

An exotic species alters patterns of marine community development

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Abstract. Predictions of ecological patterns can be strengthened through replication of foundational studies under different environmental conditions to evaluate the consistency in their underlying processes. In this study, we replicated Sutherland and Karlson’s classic ecology study that tested terrestrial paradigms of community development in a marine fouling community. The abundance patterns of marine fouling species were quantified on sequentially submerged settlement plates to investigate the effects of disturbance date on short- and long-term patterns of community development, and the original study’s data sets were reanalyzed for comparison. In both studies, community structure was initially shaped by disturbance date due to monthly and annual variation in larval recruitment; however, the influence of disturbance date diminished over time. Despite these similarities, the underlying drivers of long-term patterns of community development have shifted substantially since the 1970s. During the present study, an exotic tunicate, *Clavelina oblonga*, dominated plates over time and its dominance was associated with significant declines in species diversity. In contrast, the 1970s long-term community was characterized by a heterogeneous mixture of species that varied inter-annually, yielding increased species diversity over time. Continued observations of our settlement plates (2 yr total) indicated that *C. oblonga* remains the dominant species in this community, suggesting that these findings are not the result of a single, novel recruitment event. These results highlight how an exotic species can alter patterns of community development and biodiversity. Moreover, this study demonstrates the need to replicate foundational ecological studies to evaluate community dynamics and underlying processes in light of ongoing ecosystem change.

Key words: biodiversity; *Clavelina oblonga*; community structure; disturbance; fouling community; invasive species; marine invertebrates; North Carolina; recruitment; tunicate.

INTRODUCTION

Recent, rapid changes in marine and terrestrial ecosystems due to human alterations and environmental change present an opportunity for ecologists to evaluate the robustness of patterns and processes underlying foundational ecological concepts, such as community development. For example, well-documented biological responses to anthropogenic impacts and environmental change include (1) range expansion of species from lower to higher latitudes or elevations (Parmesan and Yohe 2003, Kelly and Goulden 2008, Rindone and Eggleston 2011), (2) changes in the timing of life-history traits (Winder and Schindler 2004), or (3) the death and local extirpation of species unable to adapt to their altered habitat (Hoegh-Guldberg 1999). Consequently, changes in species composition and associated biological interactions can alter the processes that shape community structure. These types of changes are occurring across a broad range of ecological systems that, in many cases, have served as model systems for developing and refining ecological theory (Sorte et al. 2010, Smith and Smith

2012). In this study, we revisit the processes underlying community structure and resulting patterns of community development within the marine fouling community of Beaufort, North Carolina, USA ~50 yr after a classic study by Sutherland and Karlson (1977), and describe how the long-term dominance of an exotic tunicate has altered patterns of community development.

The marine fouling community (hereafter referred to as “fouling community”) has commonly served as a model system to experimentally test the mechanisms underlying patterns of community development (Sutherland and Karlson 1977, Dean 1981, Cifuentes et al. 2007, Nydam and Stachowicz 2007), including the impact of nonnative species on community assemblage patterns (Gittenberger and Moons 2011). The fouling community is composed of species that colonize hard, subtidal structures (e.g., docks, ship hulls), such as ascidians, bryozoans, hydroids, and sponges (Nydam and Stachowicz 2007). The fouling community is an ideal model system for testing the relative importance of ecological processes underlying community structure because fouling species settle on easily replicated artificial substrates, have rapid development, and facilitate settlement of other organisms, thereby shaping community composition and development (Sutherland and Karlson 1977, Dean 1981).

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Disturbances, or discrete events in time that alter interactions among organisms, can lead to changes in resources, such as the availability of food, mates, and habitat (White and Pickett 1985), resulting in altered patterns of community development. Historically, both biological and physical disturbances have been regarded as important factors that influence community structure in marine and terrestrial environments (Dayton 1971, Grime 1977). For example, the distribution and abundance of species within marine communities can be impacted by ecological processes, including predation and competition, and physical disturbances, such as wave exposure (Connell 1972). More recent research has indicated that anthropogenic disturbances (e.g., shoreline hardening) can impact community structure by promoting the establishment of exotic species (Lambert and Lambert 2003, Bulleri and Chapman 2010). Despite our understanding of how natural disturbances structure communities, less is known about the consistency of the underlying ecological processes structuring marine communities and the resulting patterns of community development under ecosystem change.

Within fouling communities, numerous biological (e.g., competition, predation, larval supply) and physical (e.g., water temperature, salinity) factors can shape community structure (Lambert and Lambert 2003, Nydam and Stachowicz 2007). For example, in this space-limited community, dominant competitors can shape community structure by monopolizing key resources, such as space, through high growth rates or competitive overgrowth (Nandakumar et al. 1993, Claar et al. 2011, Lord and Whitlatch 2015). Similarly, predation can impact community structure by influencing the survival of recruits (Osman and Whitlatch 2004, Nydam and Stachowicz 2007), or through the preferential consumption of competitively superior species (Osman et al. 1992, Nydam and Stachowicz 2007). Other studies have identified the importance of larval recruitment in shaping community structure. For example, within fouling communities recruitment is often variable over time (Sutherland and Karlson 1977, Cifuentes et al. 2007), resulting in community structure that is shaped by the timing of available substrate for larval settlement and subsequent recruitment (Cifuentes et al. 2007).

The role of biological factors in shaping fouling community structure can be influenced by novel environmental conditions, such as increased water temperatures or habitat modification. For example, in response to elevated water temperatures, fouling species can exhibit increased growth rates in the northern portion of their range and decreased growth rates in the southern portion of their range (Lord and Whitlatch 2015), resulting in varied spatial patterns of community composition. Furthermore, competitive dominance can be affected by water temperatures as fouling species with higher growth rates tend to have higher rates of competitive overgrowth (Lord and Whitlatch 2015). Additionally, habitat modification, including coastal development and shoreline hardening, can impact community structure by increasing

the amount of available settlement substrate, resulting in enhanced opportunities for exotic species to become established and to potentially outcompete native species for limited resources (Glasby et al. 2007).

Historical patterns of community development in the fouling community of Beaufort, North Carolina, USA are well documented (McDougall 1943, Sutherland and Karlson 1977). During the 1970s, Sutherland and Karlson (1977) quantified patterns of larval recruitment and community development in the fouling community by deploying new settlement plates subtidally on a monthly basis during 1971 and 1972. Sutherland and Karlson (1977) determined that (1) larval recruitment patterns varied within and among years and, as a result, the initial community structure was highly variable and was dependent upon the date of disturbance (i.e., when new plates were deployed), (2) community development patterns varied over time, driven by the ability of some colonizers to exclude incoming recruits, as well as mortality events that yielded open space for larval recruitment, and (3) no community was dominated by a single species, but rather, the community often experienced variable, short-lived periods of a dominant species, and the dominant species varied year-to-year.

Given the potential impact of environmental variation and novel species on community structure, there is a growing need to replicate foundational studies to determine consistency in the ecological processes shaping community composition and resulting patterns of community development over time. The overarching goals of this study were to (1) characterize ecological processes and patterns of community development, using the fouling community of Beaufort, North Carolina, USA as a model system and (2) reanalyze Sutherland and Karlson's (1977) (hereafter S&K) data to determine if the ecological processes and resulting patterns of development characterized in this study were similar to those documented ~50 yr ago. Specifically, we addressed the following research questions: (1) Is the community composition of the present fouling community similar to that reported in the 1970s? (2) Are patterns of larval recruitment similar to those in the 1970s? (3) Does the timing of disturbance determine short-term and long-term patterns of community development? Are the patterns similar to those reported in the 1970s? (4) Does the fouling community exhibit patterns of biodiversity similar to those observed in the 1970s? By replicating a classic community ecology study and comparing present and historical results, our findings can provide insight into the potential impact of exotic species on patterns of community development.

METHODS

Study system

This study was conducted at the Duke University Marine Laboratory (DURL) dock located in Beaufort, North Carolina, USA (Fig. 1). This site is <3 km from

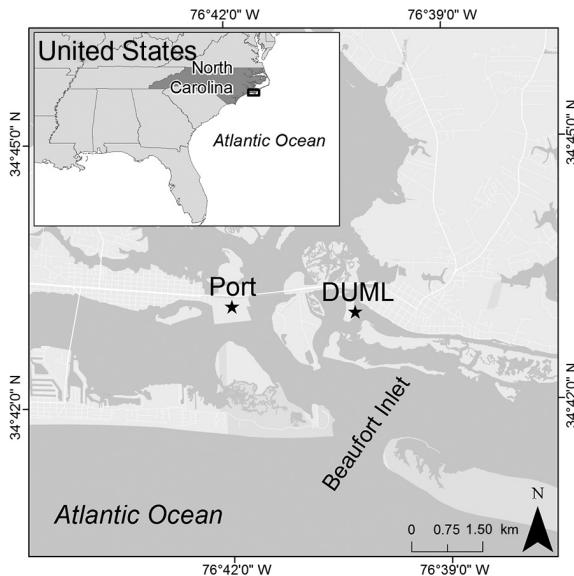


FIG. 1. Location of the study site at the Duke University Marine Lab (DUML) dock in Beaufort, North Carolina, USA in reference to the Port of Morehead City and Beaufort Inlet.

Beaufort Inlet, where waters from the Newport River Estuary System mix with water from the coastal Atlantic Ocean (Johnson et al. 2013). Beaufort Inlet serves as the primary access point for commercial vessels to the nearby (~6 km distance) Port of Morehead City. The DUML dock experiences semi-diurnal tides of ~1 m height (Kirby-Smith and Costlow 1989). Historical data (1971–1974) suggest that average monthly water temperatures generally vary from 7°C in the winter to 29°C during summer (Sutherland and Karlson 1977). Recent data (2014–2015) suggest that average monthly water temperatures have a similar range: 6°C during winter and 28°C during summer (Appendix S1: Fig. S1). Salinity tends to be relatively stable, often reaching seawater salinities (34 psu; Kirby-Smith and Costlow 1989); however, this area experiences significant variation in pH (Johnson et al. 2013). The coast of North Carolina is often considered to be the northern limit of many southern-associated marine and estuarine species, as well as the southern limit of many northern-associated species (Kirby-Smith 1983, but see Karlson and Osman 2012). This is largely due to the divergence of the warm Gulf Stream at Cape Hatteras, creating a distinct temperature difference between the subtropical environment south of Cape Hatteras and the temperate environment north of Cape Hatteras influenced by cooler waters originating from the Labrador Sea (Briggs 1974).

Experimental design

We replicated the methods of S&K to quantify patterns of larval recruitment and community development in the fouling community of Beaufort, North Carolina. As described by S&K, settlement patterns were monitored on

the lower surface of terracotta settlement plates (232 cm²) below the DUML dock. Settlement plates were individually and horizontally suspended subtidally by a vinyl-wrapped, steel cable ~0.3 m below the low tide mark and remained continuously submerged. The location of each plate along the dock was randomly assigned. We utilized the same settlement plates (i.e., material and size) positioned at the same submergence depth as S&K, thus allowing us to control for material- and position-based variation in community structure between the studies.

Larval recruitment patterns

Larval recruitment (LR) was quantified to provide monthly estimates of the species available to recruit into the fouling communities. To monitor recruitment patterns, LR plates ($n = 3$) were deployed monthly (from August 2014 to November 2015) and sampled every four weeks. LR plates were sampled from September 2014 (four weeks after August 2014) to December 2015 (four weeks after November 2015), encompassing a total of 16 months of LR sampling.

Sampling procedure.—During each sampling event, LR plates were retrieved from the dock and were immediately submerged in a plastic bin containing 1.5 cm of filtered seawater. Digital photographs were taken of the lower surface of each plate using a digital camera mounted on a custom frame (16.5 cm length × 16.5 cm width; 25 mm focal length). After each sampling event, organisms were removed from the plates and the plates were then soaked in freshwater for at least 24 h before being redeployed for the following month of LR sampling.

Quantifying settlement patterns.—A digital grid of 50 (out of 729) random points was positioned over each photograph using ArcGIS 10.3 (ESRI 2015). A new grid of random points was created for each plate and sampling period. The percent cover of basal fouling species was quantified by converting point counts (i.e., number of times a point landed on a particular species) to percent cover (Sutherland and Karlson 1977). Photographic point-count methods are a common tool used to reliably assess fouling community composition (Osman and Whitlatch 2007, Sorte and Stachowicz 2011, Lord et al. 2015). Supplemental videos of each plate were spatially referenced with each photograph to ensure accurate identification of the species under each random point. The identity and percent cover of species on the plates were then compared to the results of S&K as described in the *Statistical analyses: Larval recruitment patterns* below.

Following S&K's methods, we only quantified the abundances of basal fouling species (i.e., species attached directly to the plate surface) that had ≥10% cover at some point during the study and thus, disregarded any mobile species and extremely rare species. However, point count measurements captured the abundance patterns of mobile species (e.g., *Corophium* sp.) if sessile

components (e.g., tubes) were present on the settlement plate. Additionally, in cases where species overgrew other species, both species were counted (unless the lower species was dead), which could result in >100% cumulative cover of fouling species on settlement plates. All species were identified to the species-level where possible using available guides and taxonomic keys (Gosner 1978, Ruppert and Fox 1988, Pollock 1998).

Community development patterns

To monitor patterns of community development (CD), CD plates ($n = 3$) were deployed monthly (August 2014–September 2015) and were continuously sampled every ~12 weeks to characterize community development over time. Sequential deployment of new settlement substrates each month simulated a disturbance that resulted in the complete loss of biomass from the substrate, and thus, community development was characterized as a function of disturbance date (i.e., initial deployment date).

Short-term community development patterns.—Sampling of short-term community structure, defined as 90 d post initial plate deployment, occurred from November 2014 (90 d after August 2014 plate deployment) to December 2015 (90 d after September 2015 plate deployment), encompassing a total of 42 plates across 14 different combinations of disturbance dates. These data were compared to the 1971 and 1972 short-term community structure data obtained from S&K. Specifically, S&K's data sets encompass settlement plates that were initially deployed during May–November 1971 and May–November 1972, and sampled 90 d later.

Long-term community development patterns.—Long-term community structure (i.e., ≥ 180 d post initial plate deployment) was defined as the last sampling of the CD plates that could occur by December 2015 (following sampling every 90 d). The final sampling of CD plates occurred from October 2015 to December 2015 and encompassed 11 different combinations of disturbance dates. Note that, since the study period ended in December 2015, plates deployed after June 2015 only provided short-term community structure data. These data were compared with the 1972–1974 long-term community development obtained from S&K. Specifically, S&K's long-term data was collected during winter 1972, 1973, and 1974 for the 1971 community development series, and during winter 1973 and 1974 for the 1972 community development series. Note that four CD plates were lost during the course of this study (one deployed during September 2014, two deployed during December 2014, and one deployed during February 2015), resulting in a long-term data set consisting of 29 of 33 original plates.

Sampling procedure.—During each sampling event, CD plates were retrieved from the dock and were

immediately submerged in a plastic bin containing 1.5 cm of filtered seawater. Digital photographs were taken of the lower surface of each plate, as described in *Larval recruitment patterns: Sampling procedure*. After sampling, plates were immediately redeployed with careful attention to not disturb resident species.

Quantifying settlement patterns.—The percent cover of basal fouling species was quantified using point counts as described in *Larval recruitment patterns: Quantifying settlement patterns*. In addition to quantifying the percent cover of fouling species, we quantified the percent cover of empty space on the CD plates as an indicator of mortality events. For comparison to the amount of free space reported in the 1970s, percent free space data reported in S&K's study were extracted using ArcGIS 10.3 (ESRI 2015). To evaluate the overall availability of free space across all settlement plates, as opposed to available free space on a specific series of plates (Sutherland and Karlson 1977), percent free space was averaged across all CD plates deployed during a given month. As a result, we produced a single estimate of percent free space over time for each study.

Extended study

LR plates ($n = 3$) and a subset of the CD plates ($n = 3$) were continuously sampled beyond the December 2015 end point to determine if the LR and long-term CD trends continued to show similar patterns in following years. LR plates were sampled monthly (as described in *Larval recruitment patterns*) from January 2016 to August 2016, encompassing a total sampling period of August 2014–August 2016. The longest-running series of CD plates (i.e., plates deployed during August 2014) were continuously sampled every ~12 weeks (as described in *Community development patterns*) from November 2014 (12 weeks after the August 2014 sampling) to August 2016 (12 weeks after the May 2016 sampling), encompassing a 2-yr total sampling period.

Statistical analyses

Larval recruitment patterns.—To evaluate temporal trends in larval recruitment, the abundance patterns of fouling species on LR plates were averaged across the three replicate plates for a given month, producing a single, monthly estimate of the percent cover of recent settlers. We generated a heat map to illustrate the monthly and annual recruitment patterns of fouling species. A heat map is a graphical representation of data where the average percent cover of each species for a given month are represented with a color gradient, where white denotes the absence of a species and black indicates maximum average percent cover (Clarke et al. 2014). Temporal trends in larval recruitment were compared with the findings of S&K.

Short-term community development patterns.—The framework presented by Clarke et al. (2014) was used to evaluate patterns of community development. Specifically, similarities in the overall short-term community structure across each disturbance date were visualized with non-metric multidimensional scaling (NMDS) ordination (100 random starts) based on Bray-Curtis similarity matrices of the untransformed percent cover data. As described by Clarke et al. (2014), untransformed data can be used to evaluate the role of competitively dominant species within a community without overestimating the contribution of rare species. To compare short-term community assemblage patterns from the present study with those reported by S&K, separate Bray-Curtis similarity matrices and NMDS plots were created for each of S&K's short-term data (i.e., 1971 and 1972). Each NMDS plot is presented with a two-dimensional ordination stress value, which indicates the degree of mismatch between the two-dimensional NMDS plot and the predicted values from the regression of the similarity matrix. Smaller stress values suggest that the distances between points on the NMDS plot reflect the similarity values obtained from the similarity matrix; stress values <0.20 generally indicate an interpretable ordination (Clarke 1993).

Hierarchical cluster analysis was performed on each Bray-Curtis similarity matrix using a group-average linking method (Clarke et al. 2014). Cluster analyses were performed to group the CD plates deployed at different dates into clusters based on similar community structure. Similarity profile (SIMPROF) analyses were then performed (999 permutations, $\alpha = 0.05$) to test the null hypotheses of no differences in community structure among groups of CD plates identified in the cluster analyses. The results of the SIMPROF analyses were overlaid onto each NMDS plot to visualize significant similarities and differences in overall community structure based on disturbance date. We used similarity percentage (SIMPER) analyses to determine which species contributed to the differences among the clusters (i.e., distinct community assemblages) described above.

Analysis of similarity (ANOSIM) was also performed on each Bray-Curtis similarity matrix (999 permutations) to determine if community composition in the short-term varied significantly based on disturbance date. The significance levels, including the P and R value (an indicator of separation between groups), were determined by random permutations of each Bray-Curtis matrix. R values close to 1 indicate large differences in community assemblage patterns between plates deployed during different months (i.e., disturbance date has a large impact on community structure), whereas R values close to 0 indicate no differences in community assemblage patterns across settlement plates deployed during different months (i.e., similar community structure patterns regardless of disturbance date). All multivariate analyses were performed using PRIMER v7 (Clarke and Gorley 2015).

Long-term community development patterns.—To evaluate the effect of disturbance date on community structure over time, the methods in *Short-term community development patterns* (i.e., NMDS, cluster analysis, SIMPROF, and ANOSIM) were applied to long-term CD plates. For comparison with long-term community development patterns observed during the 1970s, these methods were also applied to each of S&K's long-term data sets. Note that for settlement plates deployed during 1971, we determined that one plate was an extreme outlier (June, replicate 1; dominated by *Hydractinia* sp.) and therefore was removed from our analyses. With the outlier included in the analyses, the remaining data could not be analyzed using NMDS because SIMPROF identified all other settlement plates as significantly similar due to the fact that all other plates lacked the dominance of *Hydractinia* sp. Removing that single data point for the long-term 1971 data set allowed us to identify differences in community composition among settlement plates deployed at different dates.

Patterns of biodiversity.—To determine if the present fouling community exhibits patterns of biodiversity similar to those observed in the 1970s, NMDS ordination (100 random starts) based on Bray-Curtis similarity matrices of the untransformed, average percentage cover data (i.e., average percent cover of species across replicates for a given month) were used to visualize the change in the community structure from the short-term to the first long-term sampling point for each study. Note that only the first long-term sampling points were used from the 1970s data set for comparison because they represent changes in community structure that occurred on similar timescales as the present study. Trajectory lines were overlaid onto each NMDS plot to visualize changes in community structure from a given sample month in the short-term to its respective long-term position. Biodiversity parameters (i.e., species richness, Pielou's evenness, Shannon's diversity index, and Simpson's diversity index) were determined from DIVERSE analyses using PRIMER v7 for each data set (Clarke and Gorley 2015), which was composed of percent cover of species across all replicate plates for each disturbance date in the short-term and the initial long-term. The null hypothesis that each biodiversity parameter in the short-term was equivalent to its respective mean value in the long-term was tested with four separate, two-tailed t tests using the R statistical software package, version 3.2.2 (R Development Core Team 2016). All data were tested for normality using the Shapiro-Wilks normality test and for homoscedasticity using Fisher's F test. Although t tests are generally robust to violations in normality, in cases where data failed to meet the assumption of homoscedasticity, denominator degrees of freedom were computed using Satterthwaite's method (Keselman et al. 1999).

RESULTS

Community composition

We observed 16 species with $\geq 10\%$ cover on either LR or CD settlement plates, as compared to the 21 species reported by S&K (Table 1). Of the 16 species observed with $\geq 10\%$ cover, 12 species were also observed during the original study in the 1970s. Species observed during both the 1970s and the present study include: barnacles (*Balanus* spp.), a brown bryozoan (*Bugula neritina*), the pleated sea squirt (*Styela plicata*), and an encrusting bryozoan (*Schizoporella errata* species complex, hereafter *Sc. errata*). The present study identified four species not reported during the 1970s: an exotic colonial tunicate (*Clavelina oblonga*), tube-building polychaetes (*Spirorbis* spp.), a colonial sea squirt (*Didemnum* sp.), and an oyster (*Crassostrea* sp.). S&K reported seven species with $\geq 10\%$ cover not observed during the present study, including three Poriferans (*Halichondria bowerbanki*, *Clathria prolifera*, and *Mycale americana*), two Cnidarians (*Astrangia poculata* and *Hydractinia* sp.), one Chordate (*Botryllus schlosseri*), and one Bryozoan (*Anguinella palmata*).

In addition to the 16 species observed during the present study with $\geq 10\%$ cover, six species were also observed, but never reached $\geq 10\%$ cover, including *Aiptasia* sp., *Botrylloides* sp., *Crepidula* spp., *Molgula manhattensis*, *Ptena colymbus*, and *Haliclona* spp. It is important to note that these species were only observed on a maximum of two plates across the entire study ($N = 120$ total settlement plates) and thus would not influence the results of our study. Of the six species observed with $< 10\%$ cover, two species were also observed during the 1970s, but with $\geq 10\%$ cover, including *Haliclona* spp. and *M. manhattensis*. Species that remained below 10% cover during the 1970s were not reported by S&K.

Average percent free space remained relatively low throughout the present study (Fig. 2a), suggesting that no substantial mortality event occurred. In contrast, during the 1970s, average percent free space peaked during August 1973 and August 1974 (Fig. 2b), indicative of an annual mortality event and subsequent sloughing

off of sessile organisms, as reported by S&K. Note that the peak free space that occurred during March 2015 is a result of averaging percent free space across settlement plates that were recently deployed (i.e., with less of a developed community) with plates that were deployed for multiple months (i.e., more substantial community developed), as depicted in the standard error bars. This effect (i.e., peaks in percent free space with associated standard error due to recent deployment) is also observed at the beginning of S&K's 1971 and 1972 series of plates.

Larval recruitment patterns

As observed by S&K, larval recruitment patterns in the present study varied within and across years (Fig. 3). For example, *Ectopleura crocea* recruitment was not captured on the LR plates during winter 2014, but was observed during winter 2015. Many species had seasonal recruitment patterns, such as *Eudendrium carneum*, which recruited most heavily during the colder months of our study. In contrast, *C. oblonga* had a single, large recruitment event during May–June 2015 where it approached 100% average cover on LR plates. Continued observations of the LR plates during 2016 suggest that *C. oblonga* continues to have a single, heavy recruitment event during May–June of each year (Fig. 4a). Recruitment patterns of *Ascidia interrupta* and *S. plicata*, dominant species observed by S&K, and *Ostrea equestris* were not captured during the course of this study. Some species, including *Bougainvillia* sp., *Crassostrea* sp., *Didemnum* sp., and *Pennaria disticha*, never reached a monthly average percent cover of $\geq 10\%$ on LR plates during the course of this study. Note that when total percent cover exceeded 100% cover, competition for space may have prevented the settlement of incoming recruits and thus the observed recruitment patterns; however, this only occurred during 3 of the 16 sampling periods.

Short-term community development patterns

Overall, short-term community composition on settlement plates deployed during 2014–2015 differed

TABLE 1. Species observed in the marine fouling community of Beaufort, North Carolina, USA during the present study (left) and the 1970s study (right; data derived from Sutherland and Karlson 1977).

Phylum	2014–2015	1970s
Annelida	<i>Hydroides dianthus</i> , <i>Spirorbis</i> spp.	<i>Hydroides dianthus</i>
Arthropoda	<i>Balanus</i> spp., <i>Corophium</i> sp.	<i>Balanus</i> spp., <i>Corophium</i> sp.
Bryozoa	<i>Bugula neritina</i> , <i>Schizoporella errata</i>	<i>Anguinella palmata</i> , <i>Bugula neritina</i> , <i>Schizoporella errata</i>
Chordata	<i>Ascidia interrupta</i> , <i>Clavelina oblonga</i> , <i>Didemnum</i> sp., <i>Styela plicata</i>	<i>Ascidia interrupta</i> , <i>Botryllus schlosseri</i> , <i>Molgula manhattensis</i> , <i>Styela plicata</i>
Cnidaria	<i>Bougainvillia</i> sp., <i>Ectopleura crocea</i> , <i>Eudendrium carneum</i> , <i>Pennaria disticha</i>	<i>Astrangia poculata</i> , <i>Bougainvillia</i> sp., <i>Hydractinia</i> sp., <i>Ectopleura crocea</i> , <i>Eudendrium carneum</i> , <i>Pennaria disticha</i>
Mollusca	<i>Crassostrea</i> sp., <i>Ostrea equestris</i>	<i>Ostrea equestris</i>
Porifera		<i>Clathria prolifera</i> , <i>Halichondria bowerbanki</i> , <i>Haliclona</i> spp., <i>Mycale americana</i>

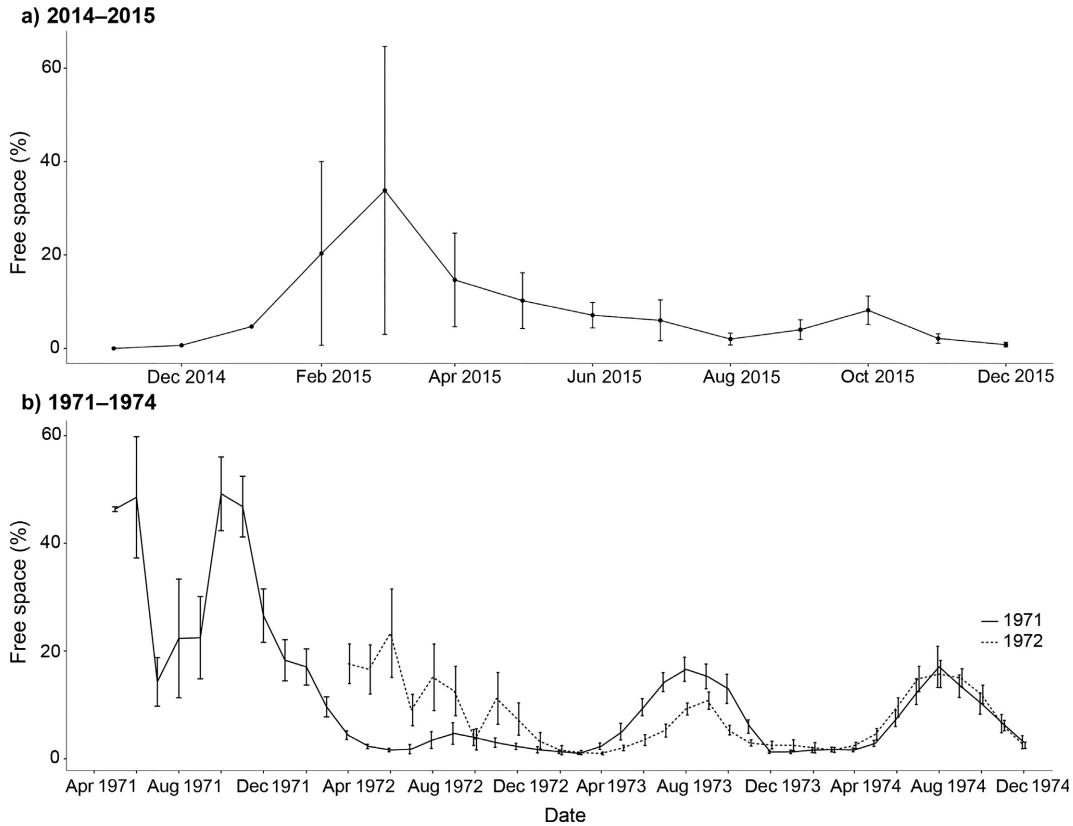


FIG. 2. Free space (mean \pm SE) on settlement plates deployed during (a) 2014–2015 and (b) 1971 (solid line) and 1972 (dashed line). Note that the 1970s data used for this analysis was obtained from Sutherland and Karlson (1977).

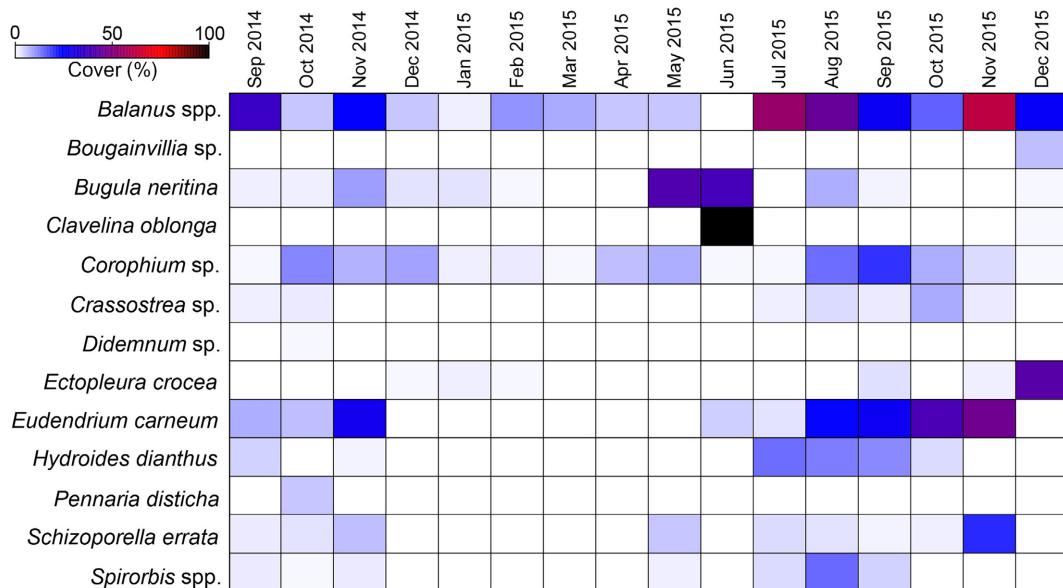


FIG. 3. Heat map of average monthly percent cover of larval species that settled on larval recruitment plates deployed from August 2014 to November 2015 and sampled four weeks later (September 2014–December 2015). Black indicates maximum abundances (100% average cover) of species and white indicates the absence (0% average cover) of a species. Recruitment patterns of *Ascidia interrupta*, *Styela plicata*, and *Ostrea equestris* were not observed during the course of this study.

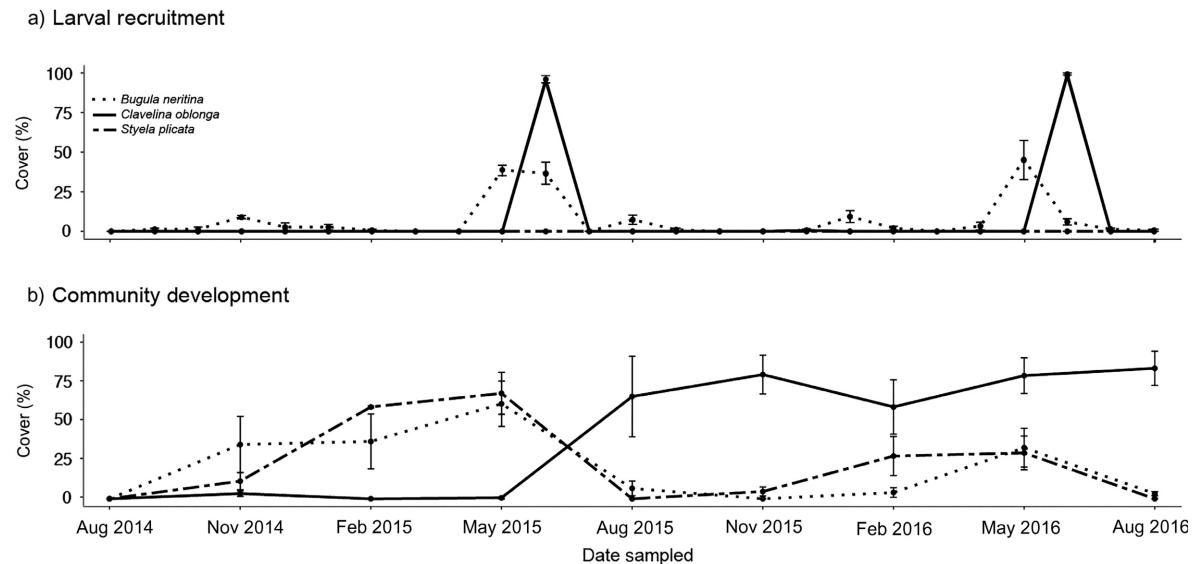


FIG. 4. Average cover (mean \pm SE) of the three most abundant species during 2014–2016 on a subset of (a) larval recruitment plates ($n = 3$) deployed during August 2014 and sampled every four weeks through August 2016 and (b) community development plates ($n = 3$) deployed during August 2014 and sampled every 12 weeks continuously through August 2016. Species include *Bugula neritina* (dotted line), *Clavelina oblonga* (solid line), and *Styela plicata* (dashed line).

significantly based on disturbance date (ANOSIM; $R = 0.865$, $P = 0.001$). For example, three distinct, short-term community assemblages were identified on plates deployed at different dates (Fig. 5a), driven largely by variable larval recruitment patterns during 2014–2015. Short-term community structure was driven by *C. oblonga* (92% average cover; 6 of 42 plates), *B. neritina* (56% average cover; 6 of 42 plates), and a mixture of species, each with relatively low abundances on the remaining 30 of 42 plates, including *Balanus* spp. (31% average cover), *Corophium* sp. (27% average cover), and *S. plicata* (24% average cover; Appendix S1: Table S1).

Similar to the present study, the short-term community structure on settlement plates deployed during 1971 and 1972 differed significantly based on disturbance date (ANOSIM; 1971, $R = 1$, $P = 0.001$; 1972, $R = 0.751$, $P = 0.001$). For example, plates deployed during 1971 displayed four distinct, short-term community assemblages according to disturbance date and associated larval recruitment patterns (Fig. 5b). The short-term cluster patterns during 1971 were driven by *S. plicata* (93% average cover; 3 of 21 plates), *P. disticha* and *A. interrupta* (74% and 72% average cover, respectively; 3 of 21 plates), *Balanus* spp. (58% average cover; 6 of 21 plates), and *S. errata* (43% average cover; 9 of 21 plates; Appendix S1: Table S1). Similarly, plates deployed during 1972 displayed five distinct short-term community assemblages on plates deployed at different dates (Fig. 5c), also driven by variable larval recruitment patterns. Short-term cluster patterns during 1972 were shaped by *Balanus* spp. (56% average cover; 3 of 20 plates) and *S. errata* (85%, 78%, 97%, and 87% average cover; 17 of 20 plates total; Appendix S1: Table S1).

Long-term community development patterns

Disturbance date significantly impacted overall long-term community composition on settlement plates deployed during 2014–2015 (ANOSIM; $R = 0.137$, $P = 0.035$); however, the effect of disturbance date is considerably lower than the 2014–2015 short-term effect of disturbance date (ANOSIM; $R = 0.865$), indicating a substantial decline in the role of disturbance date in shaping long-term community structure. It is important to note that the significance level (P value) can be largely impacted by group size and thus, the R value provides a more robust indicator of the effect of disturbance date on long-term community structure (Clarke et al. 2014). Three distinct long-term assemblage patterns were identified on plates deployed during 2014–2015 (Fig. 6), driven primarily by *C. oblonga* (27 of 29 plates total) and *S. plicata* (2 of 29 plates; Appendix S1: Table S2). Specifically, *C. oblonga* dominated (>75% cover, sensu Sutherland and Karlson 1977) nearly every plate over time with an average cover of 90%, whereas the remaining plates were composed of a mixture of low abundance species. Continued observations of a subset of the long-term CD plates suggest continued dominance by *C. oblonga* throughout 2016 (Fig. 4b) and the same overall compositional patterns as observed during winter 2015 (Appendix S1: Fig. S2).

Similar to the present study, the long-term community composition on plates deployed during 1971 and 1972 was less impacted by disturbance date than short-term community composition. For example, disturbance date had no significant impact on long-term community composition on plates deployed during 1971 (ANOSIM;

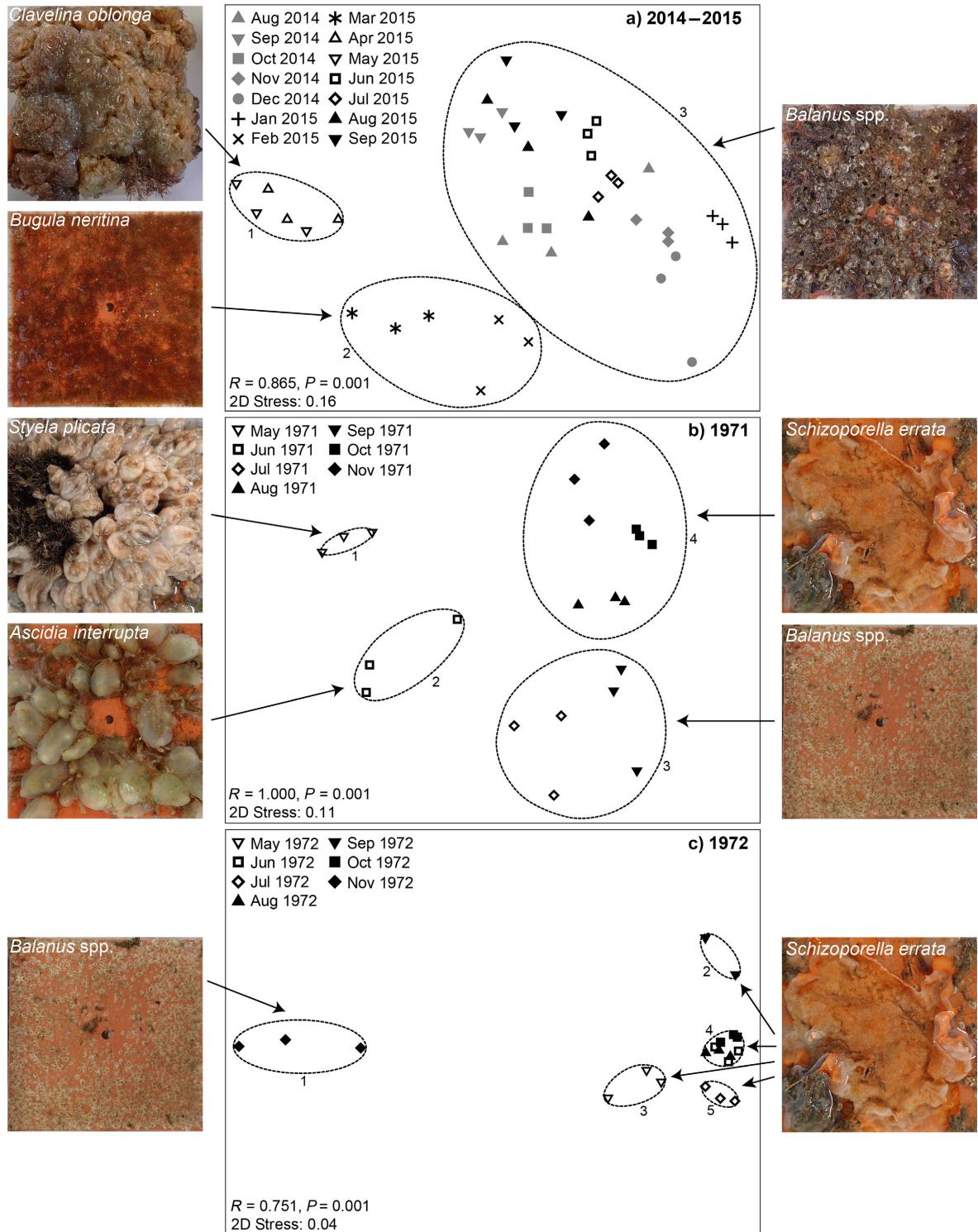


FIG. 5. Nonmetric multidimensional scaling plot depicting the (a) 2014–2015, (b) 1971, and (c) 1972 short-term fouling community composition (i.e., community composition 90 d after initial deployment date) with images illustrating the most influential species within each cluster (Appendix S1: Table S1). Symbols represent disturbance date (i.e., initial plate deployment) for each replicate plate. SIMPROF analyses (dashed line, $\alpha = 0.05$) indicate significant differences in community structure. ANOSIM results indicate the effect of disturbance date on short-term community structure. Note that the 1970s data used for this analysis was obtained from Sutherland and Karlson (1977). All images were taken by K. Theuerkauf.

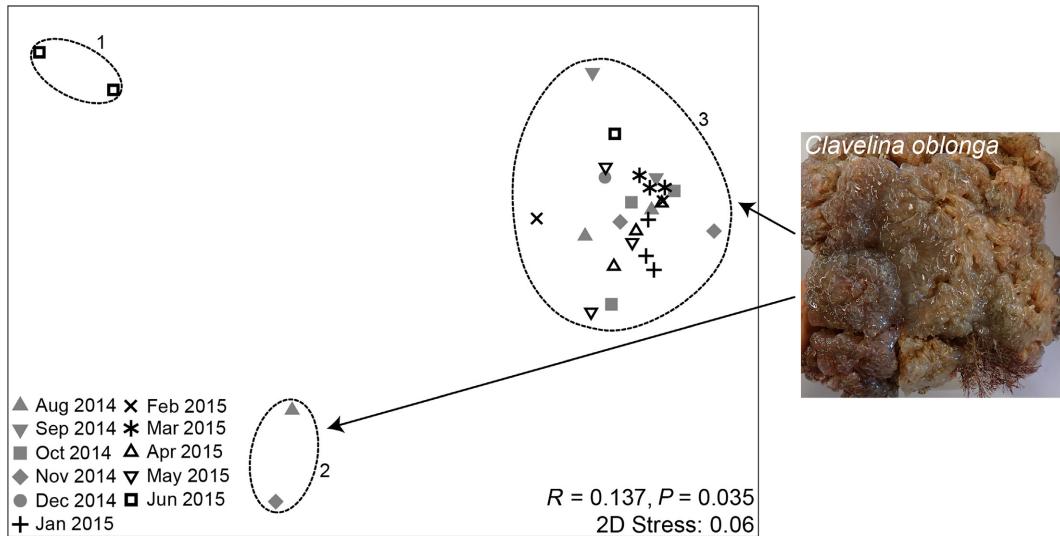


FIG. 6. Nonmetric multidimensional scaling plot depicting the 2015 long-term fouling community composition (i.e., community composition ≥ 180 d after initial deployment date) with an image illustrating the most influential species (*Clavelina oblonga*) within the largest cluster (Appendix S1: Table S2). Symbols represent disturbance date (i.e., initial plate deployment) for each replicate plate. SIMPROF analyses (dashed line, $\alpha = 0.05$) indicate significant differences in community structure. ANOSIM results indicate the effect of disturbance date on long-term community structure. Image was taken by K. Theuerkauf.

December 1972, $R = 0.067$, $P = 0.260$; December 1973, $R = 0.162$, $P = 0.068$; December 1974, $R = -0.041$, $P = 0.634$). Disturbance date had a significant impact on long-term community composition on plates deployed during 1972 (ANOSIM; December 1973, $R = 0.370$, $P = 0.001$; December 1974, $R = 0.298$, $P = 0.016$); however, the effects of disturbance date are considerably lower than the 1972 short-term effect of disturbance date (ANOSIM; $R = 0.751$).

For plates deployed during 1971, five distinct long-term assemblage patterns were identified by December 1972, one distinct assemblage pattern by December 1973, and two distinct assemblage patterns by December 1974 (Fig. 7a–c). Long-term community structure during December 1972 was driven primarily by *S. errata* (9 of 20 plates); however, *E. crocea* (20 of 20 plates) was the most influential species by December 1973, and *Haliclona* spp. (18 of 20 plates) was the most influential species by December 1974 (Appendix S1: Table S2). For plates deployed during 1972, three distinct long-term assemblage patterns were identified by December 1973 and three distinct assemblage patterns by December 1974 (Fig. 7d, e). Long-term assemblages during December 1973 were driven primarily by *S. errata* (19 of 20 plates total), though *S. plicata* (13 of 20 plates) was the most influential species by December 1974 (Appendix S1: Table S2). In contrast to the present study, which identified *C. oblonga* as a long-term dominant species on nearly every plate, no species dominated (i.e., $>75\%$ cover) the majority of the long-term 1971 or 1972 plates. Specifically, on the 1971 series, *S. plicata* only dominated three plates during December 1972 (92% average cover), while no species dominated during

December 1973 or December 1974. Similarly, no species dominated the 1972 series over time; however, *S. errata* was the most abundant species on the majority of the plates during December 1973.

Patterns of biodiversity

When comparing 2014–2015 average short-term and long-term community composition, NMDS trajectory plots (Fig. 8a) highlight the shift from a diverse assemblage of species in the short term to a less diverse assemblage of species in the long term, driven largely by the long-term dominance of *C. oblonga* (84% average cover across all settlement plates). The long-term assemblage patterns had significantly lower Simpson's diversity index ($t_{20} = 2.15$, $P = 0.04$) and Pielou's evenness ($t_{20} = 2.77$, $P = 0.01$) than the short-term assemblage. Conversely, there was no significant difference in species richness ($t_{20} = -0.61$, $P = 0.55$) or Shannon's diversity index ($t_{20} = 1.70$, $P = 0.11$) between short-term and long-term assemblage patterns.

In contrast to the present study, when comparing the 1971 and 1972 average short-term community composition with the first long-term sampling (i.e., December 1972, December 1973, respectively), NMDS trajectory plots indicate a diverse assemblage of species in both the short and long term (Fig. 8b, c). The long-term assemblage patterns in December 1972 had significantly higher species richness ($t_{12} = -3.17$, $P = 0.008$), Shannon's diversity index ($t_{12} = -5.71$, $P = 9.77 \times 10^{-5}$), Simpson's diversity index ($t_{7.54} = -5.88$, $P = 0.0005$), and Pielou's evenness ($t_{12} = -3.98$, $P = 0.002$) than the 1971 short-term assemblage. Similarly, the long-term assemblage

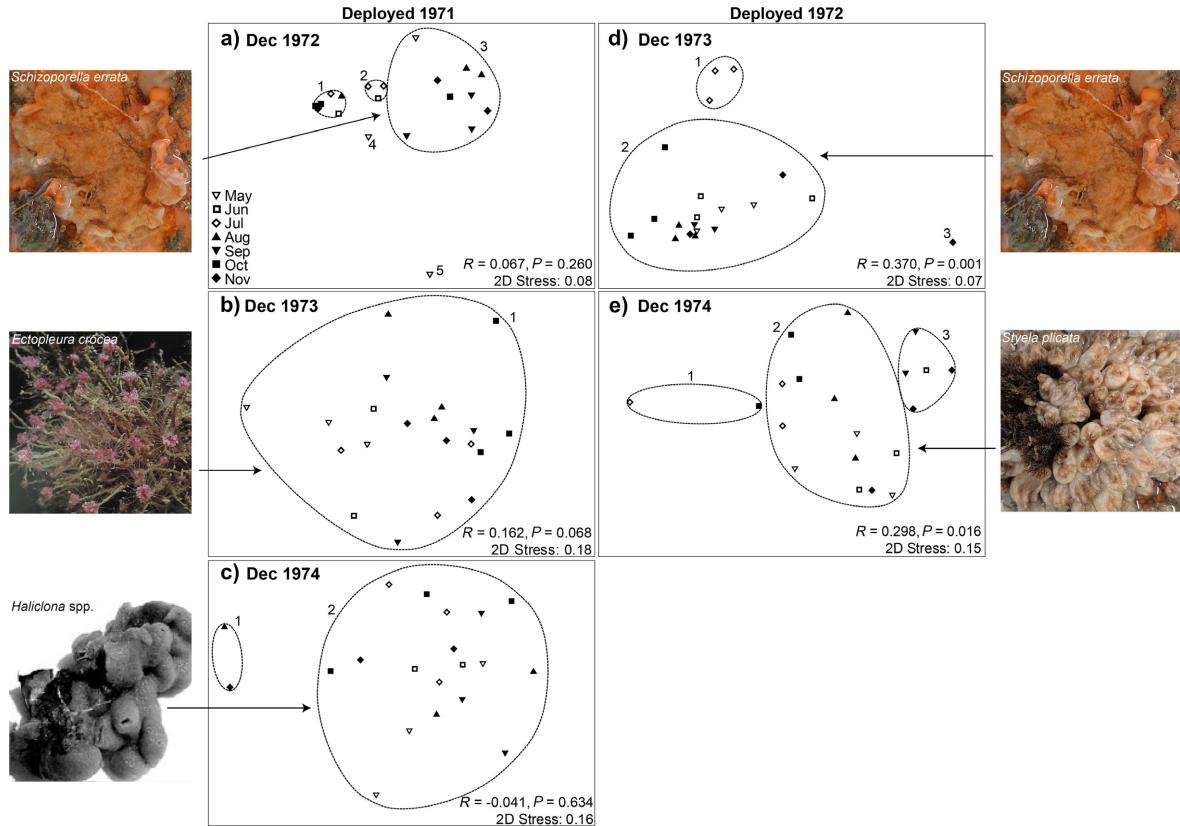


FIG. 7. Nonmetric multidimensional scaling plot depicting the long-term fouling community composition (i.e., community composition ≥ 180 d after initial deployment date) of settlement plates deployed in 1971 (left) and 1972 (right). Plates deployed during 1971 were sampled (a) December 1972, (b) December 1973, and (c) December 1974, while plates deployed during 1972 were sampled (d) December 1973 and (e) December 1974. Images illustrate the most influential species within the largest cluster (Appendix S1: Table S2). Symbols represent disturbance date (i.e., initial plate deployment) for each replicate plate. SIMPROF analyses (dashed line, $\alpha = 0.05$) indicate significant differences in community structure. ANOSIM results indicate the effect of disturbance date on long-term community structure. Note that the 1970s data used for this analysis was obtained from Sutherland and Karlson (1977). Images were obtained from K. Theuerkauf (a, d, e), National Audubon Society Field Guide to North American Seashore Creatures (b), and www.sanctuarysimon.org (c).

patterns in December 1973 had significantly higher species richness ($t_{12} = -7.16$, $P = 1.15 \times 10^{-5}$), Shannon's diversity index ($t_{12} = -4.75$, $P = 0.0005$), Simpson's diversity index ($t_{11.96} = -3.52$, $P = 0.004$), and Pielou's evenness ($t_{12} = -2.97$, $P = 0.01$) than the 1972 short-term assemblage.

DISCUSSION

This study reevaluated the ecological processes underlying community structure and the resulting patterns of community development within the marine fouling community of Beaufort, North Carolina. The present study reveals that a competitively dominant, exotic tunicate (*Clavelina oblonga*) can significantly alter patterns of community development from those observed ~ 50 yr ago. S&K's classic study from the 1970s found that the short-term fouling community structure was initially shaped by disturbance date as a result of monthly and annual variation in larval

recruitment. Disturbance date became less important in structuring the long-term community assemblage in S&K's study due to annual mortality and subsequent sloughing off of dominant species, yielding available free space to incoming larval species. As a result, the diversity, evenness, and richness of the communities on the settlement plates observed by S&K increased over time, a pattern similar to those suggested in several classic marine ecology studies (Odum 1969, Connell 1978). Though the present fouling community structure was also (1) initially shaped by disturbance date as a result of variable larval recruitment patterns and (2) disturbance date became less important over time in structuring the community, the long-term community was characterized by a dominant, exotic tunicate, *C. oblonga*. The dominance of *C. oblonga* was associated with a significant decline in diversity and evenness of the community over time, providing broader insight into the potential impact of exotic species on community development patterns. Furthermore, in light of

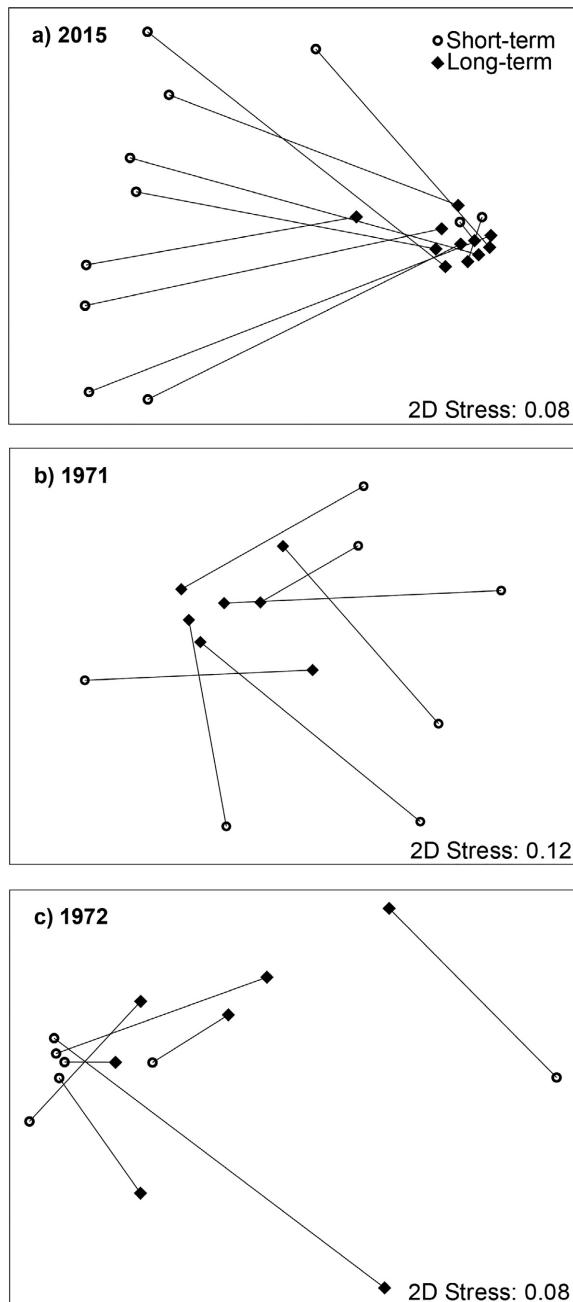


FIG. 8. Nonmetric multidimensional scaling plot depicting the (a) 2014–2015, (b) 1971, and (c) 1972 average short-term (open circles) and long-term (closed diamonds) fouling community composition. Trajectory lines connect a given sample month in the short-term to its respective long-term position. Note that the 1970s data used for this analysis was obtained from Sutherland and Karlson (1977).

ongoing and rapid ecosystem change, our results highlight the importance of replicating foundational studies to determine the consistency of ecological processes and resulting patterns of community development under environmental change.

Community composition

The observed differences in fouling community composition between the 1970s and the present study are driven primarily by both the dominance of *C. oblonga* and the lack of Poriferan species (Table 1). Four species were observed during the present study, but were not reported by S&K, including *C. oblonga*, *Spirorbis* spp., *Didemnum* sp., and *Crassostrea* sp. *C. oblonga* has not previously been reported in this area and appears to have joined the Beaufort fouling community within the past two years (D. Rittschof and J. Hawkins, *personal communication*). *Spirorbis* spp., *Didemnum* sp., and *Crassostrea* sp. have been historically observed in Beaufort (McDougall 1943, Walters 1992, Holm et al. 1997), but may not have been reported by S&K due to low abundances (i.e., below the 10% cover threshold used by S&K) during their study period. Many of the species observed during the 1970s, but not during the present study, have not been recently reported in North Carolina (Karlson and Osman 2012), likely the result of a decline in local abundances. Identifying the mechanism driving the decline in many of these fouling species over time is beyond the scope of this study and warrants further investigation.

It is important to note the potential substrate sampling bias present within both the present study and S&K's original study that may influence the observed community composition. Specifically, the suspension of settlement plates above the sea floor prevented access by benthic predators (e.g., omnivorous sea urchins), whereas nearby communities on dock pilings and other hard structures were exposed to such predation. Though qualitative observations of the communities on larger adjacent substrates revealed similar organisms, substantial oyster reefs existed on nearly every cement dock piling that appeared to limit the recruitment of other fouling organisms (K. W. Theuerkauf, *personal observation*). In contrast, similar species and abundance patterns to those recorded in the present study were observed on a large, nearby floating dock. Despite the potential for substrate characteristics to influence the species reported in the fouling community and their abundance patterns (Karlson 1978, Anderson and Underwood 1994, Holm et al. 1997), the use of identical substrate material as S&K allows for a direct comparison of community dynamics between the studies without the confounding effects of substrate type.

Larval recruitment patterns

It is well recognized that early life stages of benthic invertebrates can impact community dynamics (Connell and Slatyer 1977, Osman 1977); however, biological interactions, such as competition and predation, can play an important role in shaping recruit abundance and, ultimately, the composition of the community that develops (Jackson 1977, Osman and Whitlatch 2004). For example, predation of recruits has been identified to significantly impact marine fouling community development in

several marine benthic habitats (Osman and Whitlatch 2004, Nydam and Stachowicz 2007). Though larval recruitment varied monthly and annually in both the 1970s and the present community, some of the most striking differences in larval recruitment between the two studies were driven by *C. oblonga* and *Styela plicata*. Specifically, *C. oblonga* reached ~100% average cover on LR plates during May–June 2015 (Fig. 3). This species is known to recruit during warmer months (Ordóñez et al. 2016), but it was not observed in Beaufort during the 1970s. In contrast, recruitment of *S. plicata* can occur during spring and fall (Sutherland and Karlson 1977), yet it was not observed on any plates during the course of this study. Fish predation has been identified as a source of mortality for young *S. plicata* (Sutherland 1974), and may explain the observed lack of recruitment during this study.

Competition with resident adults (Claar et al. 2011) or among recruits may also influence settlement patterns of incoming species (Jackson 1977, Menge and Sutherland 1987). For example, previous studies in Beaufort indicated that *S. plicata* recruitment occurs during May–June (McDougall 1943, Sutherland and Karlson 1977), corresponding with the same time period that we observed *C. oblonga* recruitment. In contrast to colonial organisms, such as *C. oblonga*, solitary organisms (e.g., *S. plicata*) tend to be poor space competitors (Jackson 1977). Since space is often a limiting resource in this system, *S. plicata* may not have been able to settle on LR plates in the presence of *C. oblonga*. Identifying the specific role of competition and predation in shaping larval recruitment and community development within this invaded fouling community is the focus of ongoing research (K.W. Theuerkauf, D.B. Eggleston, and S.J. Theuerkauf, *unpublished manuscript*).

Short-term community development patterns

We identified a strong effect of disturbance date and corresponding larval recruitment on overall short-term community structure within both the present study and our reanalysis of the 1970s data (Fig. 5a–c). Due to altered recruitment patterns, however, different species were responsible for shaping short-term community structure between the 1970s and the present (Appendix S1: Table S1). For example, though the majority of CD plates were composed of a mixture of species, each with relatively low abundances, heavy recruitment by *C. oblonga* and *Bugula neritina* during the present study led to unique assemblages on short-term CD plates. In contrast, our reanalysis of S&K's data indicated that different species were responsible for the observed community structure during the 1970s, including *S. plicata*, *Penmaria disticha*, *Balanus* spp., and *Schizoporella errata*. Though our reanalysis of the 1970s data differed from the original grouping patterns of settlement plates reported by S&K (e.g., number of clusters), the same overall trends exist: short-term community development patterns varied

significantly based on timing of the disturbance date and corresponding patterns of larval recruitment. The importance of substrate deployment date and corresponding patterns of larval recruitment in shaping short-term assemblage patterns has been documented in other marine benthic habitats (Osman 1977, Cifuentes et al. 2010, Freestone and Osman 2011).

Long-term community development patterns

Though this study and S&K's study both describe a declining importance of disturbance date in shaping overall community composition patterns in the long-term, we identified considerable differences in the long-term community structure as compared to what was observed during the 1970s. During the present study, *C. oblonga* dominance on nearly every settlement plate (Fig. 6; Appendix S1: Fig. S2) highlights its ability to dominate in the long term regardless of the original disturbance date, initial assemblage of species, or the amount of available substrate for settlement. It is important to note that the lower abundance of *C. oblonga* on the June plates was likely due to the deployment of those plates after *C. oblonga*'s peak recruitment during May. The lack of *S. errata* (a dominant, calcified encrusting bryozoan observed during the 1970s) as a dominant species during this study may be explained by a shift in the dominant species present. Previous studies have found that tunicates are often dominant competitors in fouling communities (Lambert and Lambert 1998) and can overgrow or outcompete subordinate species (Cifuentes et al. 2010). Given *C. oblonga*'s ability to overgrow established communities and bare substrate, *C. oblonga* may have overgrown *S. errata* or prevented its settlement. Exclusion studies of *C. oblonga* are needed to test this hypothesis.

In contrast to this study, our reanalysis of the 1970s data indicated that no species consistently dominated the 1970s settlement plates over time, and that the species responsible for the observed assemblages varied annually (Fig. 7a–e). As species died and sloughed off the plates each fall, free space was created and thus, plates generally lacked a long-lived dominant species (Sutherland and Karlson 1977). The communities on the plates became more similar over time (i.e., decreasing number of clusters) as a result of free space increasing on plates during the same time period and subsequent exposure of plates to the same recruitment events. Further, as a result of annual variation in larval recruitment, community composition varied annually. In contrast to S&K, we did not observe any substantial increase in the amount of free space on our plates during the course of our study.

Continued observation of a subset of our LR and long-term CD plates throughout 2016 (i.e., 2 yr post initial deployment) suggests (1) continued dominance of *C. oblonga* on the settlement plates and (2) a distinct, reoccurring recruitment event of *C. oblonga* during May–June

each year (Fig. 4a, b), which likely contributes to its ability to persist over time as the dominant species. These observations suggest that there was no identifiable mortality event during the summer of 2016, highlighting the ability of *C. oblonga* to persist throughout the warmest and coolest months of the year. The multi-year dominance of an exotic ascidian contrasts the findings of a recent study (Dijkstra et al. 2011) that examined long-term changes in community structure of a New England fouling community. Particularly, Dijkstra et al. (2011) observed an increase in the abundance of invasive ascidians over time; however, the ascidians were short-lived and seasonally abundant, as opposed to long-term dominant ascidians, such as *C. oblonga*. In contrast to the temperate-subtropical climate of North Carolina, habitats within New England tend to be influenced by wider seasonal variation in physical factors (e.g., water temperature) and as a result, the dominant, exotic fouling species are often short lived (Dijkstra et al. 2011). In the absence of seasonal or annual mortality events, as appears to be the case in our study system, it is unlikely that other species can successfully invade and outcompete *C. oblonga* for space; however, this hypothesis requires further testing.

Patterns of biodiversity

C. oblonga's year-round dominance coincided with the observed significant decline in Simpson's diversity and evenness over time during the present study (Fig. 8a). The lack of a significant decline in Shannon's diversity index and species richness over time, metrics that are directly related (i.e., Shannon's diversity index increases with the number of species; Legendre and Legendre 2012), suggests that there was no change in the number of resident species on *C. oblonga*-dominated substrate. However, the decline in Simpson's diversity and evenness, metrics that are also directly related (i.e., Simpson's diversity index increases with increased evenness; Clarke et al. 2014), suggests that *C. oblonga* may limit the growth of resident species through competitive overgrowth or the monopolization of space. Conversely, the short-term fouling assemblages during 1971 and 1972 showed a significant increase in diversity (both Shannon's and Simpson's diversity), richness, and evenness over time, suggesting an overall increase in the number of species and lack of dominance by a single species over time (Fig. 8b, c).

Within competitive communities, such as the fouling community where space is often the limiting resource, the life-history characteristics or competitive exclusion of marine organisms can play an important role in shaping species diversity (Dayton 1971, Connell 1978, Sousa 1984). For example, as seen in the 1970s data from S&K described here, the seasonal dominance or short life-cycle of some fouling species can increase the availability of resources (e.g., space) for less competitive or other seasonally abundant species to become established, thus

increasing diversity (Stachowicz and Byrnes 2006, Dijkstra and Harris 2009). Alternatively, some competitively dominant fouling species, such as colonial ascidians, possess chemical defenses that can result in a reduction in diversity by preventing settlement of other organisms (Bryan et al. 2003) or by preventing predation (Lindquist et al. 1992). *C. oblonga*'s acidic tunic (i.e., outer covering) and high vanadium content (Stoecker 1980), both of which are known defenses against epizoid recruitment and predation, may contribute to its ability to dominate and reduce diversity and evenness in this community. In addition to limiting recruitment, tunicates are superior competitors in many fouling communities (Russ 1980, Lambert and Lambert 2003) and are capable of overgrowing resident species (Cifuentes et al. 2010). Life-history characteristics of ascidians that likely enhance their superior competitive ability include their ability to self-fertilize, grow rapidly, and brood larvae (see Rocha and Kremer 2005 and references therein). Given the lack of observed settlement on the surface of *C. oblonga* (K. W. Theuerkauf, *personal observation*) combined with *C. oblonga*'s fast growth rates and consistent spring recruitment, *C. oblonga* may continue to limit diversity within this community.

Clavelina oblonga: an exotic tunicate

C. oblonga was originally identified in Bermuda and has also been observed in Florida and the West Indies (Van Name 1945), and has been introduced into Brazil, the eastern Atlantic, and the Mediterranean Sea (Rocha et al. 2012, Ordóñez et al. 2016). Within the Mediterranean, *C. oblonga* has negatively impacted aquaculture practices through competitive overgrowth of equipment and species of interest, including oyster and mussel spat (Ordóñez et al. 2016). *C. oblonga* has not been identified in Beaufort, North Carolina during extensive field surveys of the fouling community historically or recently (McDougall 1943, Sutherland and Karlson 1977, Karlson and Osman 2012), but has recently been observed in high abundances on similar dock habitats in nearby areas (up to ~10 km from the DURL dock; Appendix S1: Fig. S3), suggesting that its presence and dominance is not an artifact of our experimental design.

The close proximity of the study site to the Port of Morehead City may make the area particularly susceptible to the introduction of *C. oblonga* due to the high volume of shipping traffic that reaches the state port, with many of these vessels containing ballast water (Bishop et al. 2006). Transportation on boat hulls has also been suggested as a possible mechanism for the introduction of *C. oblonga* (Rocha et al. 2012). The short dispersal distances that are characteristic of many ascidians (Olson 1985) coupled with the successful introduction of *C. oblonga* in other regions suggests that *C. oblonga* may have been introduced in Beaufort rather than establishing itself through large-scale water currents. Quantifying dispersal patterns of *C. oblonga* may provide

insight into the mechanisms driving its introduction into new habitats and should be the focus of future studies.

Future research

Novel environmental conditions, such as warming waters, are often attributed to changes in fouling community composition (Dijkstra et al. 2011, Sorte and Stachowicz 2011). Water temperature has been correlated with growth and reproduction timing of *C. oblonga* in other regions (Ordóñez et al. 2016); however, monthly average water temperatures during the course of this study do not appear to be substantially different than the 1970s (Appendix S1: Fig. S1) and thus, likely do not explain *C. oblonga*'s recent establishment in Beaufort, North Carolina. Other environmental factors, including decreased pH, have been determined to negatively impact growth rates (Kroeker et al. 2012) and diversity (Kroeker et al. 2011) of marine benthic communities, which may allow competitively dominant species, such as *C. oblonga*, to outcompete slower growing, less abundant species. However, given the paucity of available detailed environmental data at our study site from the 1970s for comparison with modern data, identifying environmental factors that may be related to the recent establishment of *C. oblonga* in Beaufort is purely speculative and the role of these factors in facilitating *C. oblonga* establishment should be the focus of future studies.

Further experimental evaluation of the role of biological interactions, including competition and predation, would provide insight into the processes that structure an invaded community. Given the significant impact of *C. oblonga* on community dynamics in Beaufort, North Carolina as observed in the present study, future work should focus on the exclusion of *C. oblonga* to determine if the fouling community of Beaufort would develop similarly to observations by S&K in the absence of the dominant competitor. Furthermore, because predators often prevent the monopolization of space by a competitively dominant species (Paine 1966), manipulating predator density may provide insight into relative importance of predation and inter-specific competition among *C. oblonga* and previously established species (e.g., *S. plicata* or *B. neritina*). This experimental manipulation is the focus of current research (Theuerkauf et al., *in preparation*). Furthermore, continued monitoring of *C. oblonga* should be a local management and research priority given its observed negative impacts in other portions of its introduced range.

CONCLUSIONS

Through replicating S&K's classic 1977 community ecology study nearly 50 yr later, we identified similar patterns of community development to those observed by S&K in the short-term (i.e., disturbance date can shape the identity of the dominant species and the overall community structure due to temporal variation in larval

recruitment) and long-term (i.e., declining importance of disturbance date in shaping community structure); however, the species that drive these patterns are dramatically different due to the presence of an exotic tunicate, *Clavelina oblonga*. Our results suggest that the recent introduction of this exotic species has reduced diversity and evenness in the marine fouling community of Beaufort, North Carolina, USA as compared to ~50 yr ago.

Our findings have important implications for understanding and predicting patterns of community development in the face of rapid, ongoing environmental changes and exotic species introductions in both marine and terrestrial environments. Because the observed impact of this exotic fouling species on community development and biodiversity is consistent with impacts associated with other invasive species in aquatic (e.g., zebra mussel) and terrestrial communities (e.g., European cheatgrass), this study highlights the widespread impact that exotic species can have on fundamental ecological processes across a broad range of environments (Pimentel et al. 2005). Furthermore, this study illuminates the need to replicate classic studies in other systems to determine the consistency of community-level ecological processes under altered ecosystem conditions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1277/full>

DATA AVAILABILITY

Data associated with this paper are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5qp96>.