Research Article

The influence of biogenic habitat created by the non-indigenous bryozoan, *Amathia verticillata*, on the resident marine invertebrate community in San Diego, California

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Abstract

The non-indigenous bryozoan, *Amathia verticillata*, has a worldwide distribution and commonly colonizes anthropogenic structures such as docks. Although widely recognized to house marine invertebrates within its structure, little is known regarding how the biogenic material produced by *A. verticillata* influences the marine community dynamics. The purpose of this study was to document the temporal patterns of *A. verticillata* and their associated marine invertebrate community in an urbanized estuary, Mission Bay, San Diego, CA, USA. We quantified *A. verticillata* percent cover and the abiotic conditions between July 2021–2022. The percent cover of *A. verticillata* varied temporally with temperature, with highest percent cover on docksides when temperatures were warmest. We also collected *A. verticillata* colonies of varying morphology and size to determine if abundance, density, and diversity of the marine invertebrate community associated with *A. verticillata* was influenced by its biogenic material and structural complexity. All invertebrates were identified to the lowest taxonomic level possible. We identified 20 families, 19 genera, and 12 organisms to species, representing 2 non-indigenous species (NIS), 2 likely NIS, 3 cryptogenic, and 5 native species. The most abundant taxonomic groups were marine amphipods, isopods, tanaids, and polychaetes. Furthermore, we identified juvenile stages and females with eggs living within *A. verticillata*. The invertebrate community varied significantly by *A. verticillata* morphotype and structural complexity. In general, there was greater invertebrate diversity in the elongated versus compact morphotype, and the invertebrate counts and diversity increased with structural complexity. Collectively, our results suggest that *A. verticillata* functions as a habitat-producing ecosystem engineer that may be providing an important nursery habitat for diverse groups of marine invertebrates, including other NIS, on anthropogenic structures.

Key words: Ecosystem engineers, structural complexity, non-indigenous species, nursery habitat, habitat-producing bryozoans

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Introduction

Non-indigenous species (NIS) are a pervasive problem in marine ecosystems (Vitousek et al. 1997; Chan and Briski 2017), driving ecological changes and threatening global biodiversity (reviewed in Bax et al. 2003). NIS are often characterized by rapid growth, and their establishment can affect resource availability for other organisms, and lead to declines in native species (Molnar et al. 2008; Katsanevakis et al. 2014; Geburzi and McCarthy 2018). Furthermore, some NIS act as ecosystem engineers that physically alter habitats by changing biotic or abiotic conditions (Jones et al. 1994; Jones et al. 1997). The effects of non-indigenous ecosystem engineers on community abundance and diversity can be variable (Guy-Haim et al. 2017), and context-dependent (Crooks 2002). For instance, if non-indigenous ecosystem engineers become established on a homogeneous surface and increase complexity by producing multidimensional biogenic habitat, the associated community often increases in abundance, richness, and diversity (reviewed by Crooks 2002). One such non-indigenous structure-producing ecosystem engineer is the ctenostome bryozoan, *Amathia verticillata* (previously *Zoobotryon verticillatum* [Delle Chiaje, 1822]), also known as spaghetti bryozoan.

Amathia verticillata is found in relatively shallow, tropical to temperate areas (Cohen et al. 2005; Galil and Gevili 2014; Obaza and Williams 2018), where it grows densely, sometimes exceeding 1.5 m in length with branching, tangled noodle-like strands (McCann et al. 2015). It has a worldwide distribution; however, there is no universal agreement on its origin (Winston 1995; Galil and Gevili 2014; Marchini et al. 2015; Nascimento et al. 2021). Some suggest that *A. verticillata* is cryptogenic with an unknown native range (Nascimento et al. 2021), while others provide evidence for a Caribbean origin (Winston 1995; Galil and Gevili 2014), or indicate that this species is native to the Atlantic Ocean (Ounifi-Ben Amor et al. 2016). Despite this uncertainty, *A. verticillata* is commonly recognized as a NIS in the northeastern Atlantic (Amat and Tempera 2009), Mediterranean Sea (Ramadan et al. 2006; Galil and Gevili 2014), southern Mexican Pacific (Humara-Gil and Cruz-Gómez 2019), Galápagos Islands (McCann et al. 2015), Madeira Island (Wirtz and Canning-Clode 2009), Brazilian waters (Miranda et al. 2018), southeast coast of India (Jebakumar et al. 2017), and southern California (Cohen et al. 2005; Obaza and Williams 2018; Zavacki et al. 2024).

Amathia verticillata generally colonizes hard anthropogenic structures such as docks (Cohen and Carlton 1995; Winston 1995; Amat and Tempera 2009; Wirtz and Canning-Clode 2009; Obaza and Williams 2018), consequently providing a complex biogenic habitat on surfaces that might otherwise have a lower ecological value (Schlaepfer et al. 2011; Katsanevakis et al. 2014). Coupled with the observation that percent cover of *A. verticillata* often exceeds that of native species on anthropogenic substrates (Obaza and Williams 2018), *A. verticillata* has the potential to substantially impact the ecology of fouling communities on docks, especially for small benthic invertebrates that can play crucial roles in connecting trophic levels and influencing the function of ecosystems (e.g., Martins and Barros 2022; Ritter and Bourne 2024). Examples of the fauna associated with *A. verticillata* include mobile crustaceans such as amphipods (Guerra-García et al. 2011; Marchini et al. 2015; Guerra-García et al. 2024; Zavacki et al. 2024) and isopods (Marchini et al. 2015; Marchini et al. 2018; Guerra-García et al. 2024; Zavacki et al. 2024), polychaetes, pycnogonids, and bivalves (Farrapeira 2011; Guerra-García et al. 2024; Zavacki et al. 2024). Additional invertebrate and fish species also use drifting *A. verticillata* patches as ephemeral estuarine habitats (Pederson and Peterson 2002; Anderson et al. 2022).

In a recent study conducted along the Iberian Peninsula and north African coast, peracarid crustaceans, especially amphipods, dominated the macrofaunal

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communities associated with *A. verticillata* collected from docks within marinas (Guerra-García et al. 2024). Amphipods utilize microhabitats created by foundation species, and the trophic pathways they support contribute to ecosystem functioning (reviewed by Ritter and Bourne 2024). For example, amphipod grazing can determine the composition of fouling community assemblages by preventing periphyton and ascidians from colonizing and overgrowing seagrasses (Duffy and Harvilicz 2001). Thus, the fouling community dynamics along docks colonized by *A. verticillata* could be driven by the macrofauna that reside within *A. verticillata*. To begin to understand the ecological role of the amphipods and other invertebrates that inhabit *A. verticillata*, a critical first step is identifying which species are present and their relative abundances. We also need to identify the invertebrate community to determine whether *A. verticillata* facilitates the establishment and spread of other NIS as has been shown along the Iberian Peninsula and north Africa where seven NIS accounted for more than 50% of the total abundance of the macrofaunal species collected in *A. verticillata* (Guerra-García et al. 2024). There is concern that if *A. verticillata* facilitates the establishment of other NIS, there could be negative synergistic impacts on native species, resulting in an invasion meltdown (Guerra-García et al. 2024).

Mission Bay, San Diego, CA, USA is an urbanized estuary where *A. verticillata* is known to colonize docks (Dexter and Crooks 2000; Tracy and Reyns 2014; Obaza and Williams 2018; Zavacki et al. 2024). While the presence of *A. verticillata* in Mission Bay has been previously documented, in this study we systematically characterized the temporal dynamics of *A. verticillata* colonization with respect to the environmental conditions at one site in Mission Bay and identified the associated invertebrate community to determine the degree to which *A. verticillata* serves as a habitat for other NIS. Furthermore, we examined if abundance, density, and diversity of the marine invertebrate community associated with *A. verticillata* was influenced by the biogenic material produced by, and structural complexity of, *A. verticillata*. To date, the role that the *A. verticillata* biogenic structure itself plays in determining the community dynamics of its inhabitants is not well understood.

Methods

The first goal of our study was to document the temporal patterns of *A. verticillata* colonization to understand how *A. verticillata* and its associated invertebrate community changed over time. Elsewhere (see Zavacki et al. 2024) we document the spatial patterns of *A. verticillata* colonization in Mission Bay. Here, we focused our efforts at one site, the South Shores (32°45.85'N, 177°13.05'W) dock in Mission Bay, San Diego, California, USA (Fig. 1), because *A. verticillata* has been consistently observed here during the last decade (Reyns, personal observation), and sampling at one site allowed for sampling on a relatively high-resolution temporal scale (usually weekly, but see below) from July 2021 to July 2022. To examine the environmental conditions that might impact the colonization of *A. verticillata*, a YSI ProDSS (digital sampling system) handheld multiparameter meter was used to record a point measure of surface temperature, salinity, and dissolved oxygen (DO). Precipitation data was also collected at the San Diego Airport (Menne et al. 2012), located ~9.65 km from the center of Mission Bay. To determine how the distribution of *A. verticillata* varied weekly, we quantified the percent cover of *A. verticillata* on the dock within 5 randomly selected 25 × 25 cm fixed quadrats. These data were used to calculate the average percent cover of *A. verticillata* per week.

To identify the invertebrate community associated with *A. verticillata*, three replicate colonies (of low, medium, and high biogenic material; see below for definitions) were collected from locations on the dock outside of the fixed quadrats, once per week
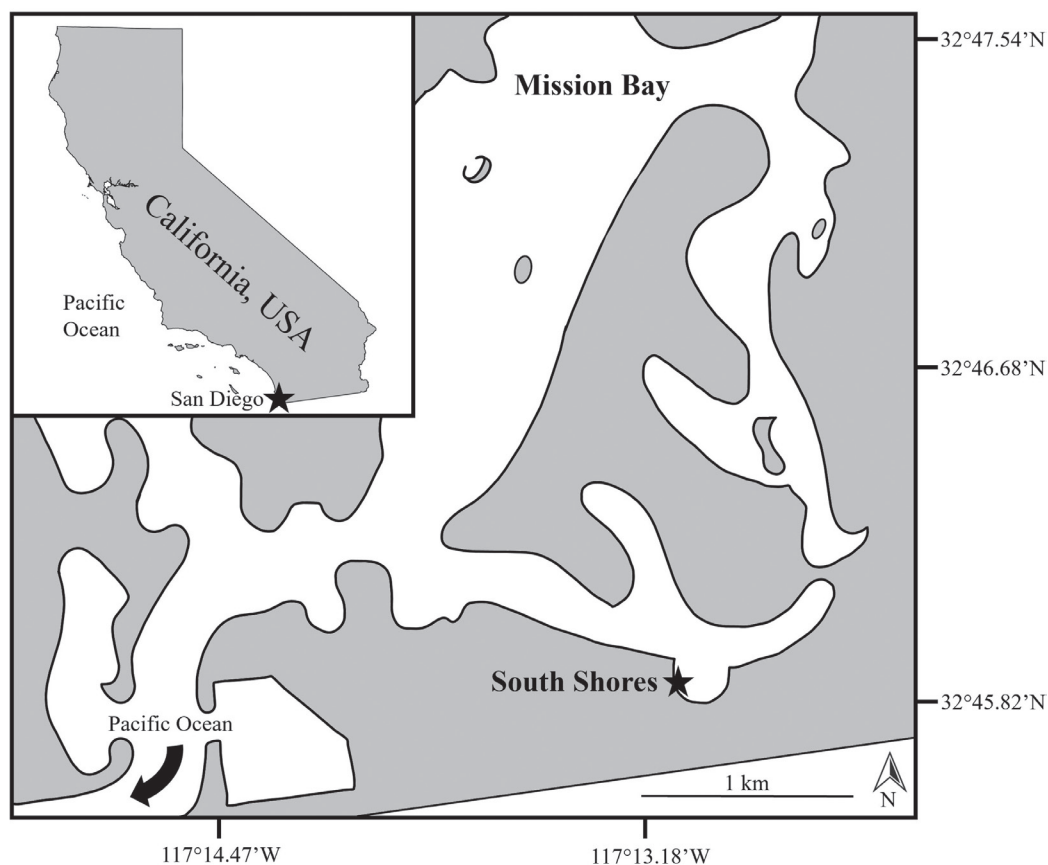
Figure 1. Map of Mission Bay, San Diego, CA with sampling station, South Shores denoted by the star. Inset shows location of San Diego in California, USA for reference.

from July through December 2021, when colonies disappeared. Collections were resumed once per month after colonies returned to the dock, from March through June 2022 (n = 84 samples). Upon collection, each *A. verticillata* colony was categorized by morphotype (compact: ≤ 25 cm or elongated: > 25 cm from the dock). *Amathia verticillata* and their associated marine organisms were collected by surrounding the colony (depending on its size) with a 100 µm, 18 × 42 cm or 10.5 × 20 cm mesh bag, placing the sample into a gallon-sized Ziplock bag, and storing it in a cooler with ice to prevent degradation during transport to the lab for further processing.

In the laboratory, each *A. verticillata* colony was removed from the collection bags and placed in a 5-gallon bucket filled with seawater. The *A. verticillata* colony was shaken 10 times by hand to remove all associated marine organisms, and the colony was returned to the Ziplock bag for processing after sample sieving. The bucket water was filtered through nested 100, 200, and 400 µm mesh sieves to collect the organisms associated with *A. verticillata*. This process was repeated three times to ensure that most of the organisms had been successfully removed from each *A. verticillata* colony (as determined by a pilot study: Zavacki 2023). Organisms were placed in containers by sieve size and preserved in 100% ethanol until they could be counted and identified.

Each *A. verticillata* colony was removed from its Ziplock bag and five random kenozooids per colony were selected to measure widths using a Meiji Techno stereo microscope with a RZ PLAN 1× lens and an ocular micrometer. Once measured, the colony was placed in a drying oven at 50 °C for 24 h to obtain the *A. verticillata* dry weight of each sample. The preserved invertebrate samples were divided using a Folsom plankton splitter if they were dense, then sorted under a Meiji Techno stereo microscope

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with a RZ PLAN 1× lens. Organisms were separated into broad taxonomic groups: amphipods, isopods, tanaids, polychaetes, copepods, unknowns, and other organisms that could be identified but were less abundant, such as gastropods, bivalves, and nematodes (called "others"). The organisms collected in the 100 μm sieve were primarily pelagic copepods which were assumed to be swimming in and around *A. verticillata* colonies and not necessarily using the bryozoan as a benthic habitat; thus, they were not identified to species and were excluded from further analysis. The 200 and 400 μm sieved amphipods, isopods, tanaids, and polychaetes were identified to the lowest taxonomic level possible using published resources (SCAMIT 2004; Fofonoff et al. 2018; SCAMIT 2023) and by working with taxonomists (Dean Pasko and Tony Phillips, personal communication). Species names and systematic arrangement of taxa were arranged following the World Register of Marine Species (WoRMS Editorial Board 2023). In addition, invertebrates were categorized into four main life history stages: immature organisms, adults (males and females without eggs), females with eggs, and unknowns. Finally, we classified the introduction status for the 12 peracarid crustaceans and polychaetes that we could identify to species as native, NIS, likely NIS, and cryptogenic using published records (Menzies 1952; Chapman 2007; Maloney 2007b, a; Fofonoff et al. 2018) and taxonomic experts (Dean Pasko and Tony Phillips, personal communication). The 'likely NIS' category were species of uncertainty because their biogeographic ranges prevented their inclusion in the other defined categories.

Given that the size of *A. verticillata* colonies varied by collection, we standardized the invertebrate counts within *A. verticillata* by dividing the number of organisms collected per colony by the dry weight of that colony. Thus, we used density (number of invertebrates per gram of dry weight of *A. verticillata*) as the response variable to compare the marine invertebrate communities associated with each *A. verticillata* morphotype (compact versus elongated). To determine if the amount of *A. verticillata* biogenic material, or structure, influenced the associated invertebrate community, we also separated the weekly *A. verticillata* samples into three bins based on the *A. verticillata* dry weight: low, defined as < 0.5 g (n = 44 replicates), medium defined as 0.5–5 g (n = 28 replicates), and high defined as > 5 g (n = 12 replicates). We considered these *A. verticillata* dry weight bins, which are a way to quantify the amount of biogenic material in each colony, to serve as a proxy for structural complexity based on observations that colonies that were larger and greater in weight, were also bushier and more developed with branching stolons. All invertebrates were counted and identified to the lowest taxonomic level possible as described above. We used the raw counts (not standardized by *A. verticillata* dry weight) to compare the marine invertebrate communities by structural complexity bin.

Statistical analyses

We examined the relationship between *A. verticillata* percent cover and the abiotic conditions (n = 45 weeks) using a Spearman's correlation (SPSS v. 28.0). To examine the community dynamics of the invertebrates inhabiting *A. verticillata*, all analyses were performed using PRIMER-e v. 7 with the add-on PERMANOVA package (Clarke et al. 2014). We focused on the most abundant taxonomic groups: peracarid crustaceans and polychaetes. To undertake a comprehensive statistical analysis of the entire invertebrate community, we combined the abundances in the 200 and 400 μm sieves; thus, the response variables used in the analyses were the total organism density for each sampling date. Species and genera were grouped to family level since not all organisms could be identified to species.

To determine if there were differences in the marine invertebrate community density by *A. verticillata* morphotype, or differences in the marine invertebrate

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community counts by *A. verticillata* structural complexity bins, we used two separate repeated measures, one-factor permutational multivariate analysis of variance (PERMANOVA) tests, with two levels for morphotype: compact or elongated and three levels for structural complexity: low, medium, and high. Prior to analysis, the invertebrate community densities and counts were fourth root-transformed. We used the Bray-Curtis similarities in the analysis, with 9999 permutations. Similarity percentage (SIMPER) tests using Euclidian distance were then used to determine which families contributed most to dissimilarities in the invertebrate communities by *A. verticillata* morphotype and structural complexity (Clarke and Warwick 2001). Given that kenozooid widths might also contribute to differences between both *A. verticillata* morphotypes, a t-test was used to compare the kenozooid widths of compact and elongated colonies (SPSS v. 28.0).

The Shannon-Wiener Diversity index (H') was also used to determine whether the invertebrate community diversity varied with *A. verticillata* structure (Shannon and Weaver 1949). Consequently, we calculated the average diversity index H' for each morphotype and structural complexity bin.

Results

When we started sampling in July 2021, the percent cover of *A. verticillata* colonies was ~20% but increased to over 80% less than one month later (Fig. 2A). During the peak of *A. verticillata* coverage, we observed colonies that extended from the dock to the sediment below (~2.6 m deep) as well as small patches that covered the benthos adjacent to the dock. Percent cover was above 20% through the fall months, before declining in October 2021, and disappearing from the dock sides from January 4 through March 15, 2022 (Fig. 2A). In the spring, *A. verticillata* percent cover increased from 0% in March to 7.6% in July 2022 when sampling was terminated. This seasonal pattern in *A. verticillata* percent cover followed the seasonal temperature patterns we observed (Fig. 2A). Although there were temperature fluctuations throughout the sampling period, temperatures decreased overall during the fall months from a 25.8 °C high in August to the 14.2 °C low in late December 2021 and increased through the spring months. Additionally, during the period of relatively low *A. verticillata* percent cover, there were periodic decreases in salinity (e.g., late October 2021, late December 2021, and early April 2022) that corresponded to rain events; indeed, the lowest salinities corresponded to the late fall through early spring months when precipitation occurred (Fig. 2B). While salinity fluctuated weekly, it generally remained between 33–34 PSU throughout the study period. Similarly, DO varied weekly, but values were above 4 mg L^{-1} throughout the study period (Fig. 2C). Generally, DO values were highest during the winter through early spring months when temperatures were the lowest (Fig. 2A, C). Overall, when we examined the relationship between the percent cover of *A. verticillata* and the abiotic conditions, there was a significant positive relationship between *A. verticillata* and temperature (Spearman correlation coefficient = 0.74, p < 0.0001). There were also significant relationships between temperature and salinity (Spearman correlation coefficient = 0.51, p < 0.0004) as well as temperature and DO (Spearman correlation coefficient = -0.87, p < 0.0001), whereby increasing temperatures corresponded to increasing salinity and decreasing DO. Given the autocorrelations between abiotic variables, we did not run additional correlations between the percent cover of *A. verticillata* and salinity or DO.

Within *A. verticillata*, we identified marine invertebrates from 20 families, 19 genera, and 12 species (Table 1). Of the invertebrates we could identify to species, we observed more native species (e.g., *Paracerceis sculpta* and *Odontosyllis phosphorea*)
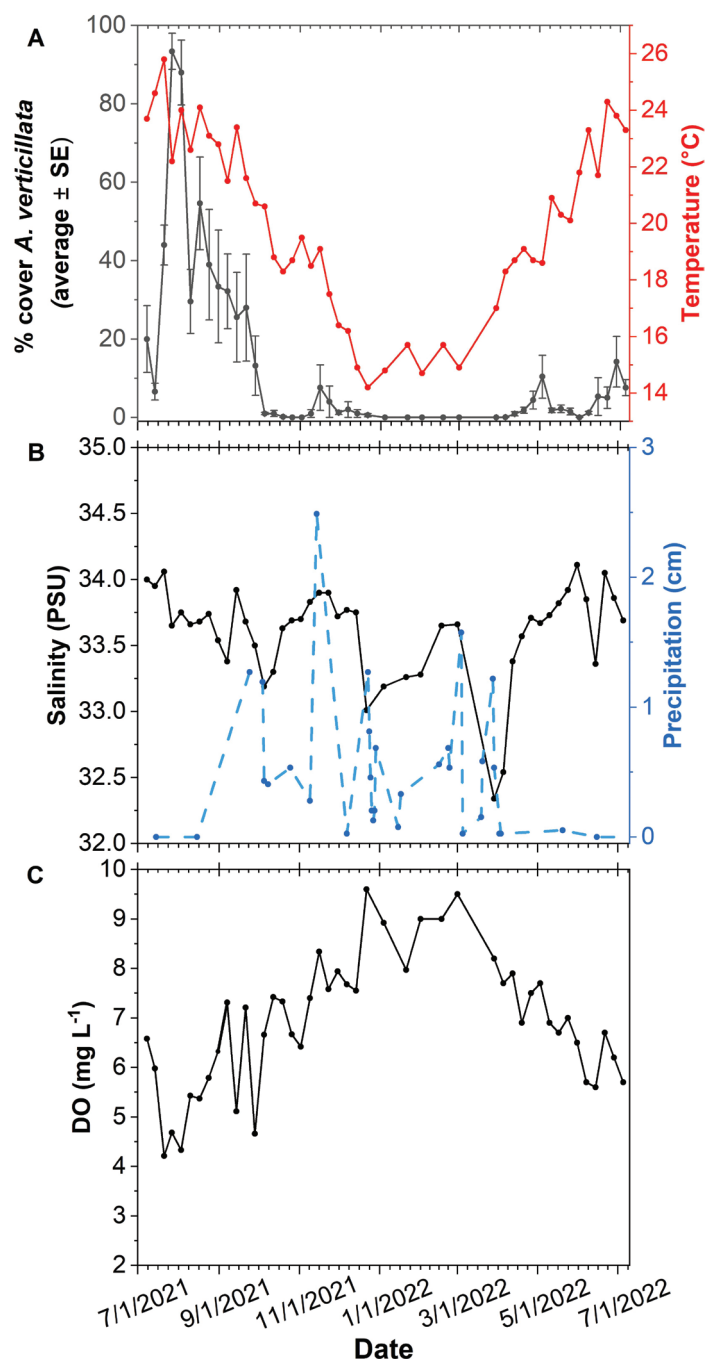
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Figure 2. *Amathia verticillata* percent cover and abiotic conditions. (**A**) *Amathia verticillata* percent cover (left y-axis) and temperature (right y-axis), (**B**) salinity (left y-axis) and precipitation (right y-axis), and (**C**) dissolved oxygen (DO) over time.

than introduced species (e.g., *Aoroides secunda* and *Paranthura japonica*) at the beginning of sampling until *A. verticillata* experienced a winter die-off (Figs 2A, 3). Interestingly, once *A. verticillata* started to grow back on the dock in March 2022, the first species to recolonize were NIS, along with possibly less common species, given the relatively high percentage (e.g., > 80%) of unknown species also observed during this time (Table 1, Fig. 3). Native species returned to the *A. verticillata* after the introduced species and appeared to increase in relative abundance as *A. verticillata* became more established (Fig. 3). An important consideration is that during most sampling dates, more than half the of the organisms we collected were immature juveniles that could not be identified to species.

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Table 1. Peracarid crustaceans and polychaetes collected within *Amathia verticillata*. When organisms were identified to species, introduction status (native, likely NIS, NIS, cryptogenic) and the source of the reference for the introduction status is also included. Species names and systematic arrangement of taxa were arranged to follow the World Register of Marine Species (WoRMS Editorial Board 2023).

Species Name	Phylum	Family	Introduction Status	Source
Dorvillea **sp.**	Annelida	Cirratulidae		
	Annelida	Dorvilleidae		
	Annelida	Spionidae		
Odontosyllis phosphorea Moore, 1909	Annelida	Syllidae	Native	Personal com.: Tony Phillips, 2023
Salvatoria **sp.**	Annelida	Syllidae		
Syllis gracilis **s.l.** Grube, 1840	Annelida	Syllidae	Cryptogenic	Personal com.: Tony Phillips, 2023
Syllis **spp**.	Annelida	Syllidae		
	Arthropoda	Amphilochidae		
Leucothoe alata J. L. Barnard, 1959	Arthropoda	Leucothoidae	Cryptogenic; Likely NIS	Maloney et al. 2007b; Chapman 2007
Ampithoe **sp**.	Arthropoda	Ampithoidae		
Aoroides secunda Gurjanova, 1938	Arthropoda	Aoridae	NIS	Fofonoff et al. 2018
Caprella californica Stimpson, 1856	Arthropoda	Caprellidae	Native	Maloney et al. 2007a, 2007b
Laticorophium baconi (Shoemaker, 1934)	Arthropoda	Corophiidae	Cryptogenic	Maloney et al. 2007b
Paradexamine **sp.**	Arthropoda	Dexaminidae		
Protohyale **sp.**	Arthropoda	Hyalidae		
Ericthonius brasiliensis (Dana, 1853)	Arthropoda	Ischyroceridae	Likely NIS	Chapman 2007; Personal com.: Dean Pasko & Tony Phillips, 2023
Ianiropsis analoga Menzies, 1952	Arthropoda	Janiridae	Native	Menzies 1952; Personal com.: Dean Pasko & Tony Phillips, 2023
Elasmopus **sp.**	Arthropoda	Maeridae		
Quadrimaera **sp.**	Arthropoda	Maeridae		
Paranthura elegans Menzies, 1951	Arthropoda	Paranthuridae	Native	Personal com.: Dean Pasko, 2023
Paranthura japonica Richardson, 1909	Arthropoda	Paranthuridae	NIS	Fofonoff et al. 2018
Podocerus **spp.**	Arthropoda	Podoceridae		
	Arthropoda	Pontogeneiidae		
Paracerceis sculpta (Holmes, 1904)	Arthropoda	Sphaeromatidae	Native	Fofonoff et al. 2018
Zeuxo normani **s.l.** (Richardson, 1905)	Arthropoda	Tanaididae	Cryptogenic	Maloney et al. 2007b

The most abundant taxonomic groups we identified inhabiting *A. verticillata* were amphipods, isopods, tanaids, and polychaetes (Fig. 4A). Amphipods dominated our samples, but the relative abundance of each taxonomic group varied slightly by *A. verticillata* morphotype, with more amphipods, isopods and tanaids collected in compact *A. verticillata* than in the elongated morphotype (Fig. 4A). In contrast, the elongated morphotype had more polychaetes (33.4% composition) than in the compact morphotype (only 7.3%; Fig. 4A). In both morphotypes, tanaids made up less than 1% of the community composition (Fig. 4A). Notably, both *A. verticillata* morphotypes housed all life history stages of these invertebrate groups with immature organisms being the most frequently observed in the compact (67.1%) and elongated (49.1%) morphotypes (Fig. 4B). There were slightly more adult stages in the compact (18.5%) than elongated (15.5%) morphotype, and relatively small percentages of reproductive females (2.3–5%; Fig. 4B). However, a number of individuals collected could not be identified, and the elongated morphotype had more than three times the percent of unknown species (i.e., immature stages) in comparison to the compact morphotype (Fig. 4B).

Overall, there were differences between the *A. verticillata* morphotypes and their associated marine invertebrate communities. A t-test indicated that there was a significant difference between kenozooid width of the two morphotypes (t_{109} = -2.634, p = 0.01), with elongated kenozooids having significantly greater widths than those

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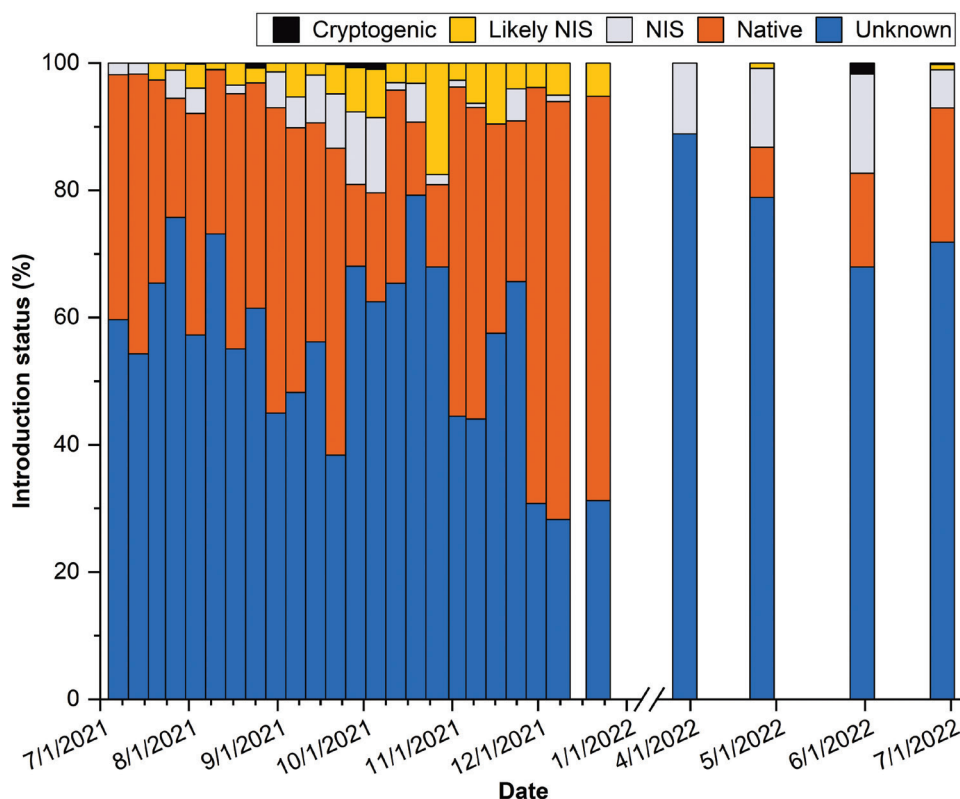
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Figure 3. Introduction status and % composition of the invertebrate community associated with *Amathia verticillata* over time. Introduction status from top to bottom are % of species in *Amathia verticillata* that were: cryptogenic (black), likely NIS (yellow), NIS (grey), native (orange), and unknown (blue) during the sampling times (once per week from July - December 2021, and once per month from March - June 2022; noted as Month/Day/Year).

of the compact morphotype. Furthermore, the marine invertebrate community varied significantly by morphotype (PERMANOVA, $F_{1,79}$ = 2.45, p = 0.02, 9956 unique permutations). The average invertebrate densities were similar in compact and elongated colonies (Fig. 5A), but invertebrate diversity was slightly higher in elongated colonies (H': 1.94 ± 0.05) than in compact colonies (H': 1.61 ± 0.06; Fig. 5B). There were also slight differences in the percent contribution of families to the invertebrate communities associated with the compact and elongated morphotypes (Table 2). Compact colonies had an average similarity of 58.08%, whereas the elongated colonies had an average similarity of 65.91% (Table 2). The highest contributions to the similarities in the invertebrate community were > 13% and by the same isopod family (Sphaeromatidae; Table 2) for both morphotypes. Additionally, the Corophiidae amphipods had a higher percent contribution to the communities in the compact than elongated morphotypes (15.83% versus 9.58%, respectively; Table 2). The Podoceridae amphipods also had a higher percent contribution to the communities in the compact than elongated morphotypes (13.69% versus 11.02%, respectively; Table 2). In contrast, the Hyalidae, Ampithoidae and Amphilochidae amphipods, and Syllidae polychaetes had higher percent contributions in the elongated colonies than the compact colonies (Table 2). The average dissimilarity between the two morphotypes was 39.25% (Table 2). Although the Hyalidae amphipods were the highest contributing invertebrate family to those differences, all invertebrate family contributions to the differences were under 8% (Table 2).

With respect to *A. verticillata* structure, the marine invertebrate community varied significantly by structural complexity bin (PERMANOVA, $F_{2,81}$ = 13.3, p = 0.0001, 9919 unique permutations). Average invertebrate count increased

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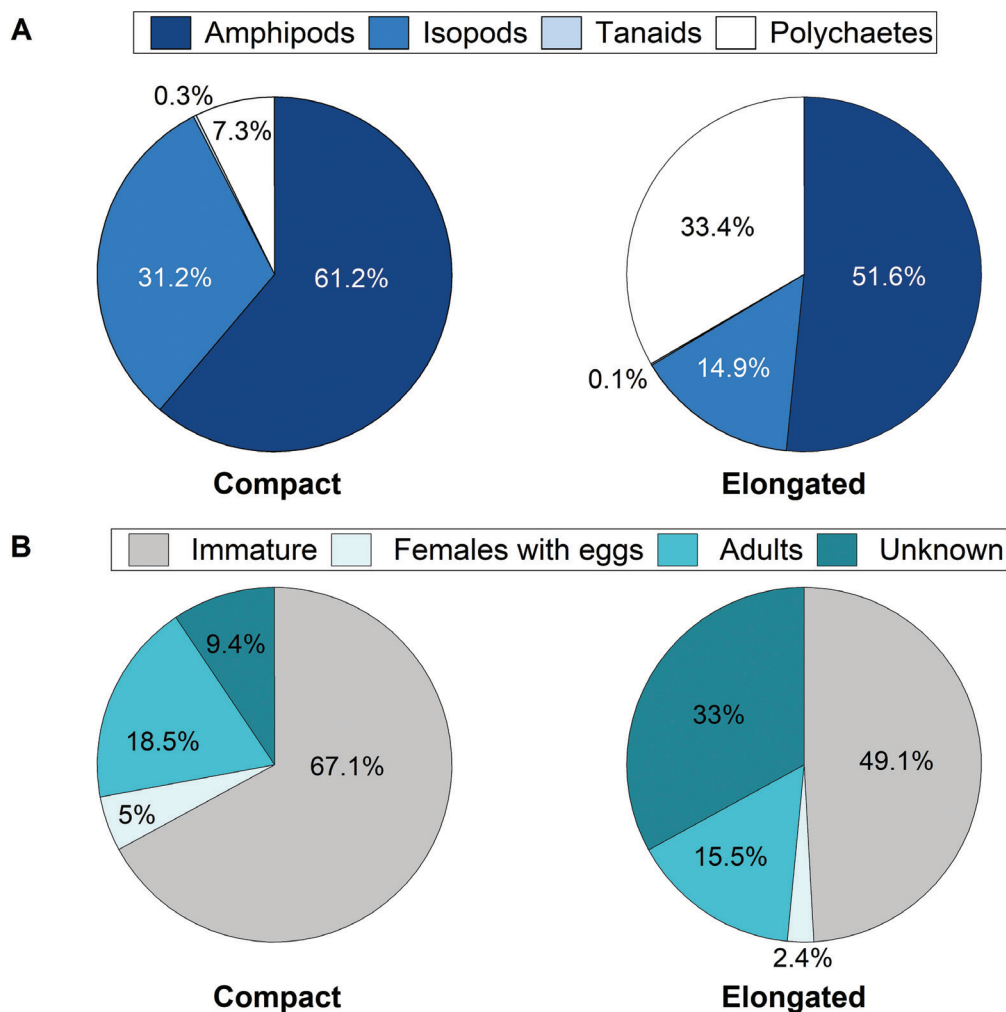
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Figure 4. *Amathia verticillata* morphotype and invertebrate composition. Composition of taxonomic groups (top row) and life history stages (bottom row) of peracarid crustaceans and polychaetes associated with *Amathia verticillata* compact (left columns) and elongated (right columns) morphotypes. Percentages by: (**A**) invertebrate groups: amphipods, tanaids, isopods, and polychaetes, and (**B**) life history stages: immature (juveniles), females with eggs, adults (males and females without eggs), and unknowns.

with increasing *A. verticillata* structural complexity from ~147 individuals in low structural complexity, ~726 individuals in the medium structural complexity, and ~2,195 individuals in the high structural complexity bin (Fig. 6A). Likewise, invertebrate diversity also increased from the low (H': 1.49 ± 0.07) to medium (H': 1.92 ± 0.05) structural complexity bins but was relatively similar between medium and high structural complexity (H'~1.9; Fig. 6B). The SIMPER analysis indicated that the average similarity among the bins was above 52%, with increasing similarity as *A. verticillata* structural complexity increased (Table 3). Sphaeromatidae isopods were the greatest contributor to these similarities, ranging ~ 12–19% contribution among each *A. verticillata* structural complexity bin (Table 3). The Corophiidae and Podoceridae amphipods had relatively high percent contributions to the community when *A. verticillata* had low structural complexity, with decreasing percent contributions as structural complexity increased (Table 3). In contrast, the Hyalidae amphipods had relatively high contributions to the communities when *A. verticillata* had medium to high structural complexity (Table 3). The low and high *A. verticillata* structural complexity bins had the greatest average dissimilarity (54.66%; Table 3). The invertebrate families all contributed less than 10% to these differences between *A. verticillata* structural complexity bins (Table 3).

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Table 2. SIMPER analysis for *Amathia verticillata* morphotypes. One-way SIMPER (**A**) among and (**B**) between morphotypes: compact (≤25 cm) and elongated (>25 cm) *Amathia verticillata* colonies on the fourth-root-transformed peracarid crustacean and polychaete data, summed to family level with a Bray-Curtis similarity. Cut off for low contributions is 70%.

| Morphotype	Avg. Similarity	Contributions	% Contribution
Compact	58.08	Sphaeromatidae	16.94
		Corophiidae	15.83
		Podoceridae	13.69
		Ampithoidae	9.15
		Hyalidae	7.47
		Syllidae	6.25
		Amphilochidae	5.89
Elongated	65.91	Sphaeromatidae	13.28
		Podoceridae	11.02
		Hyalidae	10.34
		Corophiidae	9.58
		Ampithoidae	9.52
		Syllidae	8.74
		Amphilochidae	6.93
Compact & Elongated	39.25	Hyalidae	8.16
		Syllidae	7.96
		Sphaeromatidae	7.70
		Aoridae	6.74
		Corophiidae	6.60
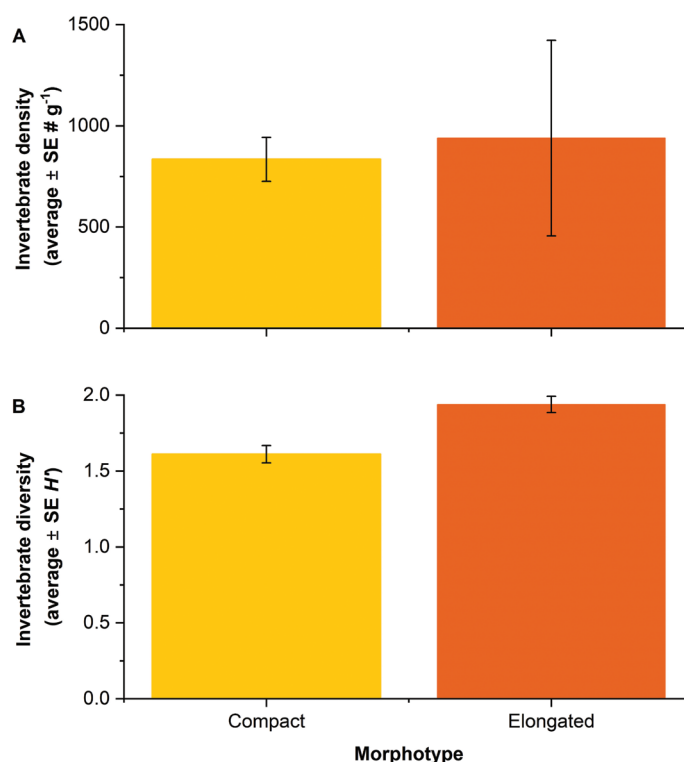
Figure 5. *Amathia verticillata* morphotype and invertebrate density and diversity. Average ± standard error of the peracarid crustaceans and polychaete invertebrate (**A**) density (# individuals/dry weight of *Amathia verticillata*) and (**B**) diversity (represented by the Shannon-Wiener Diversity index, *H'*), associated with *Amathia verticillata* compact and elongated morphotypes.

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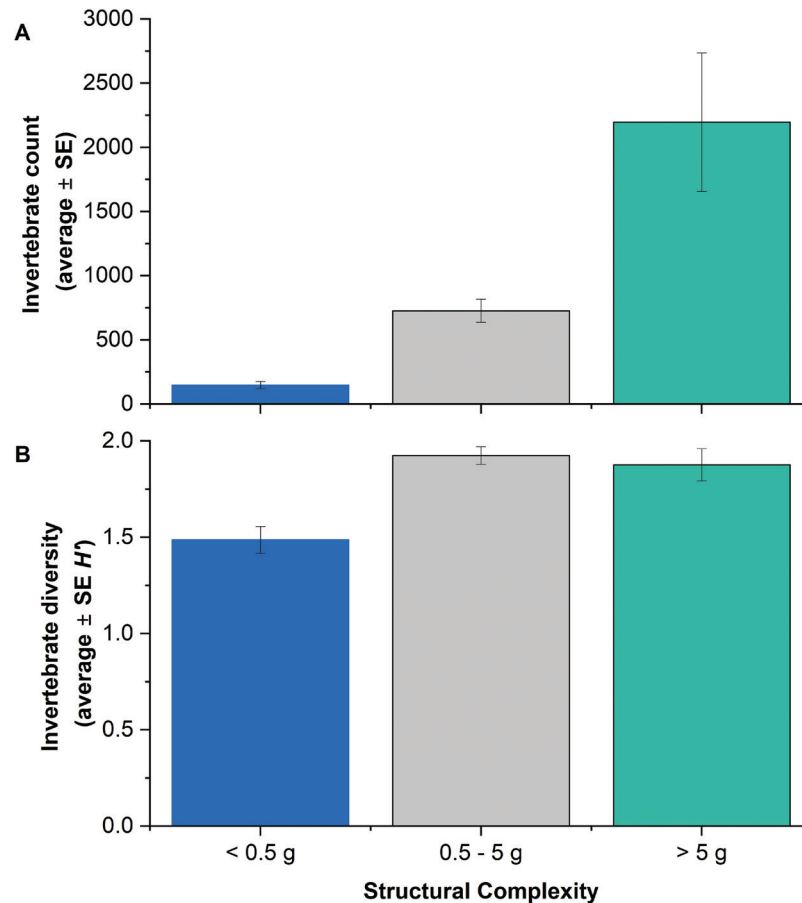
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Figure 6. *Amathia verticillata* structural complexity and invertebrate density and diversity. Average ± standard error of the peracarid crustaceans and polychaete invertebrate (**A**) counts, and (**B**) diversity (represented by the Shannon-Wiener Diversity index, H'), associated with *Amathia verticillata* structural complexity bins, low: < 0.5 g, medium: 0.5–5 g, and high: > 5 g.

Discussion

In Mission Bay, we observed seasonal changes in the percent cover of *A. verticillata*, which broadly followed observed temperature fluctuations. *Amathia verticillata* dominated the sides of the dock at the end of the summer/early fall with greater than 80% cover, but as has been reported elsewhere (Winston 1995; Coleman 1999; Micael et al. 2018; Guerra-García et al. 2024), colonies declined once temperatures decreased below 19 °C (October). Indeed, experiments indicate that growth and sexual reproduction of *A. verticillata* are limited by temperature (Bullivant 1968). In the winter (between December and February), *A. verticillata* disappeared from the sides of the dock, similar to observations from the Indian River Lagoon, Florida where *A. verticillata* died-back when the first cold fronts lowered water temperatures (Winston 1995). In addition to the quadrats we sampled on the dock sides, video surveys taken on the undersides documented the absence of *A. verticillata* on all floating dock surfaces during the winter in Mission Bay (Zavacki, personal observation). The ability of *A. verticillata* to recolonize docks relatively quickly as temperatures increased in the spring suggests that a source of new individuals might exist locally. Winston (1995) hypothesized that *A. verticillata* fragments overwinter to produce new growth the next spring. This might also be true in Mission Bay if the benthos acts as a repository for *A. verticillata* fragments that can resume sexual reproduction and release larvae in the spring. Alternatively, when a colony undergoes fragmentation, pieces of stolon may form resting buds that can eventually re-attach

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Table 3. SIMPER analysis for *Amathia verticillata* structural complexities. One-way SIMPER for (**A**) among and (**B**) between structural complexity bins: low < 0.5 g, medium 0.5–5 g, and high > 5 g on the fourth-root-transformed peracarid crustacean and polychaete data, summed to family level with a Bray-Curtis similarity. Cut off for low contributions is 70%.

Structural complexity	Avg. Similarity	Contributions	% Contribution
Low	52.40	Sphaeromatidae	18.58
		Corophiidae	17.88
		Podoceridae	14.31
		Ampithoidae	9.30
		Unknown	6.98
		Syllidae	6.18
Medium	68.10	Sphaeromatidae	13.10
		Podoceridae	11.59
		Hyalidae	11.28
		Corophiidae	10.19
		Ampithoidae	9.54
		Syllidae	7.97
High	73.94	Sphaeromatidae	12.49
		Hyalidae	10.19
		Podoceridae	9.82
		Corophiidae	8.50
		Ampithoidae	8.45
		Syllidae	7.87
Low & Medium	48.69	Hyalidae	9.09
		Sphaeromatidae	8.61
		Ampithoidae	6.87
		Podoceridae	6.69
		Aoridae	6.63
Low & High	54.66	Hyalidae	9.55
		Sphaeromatidae	9.05
		Podoceridae	7.57
		Syllidae	7.39
		Dexaminidae	6.83
Medium & High	31.62	Sphaeromatidae	7.75
		Dexaminidae	6.98
		Ischyroceridae	6.98
		Hyalidae	6.70
		Aoridae	6.51

to substrates and grow into a new colony (as discussed in Geiger and Zimmer 2002). It is unknown whether resting buds remained attached to the dock surfaces but were too small to be readily observed, or whether such buds can reside in the sediment below the docks and become resuspended during storms or by boats to foster recolonization when environmental conditions become optimal for growth.

The period with the lowest *A. verticillata* percent cover (fall through early spring months) and temperatures corresponded to increased rain events, more variable salinity, and slightly higher DO as storms occurred. Such events were often accompanied by increased winds, and coupled with the lower temperatures, may have led to more detachment from the docks and fragmentation of *A. verticillata*. Together with tidal flushing, these environmental conditions may prevent *A. verticillata* from accumulating under the docks and causing local decreases in DO when *A. verticillata* degrades. During this study, DO at South Shores did not fall below levels considered stressful

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for biological activity (< 2–3 mg/L; https://www.epa.gov/ms-htf/hypoxia-101). Overall, salinity in Mission Bay throughout the year was within the optimal salinity range (22–35 PSU) documented for *A. verticillata* (Nair et al. 1992). Thus, it is unlikely that the survival of *A. verticillata* was hindered by the salinity in Mission Bay.

While benthic, calcifying bryozoans provide complex habitats for diverse assemblages of infaunal organisms (reviewed in Wood et al. 2012; Wood and Probert 2013), non-calcifying species such as *A. verticillata* that are commonly found in fouling communities on anthropogenic structures similarly house a variety of marine invertebrates (Winston 1995; Pederson and Peterson 2002; Guerra-García et al. 2011; Minchin 2012; Marchini et al. 2015; Dailianis et al. 2016; Marchini et al. 2018; Guerra-García et al. 2024). In this study, we identified 20 families representing peracarid crustaceans (amphipods, isopods, and tanaids) and polychaetes that were associated with *A. verticillata*. While the species we observed differed at times to those observed in other studies, there were commonalities among the families represented in *A. verticillata*, including the Caprellidae, Sphaeromatidae, and Paranthuridae (Guerra-García et al. 2011; Marchini et al. 2015; Marchini et al. 2018; Guerra-García et al. 2024), suggesting that *A. verticillata* supports similar assemblages of organisms across its global distribution.

At South Shores, we identified five native species, two NIS, two likely NIS, and three cryptogenic species. If we eliminate the organisms we could not identify (e.g., the "unknowns"), unlike Guerra-García et al. (2024), we observed higher abundances of native species within *A. verticillata* compared to the cryptogenic and NIS, for most weeks. This was particularly true at the beginning of our study when *A. verticillata* was already established on the docks in Mission Bay. Interestingly, once *A. verticillata* returned to the dock in March 2022, the first organisms to recolonize were also NIS. This could imply that introduced species are among the early colonizers of *A. verticillata*. However, it is important to note that differences in sampling approaches (e.g., using fine-meshed nets to capture the *A. verticillata* community in this study verses hand collections in Guerra-García et al. 2024) may have led to the preponderance of immature stages that we observed in our samples, but could not identify to species to determine introduction status. Since many early developmental stages have subtle or difficult morphological differences to distinguish, one next step would be to incorporate molecular tools to identify these immature organisms, which would better resolve whether the relative abundance of the invertebrates using *A. verticillata* in Mission Bay are NIS or native species. As such, we do not know the degree to which invader-invader mutualism occurs at our study area. Furthermore, experimental studies that focus on the recruitment processes and interactions between native and NIS in *A. verticillata* are imperative for understanding the community dynamics among these species.

Most studies have identified and described fauna collected within *A. verticillata* without quantifying or standardizing by the amount of biogenic material collected (e.g., Winston 1995; Farrapeira 2011; Minchin 2012; Ferrario et al. 2014; Marchini et al. 2015; Dailianis et al. 2016; Marchini et al. 2018), or by using *A. verticillata* volume (Anderson et al. 2022; Guerra-García et al. 2024) rather than dry weight to standardize collections as used herein. Given this variability in sampling techniques, it is challenging to make comparisons across studies of the overall densities of marine invertebrates found in *A. verticillata*. Of the more detailed studies that have reported densities of infauna associated within bryozoans, an average of 35.9 individuals of the amphipod *Caprella scaura* Templeton, 1836 were collected per gram of the bryozoan *Bugula neritina* Linnaeus, 1758 (Guerra-García et al. 2011), and mean values ranged between 22.1–83.4 total organisms g^{-1} of dry weight of *A. verticillata* (Pederson and Peterson 2002). However, in this study we collected 1–2 orders of magnitude greater abundances of marine invertebrates within *A. verticillata* than previously reported (Pederson and Peterson 2002; Guerra-García et al. 2011). Previous studies with *A. verticillata* either

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collected the colonies with other species (Anderson et al. 2022) by scraping the dock (Ferrario et al. 2014; Dailianis et al. 2016), or by hand (Pederson and Peterson 2002; Marchini et al. 2015; Marchini et al. 2018; Guerra-García et al. 2024). These methodologies potentially characterize different assemblages than those in our study, with some potential loss of highly mobile species, and as described above, the immature stages. Our approach of collecting *A. verticillata* colonies with fine-meshed bags may have served to capture more of these small, mobile crustaceans, and likely explain why invertebrate densities within *A. verticillata* were so high in Mission Bay.

We observed two morphotypes (compact and elongated) of *A. verticillata* in Mission Bay, and as reviewed in Marchini et al. (2015). It is unclear if these morphotypes represent two different species of *A. verticillata*, but a recent study (Nascimento et al. 2021) supports the claim that there is only one species of *A. verticillata* found worldwide. There was a difference between the kenozooid width of the two morphotypes with significantly greater width of kenozooids in the elongated colonies. Elongated colonies may reach 2 m in length (Minchin 2012), and the thicker kenozooids might provide more structural support to minimize fragmentation, as bigger colonies become more vulnerable (Micael et al. 2018). It is unlikely that kenozooid width directly impacted the invertebrate community, but we observed some differences in the associated marine invertebrates based on the morphological characteristics of *A. verticillata*. In terms of taxonomic groups, the elongated *A. verticillata* colonies had more polychaetes, whereas the compact *A. verticillata* colonies had more tanaids, isopods, and amphipods. Polychaetes may readily use the elongated *A. verticillata* morphotype as a habitat if the more open configuration provides a better shelter for these organisms. In contrast, the higher abundance of amphipods in the compact *A. verticillata* colonies could result from the variety of microhabitats provided by the typically higher number of branches and nodes found in the compact colonies in comparison to the elongated morphotype. Similarly, when the algae *Sargassum* spp. had higher numbers of branches and hydroid coverage, there was a positive correlation with amphipod richness, density, diversity, and evenness (Carvalho et al. 2018; Carvalho et al. 2022). Alternatively, the amphipods that are abundant in the compact morphotype could be outcompeting the polychaetes and reducing their abundances. Therefore, more studies are needed to examine and better understand the ecological interactions between the organisms that are using *A. verticillata* as a habitat.

Overall, the invertebrate communities in the two *A. verticillata* morphotypes were relatively similar as the same invertebrate families were found in each morphotype. For example, the isopod Sphaeromatidae family contributed the highest to the invertebrate community in both morphotypes. This likely reflects the relatively high isopod abundances observed in this region of Mission Bay (Zavacki et al. 2024). Furthermore, *Paracerceis sculpta* (Holmes 1904), the main species found in the Sphaeromatidae family in our study, is distributed worldwide in warm-temperate to tropical harbors, and is considered a NIS in many areas (Fofonoff et al. 2018). *Paracerceis sculpta* was found within *A. verticillata* in the Azores Archipelago of Portugal (Marchini et al. 2018), and select locations of southeast Atlantic shelf, Alboran Sea, and west mediterranean (Guerra-García et al. 2024). This species is also associated with a variety of other organisms, including sponges, found underneath rocks, and among algae (Fofonoff et al. 2018; Stebbins and Wetzer 2023), suggesting that this is an opportunist species when it comes to finding a habitat (Stebbins and Wetzer 2023).

However, other species may choose *A. verticillata* morphotypes as a result of multiple complex interactions, such as a behavioral choice, refuge from physical stresses, predation and/or competition, as well as a place for mating or feeding (reviewed in Stachowicz 2001). In addition, species sometimes respond to local structural complexity rather than to the overall patch size of habitat (e.g., Tan-

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iguchi et al. 2003). Perhaps, the smaller localized structures of the elongated *A. verticillata* colonies provide greater refuge from predators, shelter from hydrodynamic flow, and contain more resources (Fenwick 1976; Heck and Wetstone 1977; Hacker and Steneck 1990; Russo 1990) than the overall structure of the compact *A. verticillata* colonies. This may also help explain why invertebrate diversity was slightly higher in elongated than compact *A. verticillata* colonies.

An important consideration is that the amount of biogenic material produced by *A. verticillata* might have a larger effect on the invertebrate community dynamics than the arrangement of the material (compact or elongated). For example, a previous study with the shrimp *Palaemon macrodactylus* Rathbun, 1902 determined that the total amount of material, and not how it was arranged, was the primary factor that determined the shrimp's habitat (Crooks et al. 2016). Our observations that invertebrate counts and diversity increased with *A. verticillata* structural complexity are aligned with the results from other studies indicating that structural complexity increases species diversity (Stoner and Lewis 1985; Crooks 2002; Graham and Nash 2013; Darling et al. 2017). Additionally, the similar invertebrate diversity in the medium and high complexity bins, suggests that the amount of *A. verticillata* material predominately benefited the invertebrate community diversity when the *A. verticillata* dry weight was greater than 0.5 g.

The invertebrate communities varied significantly with *A. verticillata* structural complexity (low, medium and high); however, the highest average similarity was among the most structurally complex bin (i.e., > 5 g) where the community may have been well-established. The invertebrate contributions were mainly driven by the same families, but their percent contribution to the community varied based on the *A. verticillata* structural complexity. In addition, as structural complexity increased, the invertebrate community contribution became more even, without any one family dominating the community. Again, the Sphaeromatidae isopods were the greatest contributor to the invertebrate community regardless of the structural complexity. The second highest contributor was from families Corophiidae, Podoceridae, and Hyalidae for the low, medium, and high structural complexity bins, respectively, and included species identified as cryptogenic or likely NIS to Mission Bay (Chapman 2007; Maloney 2007b, a; Fofonoff et al. 2018).

In general, the structure of *A. verticillata* colonies had marked influence on their associated peracarid crustacean and polychaete communities. These taxa appear to be especially responsive to the effects of invasive, structure-producing ecosystem engineers, including a mussel (*Arcuatula* (=*Musculista*) *senhousia* W. H. Benson, 1842) that creates dense byssal mats in Mission Bay (Crooks 1998), a tube-building polychaete worm *Ficopomatus enigmaticus* Fauvel, 1923 that creates reefs in Mar Chiquita Lagoon, Argentina (Schwindt and Iribarne 2000), and invasive seaweeds in the Gulf of Maine (Dijkstra et al. 2017). As highlighted above, many mechanisms are potentially operating simultaneously to drive the patterns of increased diversity and densities often seen within biogenically complex habitats (McCoy and Bell 1991; Crooks 2002), and it can be difficult to tease them apart (Matias et al. 2007; Crooks et al. 2016). For *A. verticillata* in Mission Bay, however, it appears that facilitative effects go beyond simply attracting and aggregating individuals, as indicated by the presence of juveniles and females with eggs (Fig. 4). It has been suggested that invasive engineers might serve as nursery habitat for resident biota (e.g., Wallentinus and Nyberg 2007; Bruschetti 2019), and in aquatic systems, examples include crabs in *F. enigmaticus* reefs (Luppi and Bas 2002), shrimp in beds of the freshwater algae *Myriophyllum spicatum* (Alford and Rozas 2019), and sea slugs in turfs of the algae *Vaucheria* sp. on tidal flats (Reise et al. 2023). Indeed, juveniles and reproductive females of *C. scaura* were also collected in *A. verticillata* along the eastern Atlantic coast (Guerra-García

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et al. 2011), suggesting that *A. verticillata* serves as a nursery habitat for other NIS. Because of the demographic implications of invaders increasing the fitness of resident organisms (whether they be native or non-native species), this topic merits further descriptive and experimental attention. Furthermore, the colonization of *A. verticillata* on floating structures such as docks is increasing the availability of structurally-complex habitats near the surface in Mission Bay, rather than along the bottom (such as those typically provided by eelgrass). This might be shifting the distribution of the peracarid crustaceans using *A. verticillata* from benthic habitats to floating anthropogenic structures. Thus, the relatively high abundance of amphipods in *A. verticillata* may result in alterations to the local trophic dynamics and benthic-pelagic coupling (e.g., Ritter and Bourne 2024) in areas with many docks. Once we characterize the species utilizing *A. verticillata* habitats, we should focus on developing experimental approaches to improve understanding the ecological interactions among these species and the possible broader ecosystem implications of their presence.

Given the rapid growth and extensive structure created by *A. verticillata*, it is often considered a nuisance biofouler where it has invaded (e.g., Pestana et al. 2020; Guerra-García et al. 2024). By their nature, ecosystem engineers typically have multi-faceted and cascading effects within ecosystems (Crooks 2002), and further comprehensive studies across a range of systems should be undertaken to better characterize the role of *A. verticillata* and inform management strategies associated with this NIS.

Conclusions

We identified an abundant and diverse marine invertebrate community associated with the habitat-forming non-indigenous bryozoan, *A. verticillata* in Mission Bay, California. The invertebrate community was primarily composed of peracarid crustaceans and polychaetes, with a mix of native, cryptogenic, and NIS. Thus, more work should be conducted to determine if *A. verticillata* disproportionately supports native or non-native species. We also observed juveniles and reproductive female life history stages living within *A. verticillata*, suggesting that these organisms are using *A. verticillata* as a nursery habitat. While *A. verticillata* morphology influenced the associated marine invertebrate community, the amount of biogenic material produced by *A. verticillata* significantly increased the abundance of organisms within *A. verticillata*, as well as the invertebrate community diversity. Overall, the results from this study suggest that *A. verticillata* is an ecosystem engineer that provides structurally complex habitat on anthropogenic substrates for many marine invertebrates, and increases invertebrate community density, abundance, and diversity.

Authors' Contribution

EMZ: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, original draft: writing - review & editing. NBR: research conceptualization, sample design and methodology, data analysis and interpretation, second draft: writing - review & editing. JAC: research conceptualization, sample design and methodology, interpretation, and final draft: writing - review & editing. MAB: research conceptualization, sample design and methodology, interpretation, and final draft: writing - review & editing.

Funding Declaration

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Permits

Scientific Collecting Permit, General Use (ID: GM-200090002-20009-001) to the Department of Environmental and Ocean Sciences.

Acknowledgements

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