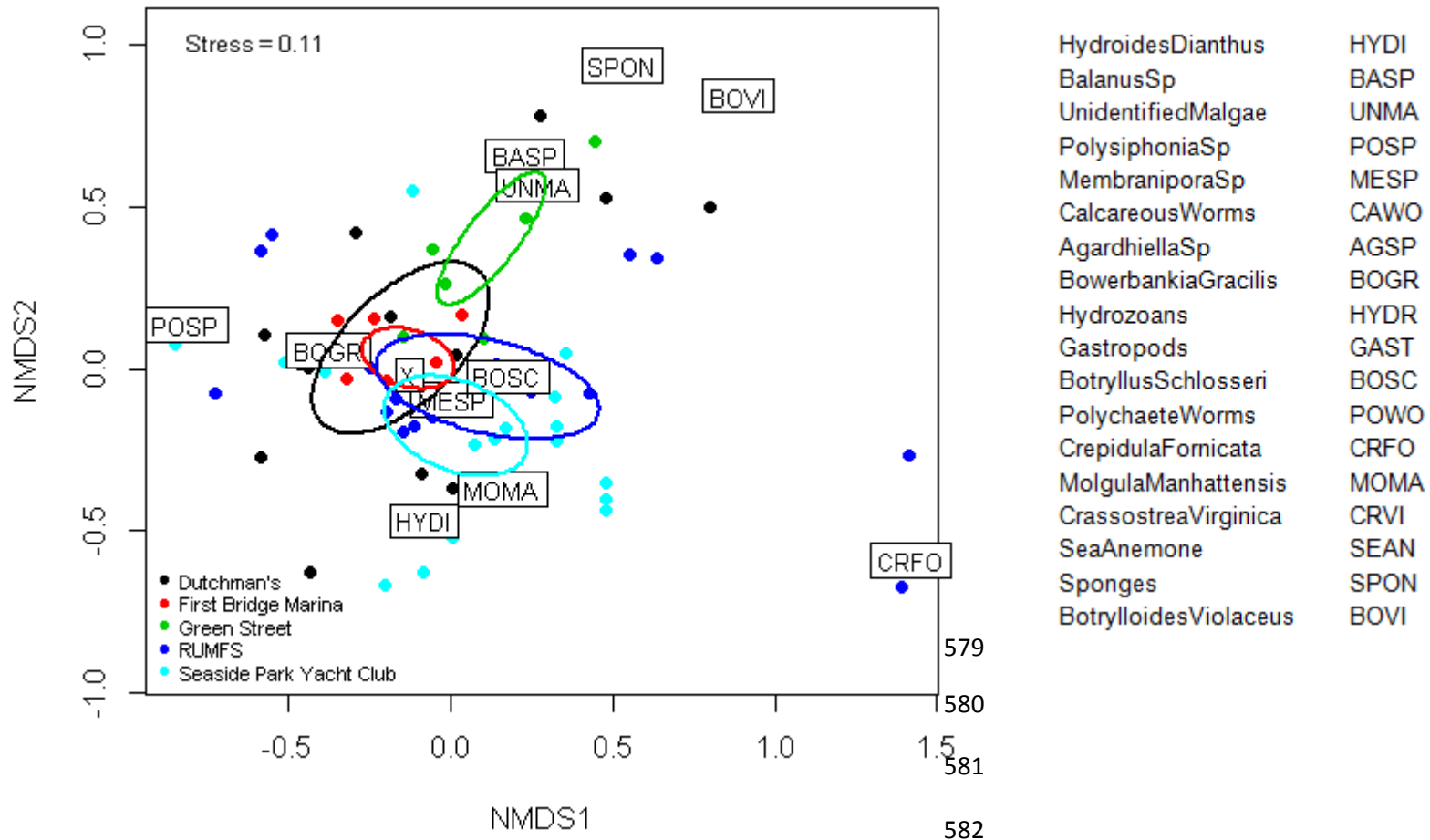


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576 Figure 4. Non-metric multidimensional scaling (NMDS) showing 176 field plots sampled in the Great Bay and Barnegat Bay estuarine

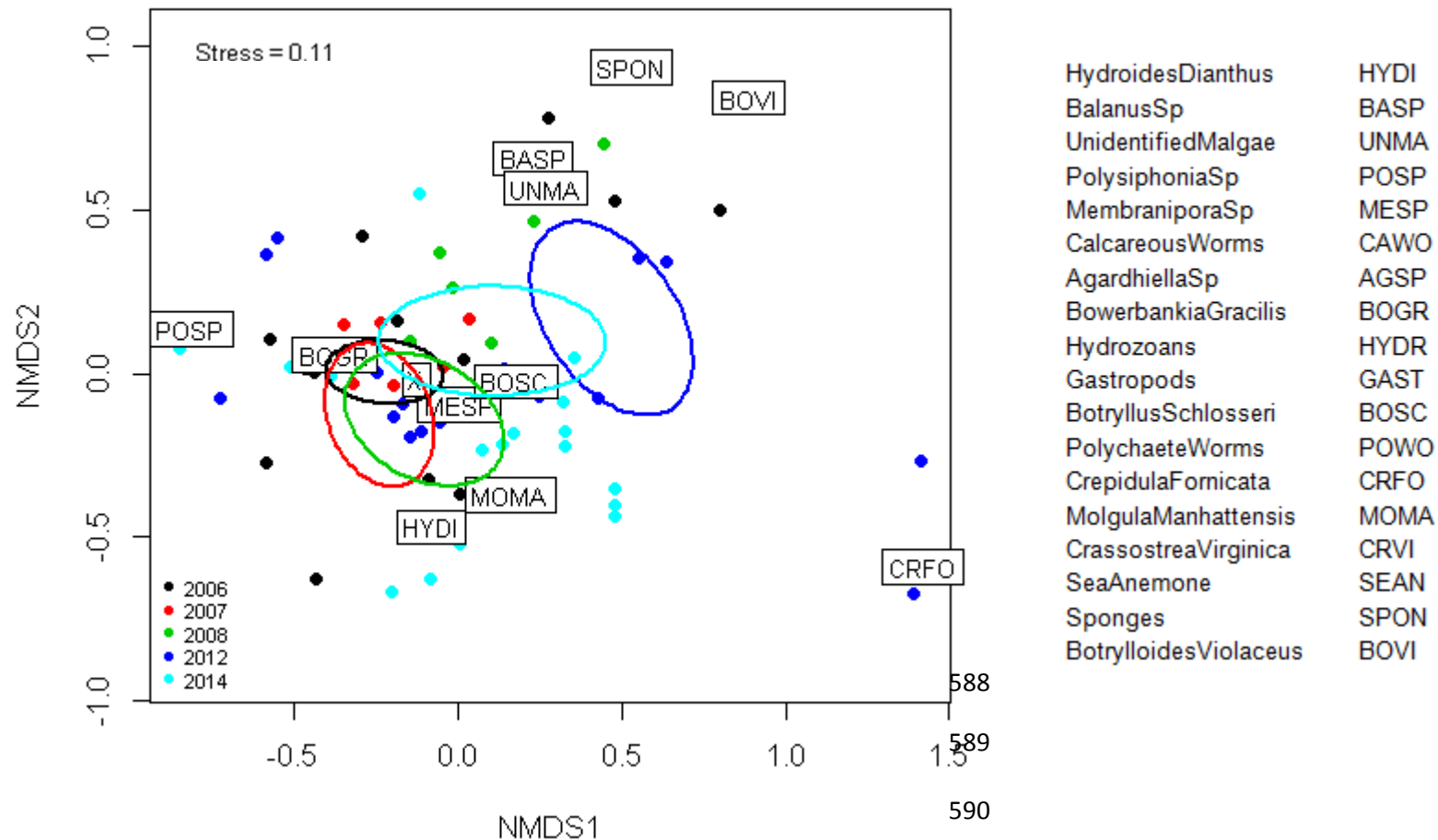
577 systems during short soak durations of 2006 to 2015, grouped by year.

578



583 Figure 5. Non-metric multidimensional scaling (NMDS) showing 72 field plots sampled in the Great Bay and Barnegat Bay estuarine
 584 systems during long soak durations of 2006-2008, 2012, and 2014, grouped by location. Figure redrawn after outlier dominated by
 585 *Gracilaria* sp was removed from the ordination.

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590

591 Figure 6. Non-metric multidimensional scaling (NMDS) showing 72 field plots sampled in the Great Bay and Barnegat Bay estuarine
 592 systems during long soak durations of 2006-2008, 2012, and 2014, grouped by year. Figure redrawn after outlier dominated by
 593 *Gracilaria* sp was removed from the ordination.

594

595

Table 1. Linear mixed model outcomes for explanatory factors (year, soak duration, plate surface, location and interaction effects of year * plate surface) and responses (richness for combined taxa and plate percent cover for combined and individual organisms). Significant results at $\alpha = 0.025$ for combined taxa and $\alpha = 0.05$ for individual organisms are bolded. Failure to converge is indicated with a dash.

| Assemblage | Response | N | Random variance | Residual variance | Year | | | | Soak duration | | | | Plate surface | | | | Location | | | | Year*plate surface | | | |
|-------------------------------|---------------------|-----|-----------------|-------------------|--------|--------|---------|-------------------|---------------|--------|---------|---------------|---------------|--------|---------|-------------------|----------|--------|---------|-------------------|--------------------|--------|---------|-------------------|
| | | | | | Num df | Den df | F value | P-value | Num df | Den df | F value | P-value | Num df | Den df | F value | P-value | Num df | Den df | F value | P-value | Num df | Den df | F value | P-value |
| Combined taxa | Richness | 264 | 0.37244 | 1.4557 | 9 | 52 | 4.44 | 0.0002 | 1 | 20.6 | 11.42 | 0.0029 | 1 | 13.6 | 3.31 | 0.091 | 4 | 14.1 | 2.69 | 0.0743 | 9 | 163 | 4.09 | <0.0001 |
| Combined taxa | Plate percent cover | 264 | 148.5773 | 625.94 | 9 | 51.1 | 5.81 | <0.0001 | 1 | 177.4 | 10.77 | 0.0012 | 1 | 12.7 | 18.2 | 0.001 | 4 | 22.53 | 2.13 | 0.1108 | 9 | 178.1 | 5.62 | <0.0001 |
| <i>Balanus</i> sp. | Percent cover | 116 | 250.83 | 0.9713 | 9 | 81.31 | 3.29 | 0.0018 | 1 | 70 | 2.82 | 0.0974 | 1 | 63.2 | 1.02 | 0.3157 | 4 | 78.56 | 4.17 | 0.0041 | 8 | 46.11 | 5.43 | <0.0001 |
| <i>Botrylloides violaceus</i> | Percent cover | 10 | 12.6519 | 0.9314 | 1 | 4 | 1.27 | 0.322 | 1 | 4 | 0.6 | 0.4814 | 1 | 4 | 57.48 | 0.0016 | - | - | - | - | 1 | 4 | 20.22 | 0.0108 |
| <i>Botryllus schlosseri</i> | Percent cover | 71 | 356.6267 | 0.4341 | 9 | 36.87 | 1.2 | 0.3233 | 1 | 34.98 | 0.37 | 0.5455 | 1 | 47 | 6.45 | 0.0144 | 4 | 36 | 0.72 | 0.5857 | 8 | 16.56 | 4.12 | 0.0071 |
| <i>Bowerbankia gracilis</i> | Percent cover | 39 | 532.0803 | 0.378 | 6 | 16.75 | 2.19 | 0.0958 | 1 | 18.31 | 2.5 | 0.1312 | 1 | 6.305 | 0.11 | 0.7514 | 3 | 16.95 | 0.2 | 0.8959 | 4 | 6.039 | 2.55 | 0.1462 |
| <i>Crossostrea virginica</i> | Percent cover | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| <i>Crepidula fornicata</i> | Percent cover | 33 | 1.1435 | 0.2315 | 8 | 15 | 35.04 | <0.0001 | 1 | 15 | 0.02 | 0.88 | 1 | 15 | 34.98 | <0.0001 | 3 | 15 | 0.38 | 0.7675 | 4 | 15 | 59.35 | <0.0001 |
| Gastropods | Percent cover | 4 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| <i>Gracilaria</i> sp. | Percent cover | 11 | 82.1577 | 0.9881 | 2 | 4 | 2.15 | 0.2318 | - | - | - | - | 1 | 4 | 1018 | <0.0001 | 1 | 4 | 1.06 | 0.3613 | - | - | - | - |
| <i>Hydroides dianthus</i> | Percent cover | 140 | 154.9705 | 1.0112 | 9 | 76.07 | 8.05 | <0.0001 | 1 | 66.06 | 0.29 | 0.5922 | 1 | 83.37 | 2.62 | 0.1091 | 4 | 80.46 | 7.05 | <0.0001 | 9 | 78.06 | 6.05 | <0.0001 |
| Hydrozoans | Percent cover | 3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| <i>Membranipora</i> sp. | Percent cover | 166 | 113.11 | 479.79 | 9 | 75.15 | 5.2 | <0.0001 | 1 | 78.88 | 0.14 | 0.7089 | 1 | 56.92 | 2.93 | 0.0922 | 4 | 75.47 | 6.15 | 0.0002 | 9 | 63.92 | 4.26 | 0.0002 |
| <i>Molgula manhattensis</i> | Percent cover | 57 | 177.8761 | 0.793 | 8 | 32.56 | 1.48 | 0.2014 | 1 | 31.55 | 1.4 | 0.2458 | 1 | 27.9 | 7.71 | 0.0097 | 3 | 34.05 | 2.13 | 0.1148 | 6 | 27.28 | 1.27 | 0.3024 |
| Polychaete worms | Percent cover | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| <i>Polysiphonia</i> sp. | Percent cover | 50 | 446.5466 | 0.576 | 7 | 21.39 | 0.98 | 0.4739 | 1 | 5.812 | 0.01 | 0.9154 | 1 | 30.41 | 6.91 | 0.0133 | 4 | 18.06 | 4.52 | 0.0105 | 4 | 16.14 | 2.17 | 0.118 |
| Sea anemone | Percent cover | 10 | 0.03333 | 0.1667 | 1 | 5 | 0.63 | 0.465 | - | - | - | - | 1 | 5 | 0.63 | 0.465 | 1 | 5 | 0 | 1 | 1 | 5 | 0.63 | 0.465 |
| Sponges | Percent cover | 27 | 114.91 | 0.6698 | 2 | 17 | 0.88 | 0.4336 | 1 | 17 | 0.47 | 0.5035 | 1 | 17 | 1.63 | 0.2183 | 3 | 17 | 2.37 | 0.1069 | 2 | 17 | 0.19 | 0.8283 |
| Unidentified macroalgae | Percent cover | 94 | 245.5293 | 1.0002 | 9 | 41.41 | 3.14 | 0.0057 | 1 | 42.48 | 3.14 | 0.0834 | 1 | 58.4 | 1.04 | 0.3127 | 4 | 38.39 | 8.09 | <0.0001 | 7 | 25.14 | 2.73 | 0.0297 |

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Table 2. Least squares means and standard errors (SE) for richness and plate percent cover for year, soak duration, plate surfaces (top/bottom) and location.

| Factor | Richness | | Plate Percent Cover (%) | | |
|---------------|-------------------------|------|-------------------------|-------|-------|
| | Mean | SE | Mean | SE | |
| Year | 2006 | 2.67 | 0.30 | 84.97 | 6.29 |
| Year | 2007 | 2.96 | 0.28 | 55.11 | 6.05 |
| Year | 2008 | 3.43 | 0.33 | 52.56 | 7.20 |
| Year | 2009 | 3.02 | 0.35 | 59.59 | 7.50 |
| Year | 2010 | 4.20 | 0.32 | 95.75 | 6.81 |
| Year | 2011 | 4.28 | 0.31 | 91.86 | 6.55 |
| Year | 2012 | 3.83 | 0.29 | 71.40 | 6.21 |
| Year | 2013 | 2.53 | 0.41 | 52.03 | 8.95 |
| Year | 2014 | 4.01 | 0.33 | 71.48 | 7.20 |
| Year | 2015 | 3.90 | 0.35 | 76.38 | 7.50 |
| Soak duration | Short | 3.09 | 0.18 | 64.13 | 3.24 |
| Soak duration | Long | 3.87 | 0.22 | 78.10 | 4.35 |
| Plate surface | Bottom | 3.71 | 0.21 | 80.91 | 3.93 |
| Plate surface | Top | 3.26 | 0.21 | 61.31 | 3.93 |
| Location | Dutchman's | 2.72 | 0.29 | 57.19 | 5.05 |
| Location | First Bridge Marina | 4.16 | 0.49 | 76.98 | 10.09 |
| Location | Green Street | 3.84 | 0.37 | 75.80 | 7.21 |
| Location | RUMFS | 3.07 | 0.31 | 75.02 | 5.54 |
| Location | Seaside Park Yacht Club | 3.62 | 0.29 | 70.58 | 5.03 |

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Table 3. Composition of the epifaunal community in Barnegat Bay and surroundings, New Jersey during three time periods: 1971-1972, 1982, and 2006-2015. Samples from October 1971 - October 1972 were collected monthly at nine sites in Barnegat Bay from wooden panels (Shafto 1974). Samples from June - August 1982 were collected from nineteen sites in Barnegat Bay and its tributaries using wooden panels, aluminum racks, and cement blocks (Hoagland 1982). Samples from 2006-2015 were collected at five sites in Great Bay and Barnegat Bay using PVC settlement plates. Generic taxa were removed from current sample list (gastropods, hydrozoans, polychaete worms, sea anemones, sponges, and unidentified macroalgae). Loveland and Shafto (1984) was the source for historic data.

| Taxa | Present 1971-1972 | Present 1982 | Present 2006-2015 |
|----------------------------------|-------------------|--------------|-------------------|
| <i>Aeolidia</i> sp. | | X | |
| <i>Amathia</i> sp. | | X | |
| <i>Ampelisca</i> sp. | X | | |
| <i>Anachis avara</i> | | X | |
| <i>Anthamnian</i> sp. | | X | |
| <i>Balanus</i> sp. | X | X | X |
| <i>Barentsia</i> sp. | | X | |
| <i>Bittium alternatum</i> | X | | |
| <i>Botrylloides violaceus</i> | | | X |
| <i>Botryllus schlosseri</i> | X | X | X |
| <i>Bowerbankia gracilis</i> | X | X | X |
| <i>Callipallene brevis</i> | X | | |
| <i>Campanularia</i> sp. | | X | |
| <i>capitella capitata</i> | X | | |
| <i>Caprella penantis</i> | X | | |
| <i>Ceramium</i> sp. | | X | |
| <i>Champia parvula</i> | | X | |
| <i>Chondria</i> sp. | | X | |
| <i>Cirrolana concharum</i> | X | | |
| <i>Codium fragile</i> | | X | |
| <i>Carophium</i> sp. | X | X | |
| <i>Crassostrea virginica</i> | | | X |
| <i>Crepidula convexa</i> | | X | |
| <i>Crepidula fornicata</i> | X | | X |
| <i>Cyathura polita</i> | X | | |
| <i>Dasya pedicellata</i> | | X | |
| <i>Diadumene leucolela</i> | X | | |
| <i>Diopatra cuprea</i> | X | | |
| <i>Doridella obscura</i> | X | X | |
| <i>Edotea triloba</i> | | X | |
| <i>Electra crustulenta</i> | | X | |
| <i>Electra hastingsae</i> | X | | |
| <i>Enteromorpha intestinalis</i> | | X | |
| <i>Erichsonella</i> sp. | X | | |
| <i>Eteone lactea</i> | X | | |
| <i>Euplana gracilis</i> | X | | |
| <i>Gammarus mucronatus</i> | | X | |
| <i>Geukensia demissa</i> | | X | |
| <i>Gobiosoma</i> sp. | | X | |
| <i>Goniada maculata</i> | X | | |
| <i>Gracilaria</i> sp. | X | X | X |
| <i>Haliclona canaliculata</i> | X | | |
| <i>Haliclona loosanoffi</i> | | X | |
| <i>Haliplanella luciae</i> | X | X | |
| <i>Hydroides dianthus</i> | X | X | X |
| <i>Idotea baltica</i> | | X | |
| <i>Ilyanassa obsoleta</i> | X | X | |
| <i>Lepidonotus squamatus</i> | | X | |
| <i>Leptochelia savignyi</i> | X | | |
| <i>Melita nitida</i> | X | | |
| <i>Membranipora</i> sp. | X | | X |
| <i>Microciona prolifera</i> | | X | |
| <i>Mitrella lunata</i> | X | X | |
| <i>Molgula manhattensis</i> | X | X | X |
| <i>Mytilus edulis</i> | X | X | |
| <i>Neopanope</i> sp. | | X | |
| <i>Nereis succinea</i> | X | X | |
| <i>Phylloacid</i> sp. | X | | |
| <i>Polydora ligni</i> | X | X | |
| <i>Polysiphonia</i> sp. | | X | X |
| <i>Sabella microphthalmia</i> | | X | |
| <i>Sabellaria vulgaris</i> | X | X | |
| <i>Schizotracha tenella</i> | | X | |
| <i>Sertularia argentea</i> | | X | |
| <i>Solemya velum</i> | X | | |
| <i>Spirarbus</i> sp. | | X | |
| <i>Stiliger fuscatus</i> | | X | |
| <i>Stylochus ellipticus</i> | X | | |
| <i>Tellina agilis</i> | X | | |
| <i>Tendipedida</i> sp. | X | | |
| <i>Ulva lactuca</i> | | X | |
| <i>Urosalpinx cinerea</i> | | X | |