

Investigating Inter-Annual Variation in Cobble-Bottom Assemblages of Fish and Decapod Crustaceans in the Beaver Harbour Region of the Bay of Fundy Over the Last 17 Years

by

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Abstract

Gradual or sudden changes in biotic or abiotic factors can drive inter-annual variation in benthic communities. Despite their role as important nurseries, subtidal cobble ecosystems are understudied because of their interstitial nature, making monitoring difficult. This study quantifies changes in a community of fish and decapod crustaceans colonizing cobble-filled bio-collectors deployed from 2007-2024 at four sites in the Beaver Harbour region of the Bay of Fundy. Fish + large decapods at all sites, and fish + large decapods + small shrimp at both Beaver Harbour Lighthouse and Beaver Harbour East sites, showed significant seriation, progressively becoming dissimilar from the initial community. These two sites also showed two more pronounced sudden community shifts during this time. Community trends were mainly driven by changes in abundances of three fish (Cunner, Radiated Shanny, Shorthorn Sculpin) and two crab (Jonah, Atlantic Rock) species. These findings provide information on inter-annual changes of an understudied cobble bottom community potentially linked to condition changes in the Bay of Fundy.

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List of Symbols, Nomenclature, or Abbreviations

MHW – Marine heat wave

GoM – Gulf of Maine

BoF – Bay of Fundy

°C – degrees Celsius

BH – Beaver Harbour

cm – centimeters

mm – millimeters

kg – kilograms

m – meters

DW – Dispersion Weighting

SQ – Square Root

Spp – species (plural)

NAO – North Atlantic Oscillation

1.0 Introduction

1.1 Inter-annual changes in marine benthic communities

Inter-annual changes in marine benthic communities are expected due to alterations to species' distributions, abundances, spawning phenologies, growth rates, and body sizes (Perry et al. 2005; Nye et al. 2009; Simpson et al. 2011; Simpson et al. 2013; Fredston-Hermann et al. 2020; Hastings et al. 2020; Fredston et al. 2021). These alterations can result from variation of a multitude of biotic processes such as competition, predation, or reproductive success (Warwick et al. 2002; Vindenes & Engen, 2017), as well as abiotic factors such as temperature (sea surface or bottom), pH levels, or oxygen levels (Simpson et al. 2013; Penn & Deutsch, 2022; Calvin et al. 2023). Changes in presence/absence and abundance of individual species can alter the greater community through changes in dominant species (Simpson et al. 2011; Simpson et al. 2013), species richness (Friedland et al. 2025), and diversity (Nye et al. 2010; Friedland et al. 2025), resulting in changes in community structure and associated ecosystem services (Burrows et al. 2019; Hastings et al. 2020; Calvin et al. 2023).

The changing conditions of the ocean contribute to inter-annual changes in benthic communities, continuously altering habitat, spawning success, food availability, and abundance of species (Simpson et al. 2013; Fredston et al. 2021; Meyer-Gutbrod, 2021; Penn & Deutsch, 2022; Calvin et al. 2023). Many studies attribute larger changes in communities and species to extreme changes in oceanographic conditions resulting from climate change, particularly the increasing rate of ocean warming (e.g., Nye et al. 2009; Simpson et al. 2011; Simpson et al. 2013; Burrows et al. 2019; Hastings et al. 2020; Penn & Deutsch, 2022; Friedland et al. 2025). Increases in sea surface and bottom

temperatures can cause changes to species' distributions, abundances, or ranges, either latitudinally or with depth, as species attempt to remain within their thermally preferred niche to ensure their survivability and successful reproduction (Perry et al. 2005; Nye et al. 2009; Simpson et al. 2011; Simpson et al. 2013; Hastings et al. 2020; Fredston-Hermann et al. 2020; Fredston et al. 2021; Penn & Deutsch, 2022). Increases in temperature can also influence abundance by affecting availability of preferred food sources (Davies et al. 2019; Meyer-Gutbrod et al. 2021; Calvin et al. 2023), limiting or increasing thermally preferred nursery habitat, or altering timing of spawning (Simpson et al. 2013; Woodard, 2018; Calvin et al. 2023). Other effects of climate change, such as decreasing pH levels resulting in ocean acidification or changes to oxygen levels, can also directly affect species and hence alter the community (Simpson et al. 2013; Penn & Deutsch, 2022; Calvin et al. 2023).

1.1.1 Gradual community changes

Long-term gradual community changes can be evaluated through analysis of seriation, which is defined as progressive dissimilarity in a community over time, with greater similarity in years closer than years farther apart (Clarke et al. 1993). Community seriation trends over time are expected first and foremost because of temporal auto-correlation, i.e., the non-independence of communities in years that are closer to one another. Temporal auto-correlation arises from (i) persistence of individuals or cohorts across years, because many individuals present in year $x+1$ were also present in year x , and (ii) ecological memory, whereby biotic and abiotic processes in one year influence community structure in the following year (Warwick et al. 2002; Vindenes & Engen, 2017; Postuma et al. 2020). Biotic “memory” can include interactions that link across

years such as reproduction, competition, or predation (Warwick et al. 2002; Vindenes & Engen, 2017). Abiotic “memory” can include oceanographic conditions such as temperature or salinity levels that impact conditions and the community in the next year (Postuma et al. 2020). However, in addition to the influence of auto-correlation, abiotic and biotic “forcing” can also contribute to seriation trends through directional and persistent changes in variables, such as a consistent rate of increasing temperature or predation intensity (Drinkwater et al. 2010; Voje et al. 2015). Distinguishing the causes of seriation is challenging, and unfortunately rarely attempted in community studies.

Several studies have documented seriation trends in marine benthic communities (Warwick et al. 2002; Collie et al. 2008; Trott, 2016; Franz et al. 2019). For example, Warwick et al. (2002) reported seriation in a subtidal soft-bottom macroinvertebrate community over 24 years caused by changes in total number of species and total abundance. Collie et al. (2008) found seriation of benthic fish and invertebrate species over 47 years associated with an increased taxonomic distinctness and an increasing pelagic:demersal ratio. Many studies looking at seriation did not statistically distinguish the contribution of forcing (abiotic or biotic) from that expected from temporal auto-correlation but have nevertheless attributed seriation to changes in oceanographic conditions. For instance, Warwick et al. (2002) hypothesized that decreasing oxygen and increased temperature caused community changes, and Collie et al. (2008) attributed community trends to changes in yearly sea surface temperatures and chlorophyll *a* concentration, although they conducted no analyses to assess the contribution of auto-correlation to these trends.

1.1.2 Sudden community shifts

Sudden shifts in marine benthic communities can occur through sudden ecological or abiotic changes, increased commercial exploitation, and industrialization. These sudden shifts can result from drastic changes in the abundances or distributions (including presence/absence) of dominant species within the community (Warwick et al. 2002; Collie et al. 2008; Mills et al. 2013). Events causing sudden shifts include rapid intensification of commercial exploitation (Trott, 2016), industrialization of the area (Warwick et al. 2002), or abrupt shifts in ocean conditions such as extreme weather events and marine heat waves (MHWs) (Mills et al. 2013; Smale et al. 2019; Marshak & Link, 2024). For example, MHWs can cause sudden changes in species' distributions, including geographic expansions near the "cold limit" of their range and contractions near the "warm limit" of their range (Mills et al. 2013; Smale et al. 2019; Marshak & Link, 2024). MHWs have also caused sudden changes in abundance and shifts in the dominant species or species group in a community (Quinn, 2018; Pershing et al. 2018; Smale et al. 2019; Marshak & Link, 2024). For example, Marshak & Link (2024) reported a decrease in the pelagic:demersal ratio in fisheries landings in the Gulf of Maine (GoM) after the 2012 MHW.

Many studies that detected significant seriation also identified sudden shifts in the same community within the serial trend (Warwick et al. 2002; Collie et al. 2008; Trott, 2016). For example, Warwick et al. (2002) reported a sudden shift in community composition coinciding with the construction of a barrage within the Tees estuary, and Collie et al. (2008) found a sudden shift to a community of species with higher temperature preferences following accelerated warming.

1.2 Conservation and long-term monitoring

Conservation of changing benthic communities, and natural biodiversity more generally, is important because conservation increases the likelihood of resilience against changing conditions through resistance to disturbance and increased likelihood of species recovery (Palumbi et al. 2009). Effective conservation and management require monitoring of biodiversity and species distribution shifts. Long-term ecosystem-based monitoring can provide early detection and better understanding of both long term and short-term changes that may not be seen in periodic sampling, in turn enabling improved ecological forecasting (Melbourne-Thomas et al. 2020; Ward et al. 2022). Long-term monitoring can also inform decisions concerning the location of marine protected areas or the management of fisheries (Lundquist & Granek 2005; Melbourne-Thomas et al. 2020; Ward et al. 2022).

1.3 Gulf of Maine and Bay of Fundy

1.3.1 Ocean conditions

The Gulf of Maine (GoM) is a large macro-tidal, semi-enclosed sea in an oceanographically unique region with high productivity and biological diversity (Wilkinson et al. 2009; Townsend et al. 2015; Burkholder et al. 2024). At the northeastern end of the GoM is the Bay of Fundy (BoF), an area whose funnel shape gives rise to very large tides. High biodiversity and productivity in the BoF reflect a range of habitat types, high interannual temperature variability, and a distinctive sub-Arctic ecosystem, making it a priority location for investigation and management (Wilkinson et al. 2009; Wahle et al. 2013; Todd et al. 2019; Pershing et al. 2021).

The GoM has one of the highest rates of warming around the globe, with average yearly sea surface temperature warming at 0.47°C per decade from 1982-2024, compared

to 0.17°C globally (Gulf of Maine Research Institute, 2025). A complex circulation system in this region dictates the proportions of cold/fresh Labrador Slope Water and deep warm/salty Gulf Stream Slope Water that enters through the North-East Channel (Townsend et al. 2015; Brickman et al. 2018; Pershing et al. 2021; Townsend et al. 2023; Burkholder et al. 2024). The proportions of Gulf Stream and Labrador Slope Water entering the GoM vary from year to year, with more pronounced changes on an approximately decadal time scale, altering the rate of warming while maintaining the overall warming trend (Townsend et al. 2015; Pershing et al. 2021; Townsend et al. 2023). The GoM and BoF have had consistently higher temperatures following a cooler decadal period around the mid-1990s, during which a higher proportion of Labrador Slope Water entered the GoM (Pershing et al. 2021; Hebert et al. 2024; Koul et al. 2024). From the mid-1990s to approximately 2010 the regional temperature approached the climatological mean (Hebert et al. 2024; Koul et al. 2024). Around 2010 a northward shift of the Gulf Stream allowed a higher proportion of deeper warmer water to enter the GoM, causing a warmer decadal period (~2012-2023, peak 2021) that was the hottest on record (Brickman et al. 2018; Pershing et al. 2021; Townsend et al. 2023; Hebert et al. 2024; Koul et al. 2024; Galbraith et al. 2025). In addition to increased warming rates, a higher ratio of Gulf Stream Slope Water increased the occurrence of MHWs in the GoM. Since 2010 there have been three major MHWs, which occurred in 2012, 2016, and 2018 (Mills et al 2013; Pershing et al 2018; Quinn, 2018; Pershing et al. 2021).

Since the early fall of 2023, ocean conditions in the GoM and BoF have changed relative to the intense warming period of the previous decade. Since then, decreases in bottom and sea surface temperature within the GoM (Hebert et al. 2024; Record et al.

2024), have been attributed to a southward shift of the Gulf Stream in 2023 allowing higher proportions of colder Labrador and Scotian Shelf Slope Waters to enter the GoM and BoF, potentially indicating the start of a cooler decadal period (Hebert et al 2024; Record et al. 2024; Galbraith et al. 2025).

1.3.2 Community and species changes

Studies in the GoM and broader Northeast shelf report significant distribution and abundance changes in benthic species in the last 50 years, attributing many of these to changes in oceanographic conditions (Nye et al. 2009; Nye et al. 2010; Fredston-Hermann et al. 2020; Fredston et al. 2021; Pershing et al. 2021; Williams, 2025). For example, Nye et al. (2009) showed poleward shifts in the annual centre of biomass of 17/36 demersal fish stocks on the Northeast shelf from 1968-2008 related to warming, with range expansions in 10 species and range contractions in six. Nye et al. (2010) showed increased total biomass of demersal fish species in the GoM from the early 1990s to 2007 and changes in biomass of individual species from 1970-2007 related to condition changes. Williams (2025) reported a higher percentage of significant shifts in median distributions of coastal demersal fishes on the Northeast shelf from 1982-2023 compared to other benthic and pelagic fish groups, with northward shifts in most species potentially associated with warming.

Several studies associate sudden shifts in abundance or distributions of species in the GoM to MHW's. For example, the 2012 heatwave was associated with the first occurrence and subsequent continued presence of juvenile Cunner (*Tautoglabrus adspersus*) in bio-collectors deployed on subtidal cobble-bottom in the Southern (outer) BoF (Woodard, 2018), and the first recorded presence of Cunner from fisher observations

in the Northern (inner) BoF (Quinn, 2018). Following this MHW there was also evidence of decreases in Green Crab (*Carcinus maenas*) in the Northern BoF (Quinn, 2018), increases in Jonah Crab (*Cancer borealis*) in the GoM (Truesdale et al. 2019), and increases in Blue Crab (*Callinectes sapidus*) in the Southern GoM (Pershing et al. 2018).

1.4 Subtidal cobble habitat

A diverse range of benthic habitats and geo-morphological settings characterize the BoF, both intertidally and subtidally, including bedrock, boulders, cobbles, gravel, sand, and mud (Shaw et al. 2012; Todd et al. 2019). The geo-morphology of the BoF is primarily a mixture of sand/mud and small gravel, with pockets of bedrock and cobble areas around the coastline, especially in the outer BoF (Shaw et al. 2012; Todd et al. 2019). Subtidal cobble is both one of the rarer and the most important habitats in this region, because its structural complexity and interstices provide nursery grounds for many species, including American Lobster (*Homarus americanus*), crabs, shrimp, and crypto-benthic fishes (Wahle et al. 2013; Ellis et al. 2015; Hunt et al. 2017). This habitat is, however, challenging to sample. Cores and grabs cannot penetrate the cobble, and rocky substrates can damage seines (Ellis et al. 2015; Hunt et al. 2017). Trawls and scuba can provide information on this habitat, but trawls effectively sample only relatively level bottoms and deeper waters, and scuba has a limited depth range and is less successful in areas of low visibility or strong currents (Wahle et al. 2009; Ellis et al. 2015; Hunt et al. 2017). These constraints contribute to a paucity of long-term data on this habitat in the BoF.

Subtidal passive cobble-filled bio-collectors were developed to measure American Lobster settlement and recruitment (Wahle et al. 2009; Wahle et al. 2013; Dinning &

Rochette, 2019) and have since been used to assess biodiversity of fish and invertebrates (Wilson, 2013; Ellis et al. 2015; Hunt et al. 2017; O'Malley & Hunt, 2020), increased recruitment of Cunner in the BoF (Woodard, 2018), and effects of aquaculture on cobble communities (Fischer-Rush, 2019; Jones, 2025). A previous field study showed that the community in bio-collectors is representative of the fauna in prime cobble habitat, noting that the bio-collectors captured 32/35 (91%) of “settler” species (larvae settling from the water column) and 41/46 (89%) of “crawl-in” species (mobile juveniles and adults from surrounding habitat) documented in adjacent scuba quadrats (quadrats assessed without suction sampling) (Wittig, 2018). The bio-collectors were actually more effective than scuba quadrats at capturing some cobble species, with 14/49 (29%) of “settler” species (all Decapoda, Echinodermata, and Porifera settlers, and 4/5 species of Ascidiacea) present in bio-collectors only (Wittig, 2018), potentially because this tool provides more interstices than the natural cobble habitat. Furthermore, 30/76 (39%) of “crawl-in” species (all Decapoda, Isopoda, and Actinopterygii species, 8/18 Gastropoda species, and 6/20 Polychaeta species) were present in bio-collectors only (Wittig, 2018), potentially reflecting the greater likelihood of mobile species evading capture when sampling using quadrats. A previous field study showed that bio-collectors placed on cobble bottom had a significantly different community and higher abundance of rock-dwelling species than bio-collectors placed on soft substrate (Ellis et al. 2015), suggesting that larvae of some species respond to substrate at a larger spatial scale than their immediate location of settlement. The use of rounded rocks in bio-collectors provides a habitat more similar to natural substrate compared to other artificial substrates (e.g. brick, gravel, tiles). Note that the community within bio-collectors may differ from that on

1.5 Objectives

This study investigates inter-annual changes in a community of fish and decapod crustaceans on subtidal cobble-bottom habitat in the Beaver Harbour region of the South-West Bay of Fundy from 2007-2024. We (1) use multivariate tools to identify inter-annual changes of this community, including gradual changes and sudden shifts, (2) identify focal species that contribute most to observed inter-annual community changes, and (3) quantify inter-annual trends in the abundance of these focal species.

2.0 Methods

2.1 Bio-collector design

Passive cobble-filled bio-collectors, based on the design from Wahle et al. (2009), (see Introduction) were used to collect data on fish and decapod crustaceans in the Beaver Harbour (BH) region of the Southwest Bay of Fundy (BoF) from 2007-2024. Bio-collectors measured 92 x 63 x 15 cm (L x W x H) and were made of 10-gauge vinyl-coated wire square mesh (5.4 cm diagonal opening) with a hinged lid. They were lined with 1 x 1 mm plastic PetScreen along the bottom and sides to retain specimens during and after retrieval from the water, including preventing transfer of specimens between bio-collectors after retrieval. A thicker Vexar 4-mm mesh screen laid on top of the PetScreen in the bottom of each bio-collector prevented tearing by rocks. Bio-collectors were filled with cobble (ranging from 9-22 cm in diameter) and weighed approximately 115 kg when filled. Organisms with a width $< \sim 5.4$ cm could enter the bio-collectors by settling out of the plankton into the cobble or by crawling/swimming through the wire mesh opening from the benthos (Ellis et al. 2015; Hunt et al. 2017; Wittig, 2018; O'Malley & Hunt, 2020).

2.2 Sites and deployment

The bio-collectors were deployed by boat on subtidal cobble bottom at a depth of 5-10 m relative to 0 chart datum, each with a line and buoy attached to a rope bridle for individual deployment and retrieval. A HOBO Water Temp Pro v2 temperature logger attached on 1-2 bio-collectors per site recorded bottom temperature every 30 minutes. Bio-collectors were deployed yearly during summer months (defined as end of June/mid July to mid October/mid November) at four sites within the BH region of the South-West

BoF over different time spans: BH Lighthouse (2007-2024, with exception of 2012), BH East (2009-2024, with exception of 2010, 2012 and 2015), Pocologan (2013-2023), and Deadman's Harbour (2013-2023) (Fig 1, Table 1). Five-24 bio-collectors were deployed per site (Table 1). Summer months were chosen to cover the period when larval stages of most species would be present in the habitat, while also to take advantage of the summer closure of the lobster fishing industry to reduce lost bio-collectors from boat activity or fishing interference (Wahle et al. 2009; Ellis et al. 2015). A previous field study found no significant difference in communities present in bio-collectors deployed on May 19 and July 8 in Beaver Harbour (Wittig, 2018), indicating that earlier deployment would likely not have resulted in greater colonization.

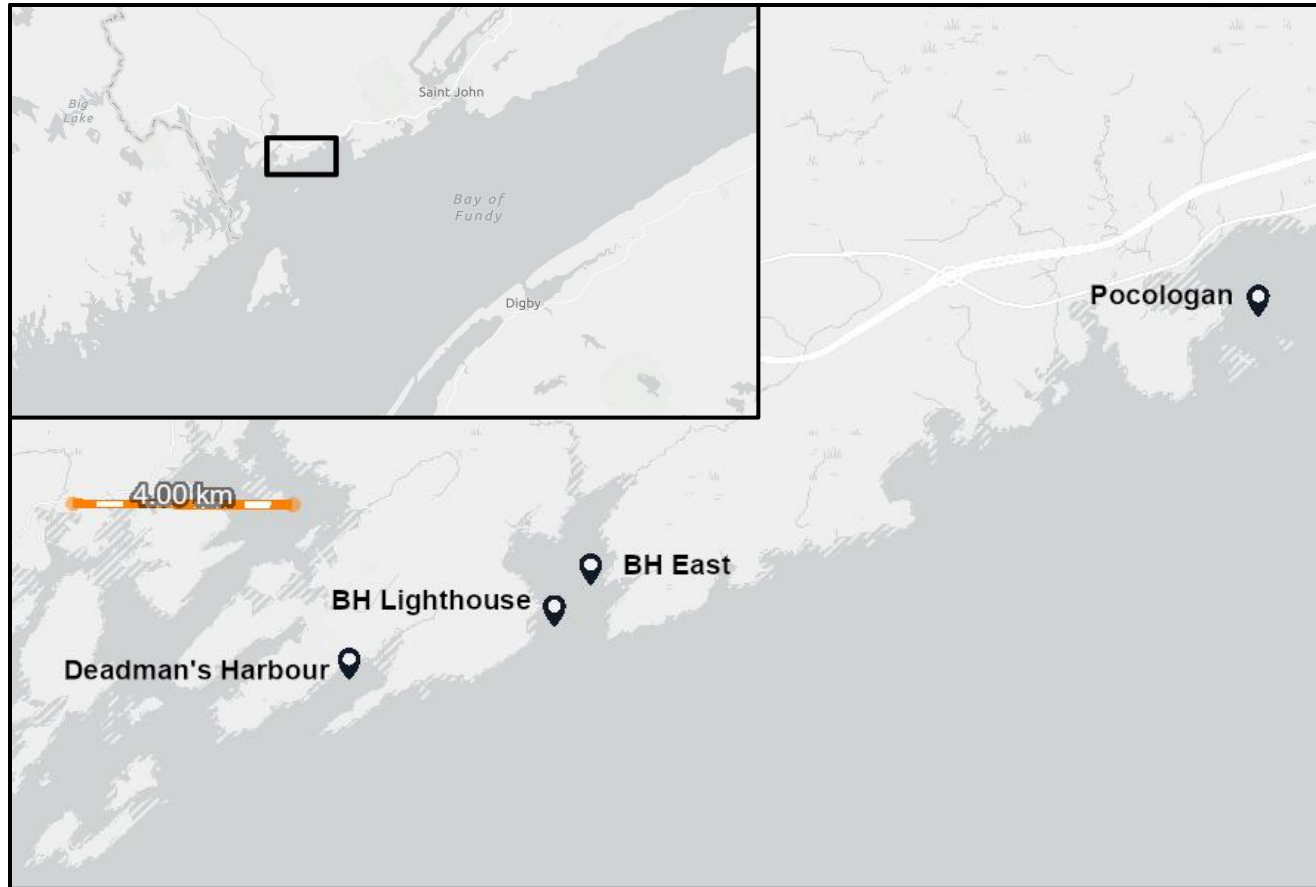


Figure 1: Location of study sites within the Beaver Harbour region of the South-West Bay of Fundy where bio-collectors were deployed. Bio-collectors were deployed yearly at BH Lighthouse (45:03:699N, 66:43:999W) from 2007-2024 (except 2012), BH East (45:04:086N, 66:43:142W) from 2009-2024 (except 2010, 2012 and 2015), and Deadman's Harbour (45:02:992N, 66:46:894W) and Pocologan (45:06:544N, 66:34:013W) from 2013-2023. Hatched lines represent the intertidal zone. Map was created using ArcGIS software by Esri. Basemap sources from: Province of New Brunswick, Esri Canada, Esri, TomTom, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, EPA, USDA, USFWS, NRCan, Parks Canada.

Table 1: Number of cobble-filled bio-collectors deployed (NA = 0) at each of four study sites in the Beaver Harbour region of the South-West Bay of Fundy between 2007 and 2024, along with the date these were deployed and retrieved. Numbers with boxes around them indicate the years when small shrimp were processed from at least 5 bio-collectors from the BH Lighthouse and BH East sites.

Site	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024
Lighthouse (BH)	17	24	5	8	7	N/A	21	17	16	7	7	19	20	20	19	19	20	14
East (BH)	N/A	N/A	10	N/A	10	N/A	19	17	N/A	5	7	20	20	20	19	20	18	17
Pocologan (MB)	N/A	N/A	N/A	N/A	N/A	N/A	20	17	18	7	7	19	20	20	19	19	19	N/A
Deadman's Harbour (DH)	N/A	N/A	N/A	N/A	N/A	N/A	18	24	6	7	7	20	20	20	19	19	20	N/A
Deployment Date(s)	26-Jul	11-Jul	03-Jul	07-Jul	19-May/ 08-Jul	N/A	03-Jul/ 04-Jul	03-Jul	04-Jul	30-Jun	04-Jul/ 05-Jul	11-Jul/ 12-Jul	07-Jul	21-Jul	12-Jul	14-Jul	09-Jul	03-Jul
Retrival Date(s)	18-Oct	24-Oct	22-Oct	21-Oct	22-Oct	N/A	10-Oct	31-Oct	10-Nov/ 15-Nov	12-Oct/ 14-Oct/ 27-Oct	20-Oct/ 28-Oct	19-Oct/ 27-Oct	26-Oct	31-Oct	29-Oct	29-Oct	04-Nov/ 11-Nov	19-Oct

2.3 Bio-collector processing

Bio-collectors were retrieved by the line attached to them using a lobster pot hauler and stacked on pallets on the boat. The pallets of bio-collectors were then transferred onto a flatbed truck using a boom, transported, and unloaded at the Huntsman Marine Science Center in Saint Andrews, New Brunswick. Processing occurred outdoors at this location usually within 24-30 hours of removal, but in a few years as long as 96 hours. An initial visual inspection of each bio-collector qualitatively assessed organic matter level and potential anoxia based on presence of black staining (from none to high); bio-collectors with high levels of muddy sediment or anoxia were not processed. Bio-collectors with mid-high levels of organic matter were still processed. Once a bio-collector was opened, all the cobbles were removed, and all non-sessile species were brushed back into the bio-collector. All visible organisms $> \sim 1$ cm (maximum linear dimension) were then removed from the bio-collector and placed in a Ziploc bag. Bio-collectors were rinsed, and all leftover material (e.g., shell hash and algae) was placed in a separate Ziploc bag to be processed for missed organisms $> \sim 1$ cm and for organisms $< \sim 1$ cm. All samples were placed on ice, transported to the University of New Brunswick Saint John campus and then frozen.

The first bag, comprising organisms $> \sim 1$ cm (maximum linear dimension), was thawed, and all individual fish and decapod crustaceans were counted, identified to the species level, and measured for length (total length for fish, carapace width or length for decapods). The second bag, comprising the leftover material (e.g., shell hash and algae), was similarly thawed and inspected under a magnifying light to pick out any individuals larger > 1 cm that may have been missed while sorting in the field. Some of the smaller

individuals (e.g., lobster, small shrimp) were damaged, so only heads were counted to avoid counting individuals more than once.

For BH Lighthouse in 2007-2011, 2014-2015, 2022-2024, and BH East in 2009, 2011, 2014, 2022-2024 (Table 1), material in the second bag (see previous paragraph) was also examined for small shrimp species $< \sim 1$ cm (down to ~ 1 mm) (e.g., *Eualus* species, *Caridion gordonii*), which were identified, counted, and their carapace length measured (for the first 20 individuals) under a dissecting microscope. Length measurements of organisms were not used in the present study. The three species of *Eualus* shrimp (Appendix 1) sometimes could not be identified to species because of preservation status. To account for this constraint, the total number of individuals for each *Eualus* species for a given sample was estimated based on the proportion of individuals of each species among the shrimp that could be identified, i.e., the individuals not identified were assigned to species groups based on the known proportion of each species within the sample. All species identifications were validated by the Hunt/Rochette lab taxonomist (Marie-Josée Maltais).

2.4 Statistical analyses

Two different fish and decapod communities were considered and analyzed separately, given that small shrimp species were only processed in certain years and sites (Table 1). The first dataset was defined as the “fish + large decapods” community, which comprised 20 species $> \sim 1$ cm (Appendix 1) that were evaluated at all 4 study sites. The second dataset was defined as “fish + large decapods + small shrimp”, which comprised the same 20 species as the first community, in addition to the seven small shrimp species (Appendix 1); this second community was only evaluated at the two BH sites and only

for some years (Table 1). Each site and community data set was analyzed separately. All multivariate analyses were done using PRIMER V7, and all univariate analyses were done using RStudio 4.2.2.

2.41 Multivariate inter-annual analyses

Bray-Curtis similarity matrices were generated to compare communities in all bio-collectors of a same site, across all years, resulting in a triangular matrix of similarity values from 0 (no species in common) to 100 (identical community) for each bio-collector compared to every other bio-collector for each site. I built these matrices using the raw abundance data and based on different transformations of each data set, to assess the contribution of species identity and abundance to similarity/dissimilarity among communities. The first of these transformations was “dispersion weighted” (DW) data, an initial transformation that controlled for high variability in abundance of species across replicates (i.e., bio-collectors) of a given site and year, as recommended by Dr. Marti Anderson (Director at PRIMER-e). Additional transformations were done on top of DW transformed data to progressively decrease the influence of the most abundant species: DW + square root (SQ) transformed data, DW + Log transformed data, and DW + presence/absence transformed data.

The similarity matrices based on raw and transformed data were each used to create non-metric Multi Dimensional Scaling (nmMDS) plots to visually depict the similarity between individual bio-collectors within and across years at each site. The PERMANOVA+ function “distance between centroids” used for each similarity matrix created a second matrix of similarity values based on the centroid of each year, calculated from the similarity values of bio-collectors within that year. The distance between

centroids matrix was used to create a second nmMDS plot to depict similarity between centroids of different years for each site visually.

To test for seriation, RELATE tests compared the “complete” community similarity matrices (i.e., not the centroid matrices) for raw and transformed data for each site and community, to corresponding year-based matrices of distances between years; this approach tested the hypothesis that communities from consecutive years were closer together are more similar than those from years farther apart. The year-based matrix included the bio-collector sample labels, with rank orders based on distances between years, taking into account unequal steps (e.g. 2007:2007 = 0, 2010:2011 = 1, 2011:2013 = 2), assigned to each comparison between bio-collectors instead of Bray-Curtis similarity values. The RELATE test compared the distance between samples in the similarity matrices to the distance between rank orders of years for the same samples in the created year-based matrices defined above. The test then assessed whether samples one rank (year) apart were the most similar, samples two ranks (years) apart were the next closest, and samples farthest apart were the least similar. The RELATE test calculated a non-parametric rank correlation coefficient (Spearman’s Rho), also referred to as an Index of Multivariate Seriation (Clarke et al. 1993), for each community similarity matrix. If the distance between samples in the community similarity matrix was identical to the distance between years with the same labels in the year-based matrix, the Spearman’s Rho value would be 1. To estimate a significance level (i.e., p value), the test then compared the observed Rho to a theoretical distribution of Rho values calculated assuming no seriation and obtained by randomizing all rank order labels in the year-based matrix 9999 times.

Comparison of nmMDS plots and RELATE output from all transformations discussed above (raw, DW, DW + SQ, DW + Log, DW + Presence/absence) allowed us to choose the DW + SQ transformation to use in further analyses to assess species contributing to seriation trends, and to identify sudden community shifts from nmMDS plots visually. DW was used to allow more consistently occurring species to contribute more to trends than species that varied greatly in abundance across replicates of a site and year. The DW transformation also yielded larger Rho values than raw data for both communities at BH Lighthouse and fish + large decapods at BH East, which are the sites with the longest time span (BH Lighthouse: 2007-2024, BH East: 2009-2024). An additional SQ transformation was also chosen, because the RELATE test Rho values based on DW + SQ transformations yielded the highest, or very close to the highest, for all sites. For simplicity, we present all further analyses (and associated nmMDS plots) only for the DW + SQ transformed data. The centroid nmMDS plots based on DW + SQ transformed data were visually assessed to identify the most sudden community shifts over the sampling period. This selection was based on the magnitude of change of community centroids between years as well as the direction of such changes across multiple years.

To illustrate further how community similarity decayed over the deployment time series, we obtained similarity values for each year comparison for each site and community (y axis) from pairwise PERMANOVA tests (run on the DW + SQ transformed Bray-Curtis similarity matrix) and plotted against distance between years (x axis). Scatter plots were created in RStudio with the `ggplot()` function from the `ggplot2` package (v4.0; Wickham, 2016). Generalized linear models with a Gamma distribution

were run with the `glm()` function from the R stats package (v3.6.2; R core team, 2013) to assess significance of the relationship.

2.42 Identifying species contributing to inter-annual trends

To assess the contribution of each species to seriation at each site, for each community, I ran RELATE tests, removing a single species each time, providing a Spearman's Rho value for the community minus that species. I then used the difference in Spearman's Rho between the full community and the value excluding a particular species as an index of that species' contribution to seriation. Then, to determine how combinations of these species contributed to the statistical significance of the seriation trend, I sequentially removed species whose individual removal caused a decrease in Spearman's Rho, beginning with that with the largest "contribution index" (i.e., change in Rho) to that with the smallest one, and re-estimated Rho after each removal. Once a species was removed from the RELATE test it was not put back in. This process was repeated until all species whose individual removal decreased Rho were removed, or the Rho value neared 0 (within 0-0.015), whichever came first. Excel scatter plots visualized the relationship between number of species removed (x axis) and Spearman's Rho value (y axis).

2.43 Individual species analysis

Species identified as significant contributors to seriation from the sequential removal RELATE tests were assessed individually for monotonic changes in abundance over time using Rstudio. Scatter plots to visualize the relationship between year (x axis) and density per bio-collector (y axis) were created using the `ggplot()` function from the `ggplot2` package (v4.0; Wickham, 2016), and overlaid with a generalized linear

regression line using the `ggplot2` package's `stat_smooth()` function. The generalized linear models were run with the `glm()` function from the `R stats` package (v3.6.2; R core team, 2013) to assess the significance of the relationship. The presence of overdispersion was tested using the `check_overdispersion()` function from the `performance` package (v0.12.4; Lüdtke et al. 2021). If no overdispersion was present I used a Poisson distribution. If overdispersion was present, I used a negative binomial distribution with the `glm.nb()` function from the `MASS` package (v7.3-65; Venables & Ripley, 2002). Model diagnostics were also assessed using the `performance` package's `check_model()` function. Craig and Uhler's Pseudo- R^2 were calculated for each model using the `pR2()` function from the `pscl` package (v1.5.9; Jackman, 2024). Densities per bio-collector per year and standard error were calculated using the `SummarySE()` function from the `Rmisc` package (v1.6; Hope, 2014). Inter-annual trends were not analyzed if a species was not present for at least 4 years.

After noting two sudden shifts in nmMDS plots for fish + large decapods in BH sites, I determined which species identified as contributors to seriation appeared to contribute to the two sudden shifts observed in the community. I created bar plots for each site comparing mean density of focal species per time span with standard error bars in RStudio using the `ggplot()` function from the `ggplot2` package (v4.0; Wickham, 2016). Welch's t or Kruskal-Wallis tests assessed differences in density of individual species in BH Lighthouse between two time spans on either side of the first sudden shift. This test was not done at BH East because I had only two years of data at this site before the first shift (2009, 2011). Similarly, differences in density were not assessed between time spans on either side of the second observed shift in either BH site because the last time span

encompassed only two years (2023, 2024). Shapiro-Wilk's tests assessed normality of data using the `Shapiro.test()` function from the `stats` package (v3.6.2; R core team, 2013). T-tests compared species with normally distributed data for both time spans on either side of the sudden shift using the `stats` package's `t.test()` function. Kruskal-Wallis tests compared species with 0 individuals in a year within a particular time span, and for species where the data were not normally distributed in either or only one time span, using the R `stats` package's `kruskal.test()` function. Mean densities and standard errors for each time span were calculated using the `SummarySE()` function from the `Rmisc` package (v1.6; Hope, 2014).

3.0 Results

3.1 Community composition

The community I identified in the bio-collectors comprised 27 species of fish and decapod crustaceans (Appendix 1). All fish (11 spp.) were larger than one cm, while I separated decapods into large decapods > 1 cm (9 spp.) and small shrimp < 1 cm (7 spp.) (Appendix 1). Small shrimp species were only processed in a subset of years (2007-2011, 2014-2015, 2022-2024) at the two Beaver Harbour (BH) sites (Table 1). The most abundant fish species were *Tautoglabrus adspersus*, *Pholis gunnellus*, *Myoxocephalus scorpius* and *Ulvaria subbifurcata*. The most abundant large decapods were *Homarus americanus*, *Cancer borealis*, and *Cancer irroratus*. The most abundant small shrimp species were *Eualus fabricii*, *Eualus pusioulus*, and *Caridion gordonii*. No fish or crustacean taxa were unidentifiable, but some *Eualus* could not be identified to species (see Methods).

3.2 Multivariate inter-annual patterns

3.2.1 Seriation analysis

The fish + large decapods community at both BH sites showed evident inter-annual change (Fig 2, Fig 3) and significant seriation trends for all transformations applied (Table 2). Inter-annual change in BH sites was indicated by some regularity in how the community changed over time, with centroids of consecutive years closer together than centroids of years farther apart in nmMDS plots (Fig 2), and by the significant negative relationships between pairwise community similarity values and the number of years between their sampling (Fig 3). The fish + large decapods community at Pocologan and Deadman's Harbour also showed evident inter-annual change (Appendix

2 and 3) with significant seriation trends for all transformations applied (Appendix 4) but exhibited less of a directional trend over the smaller time scale sampled (2013-2023) (Appendix 2). Significant seriation for all sites with all transformations for fish + large decapods indicates that both identity and abundance of species contributed to seriation.

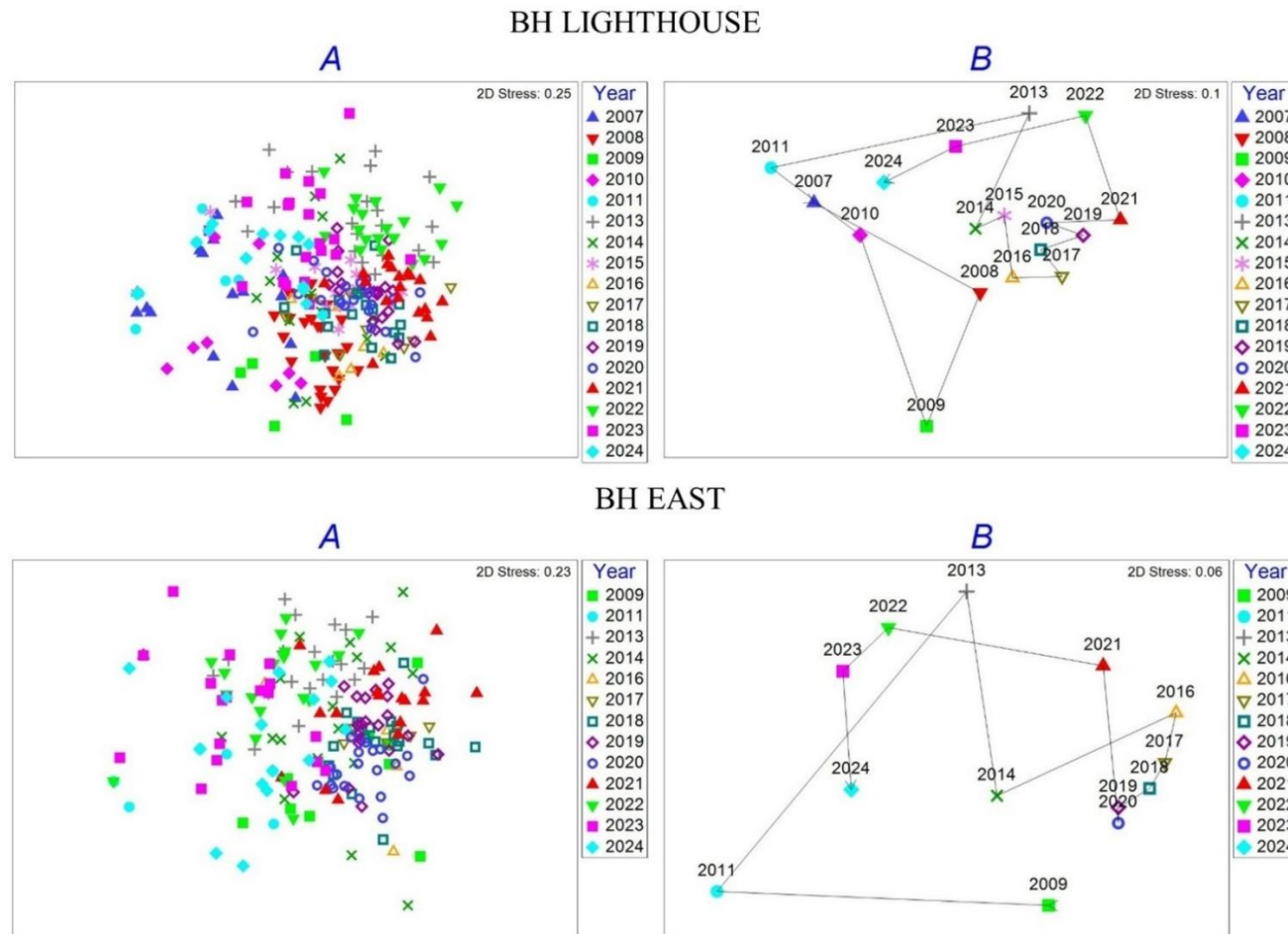
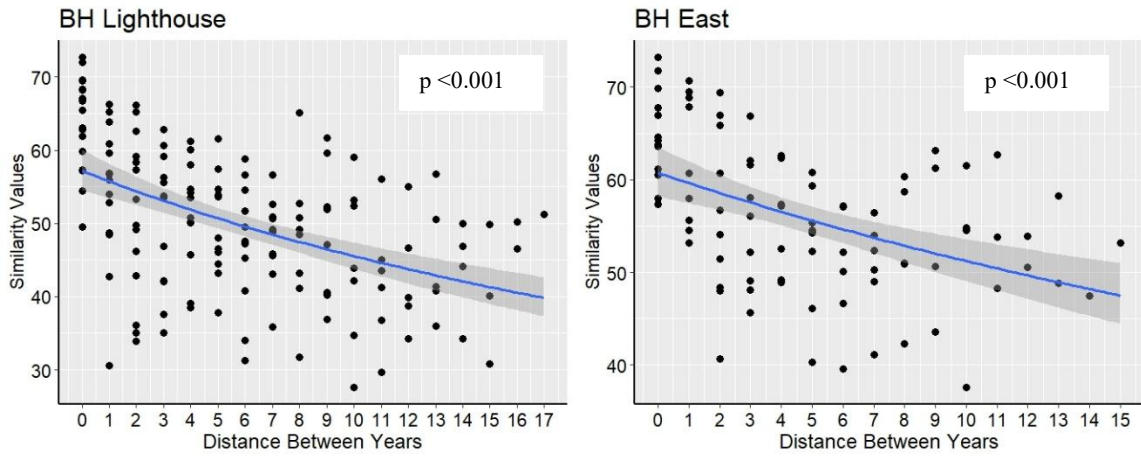


Figure 2: nmMDS plots created from dispersion weighted, square root transformed abundance data of fish + large decapods from cobble-filled bio-collectors deployed at BH Lighthouse in 2007-2024 (except 2012), and BH East in 2009-2024 (except 2010, 2012, 2015), showing similarity between (A) each bio-collector and (B) the centroids of similarity among bio-collectors deployed in a same year; lines are used to connect consecutive years to help visualize the “community trajectory” over time

FISH + LARGE DECAPODS



FISH + LARGE DECAPODS + SMALL SHRIMP

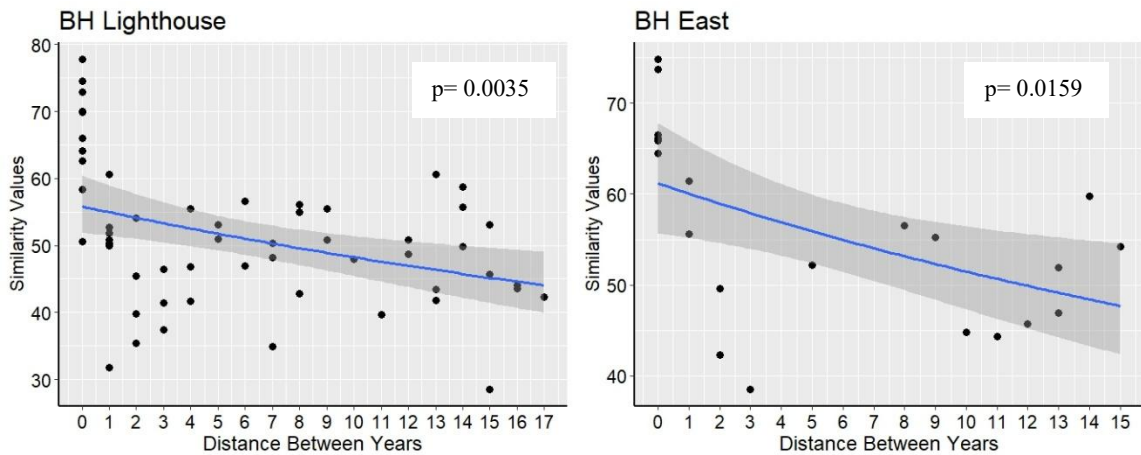
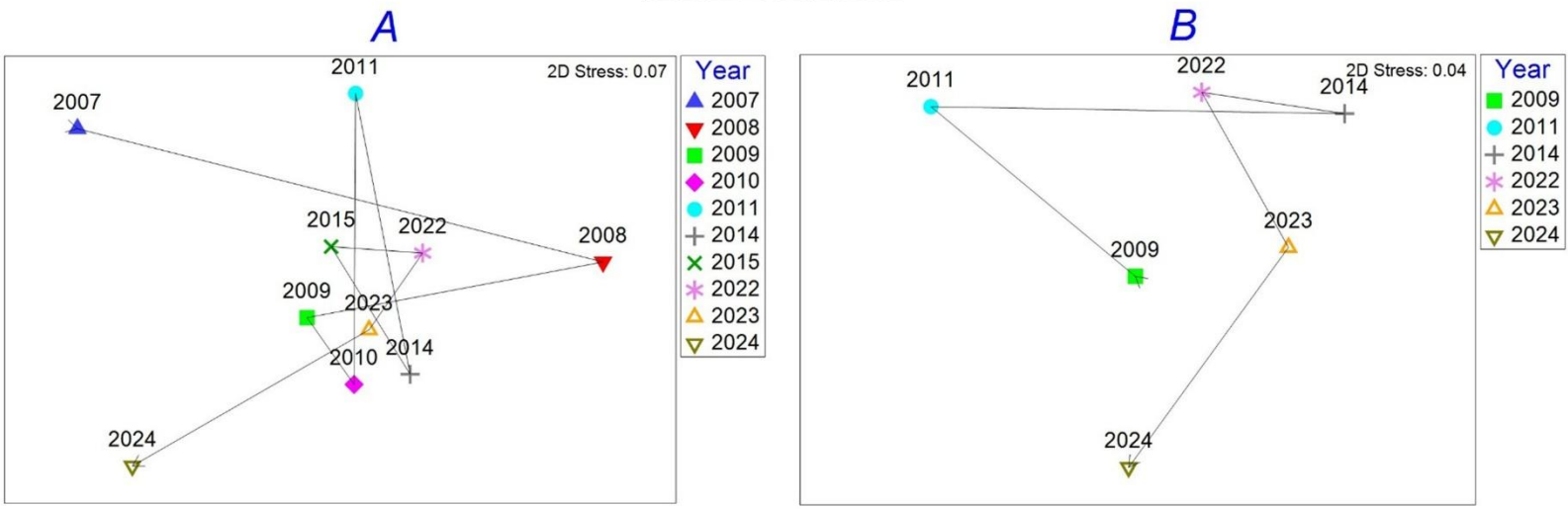


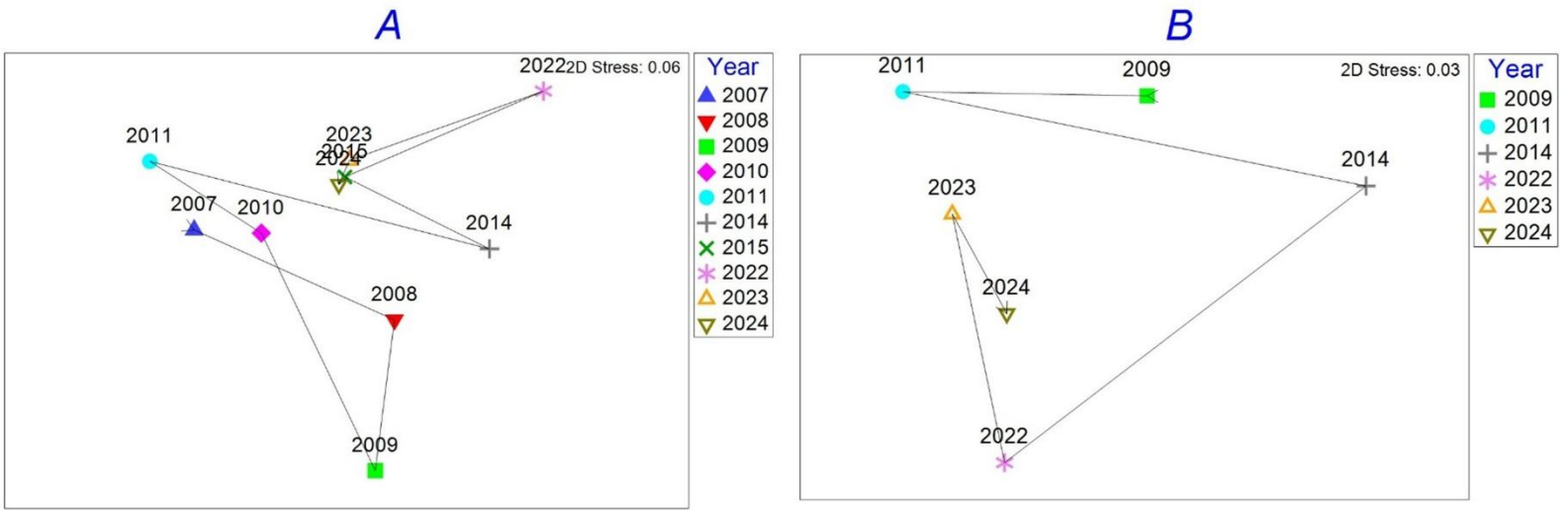
Figure 3: Scatter plots showing the relationship between pair-wise community similarity values between years and distance between the two years being compared. Similarity values are estimated based on PERMANOVAs of dispersion weighted square root transformed abundance data for fish + large decapods as well as fish + large decapods + small shrimp communities at BH Lighthouse from 2007 – 2024 (except 2012) and BH East from 2009 – 2024 (except for 2010, 2012, 2015). Also shown are Gamma regression lines ($\pm$ 95% Confidence Interval) and their associated p-value.

Figure 4 (next 2 pages): nmMDS plots created from dispersion weighted, square root transformed abundance data considering only the years when small shrimp were sampled, of small shrimp alone (top panels), fish + large decapods (middle panels), and fish + large decapods + small shrimp (lower panels) from cobble-filled bio-collectors deployed at (A) BH Lighthouse from 2007-2011, 2014-2015, 2022-2024, and (B) BH East in 2009, 2011, 2014, and 2022-2024, showing the centroids of similarity for each year; lines are used to connect consecutive years to help visualize the “community trajectory” over time.

SMALL SHRIMP

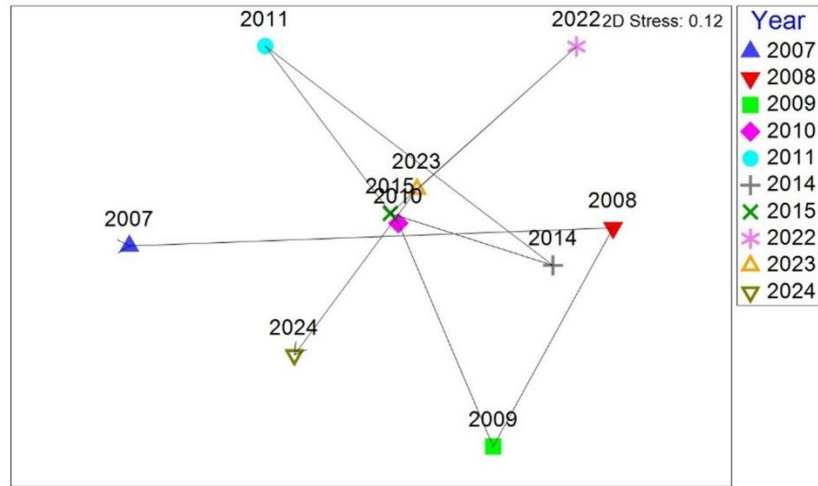


FISH + LARGE DECAPODS (SHRIMP YEARS)

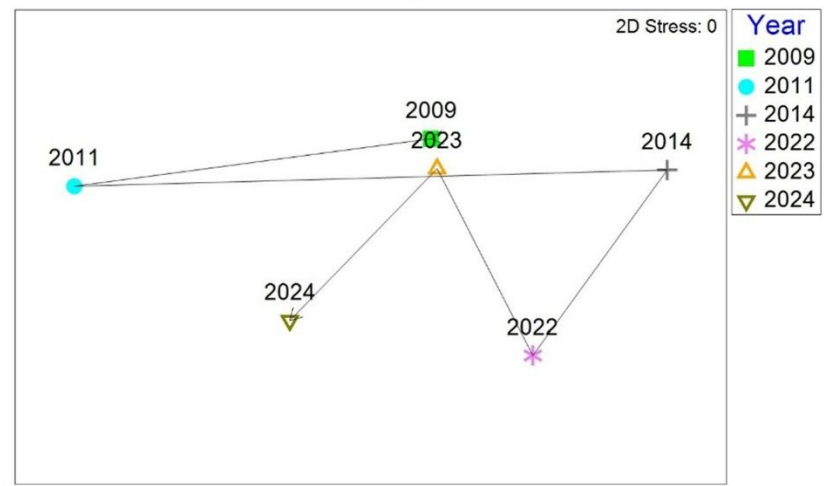


FISH + LARGE DECAPODS + SMALL SHRIMP

A



B



The fish + large decapods + small shrimp community showed evident inter-annual change (Fig 3, Fig 4) and significant seriation trends at both BH sites for all transformations applied (Table 2), but a weaker directional trend than fish + large decapods (Fig 4). At BH Lighthouse, fish + large decapods (2007-2024, except 2012) had higher Spearman's Rho values than fish + large decapods + small shrimp (2007-2011, 2014-2015, 2022-2024), for all transformations (Table 2), indicating that seriation trends were stronger without the addition of small shrimp species at this site; this pattern was not evident at BH East (Table 2). Rho values were not particularly large (≤ 0.269) for any of the analyses (Table 2), i.e., either of the two communities at any of the four sites, indicating the community was not becoming less similar to the initial community throughout the sampling period (Fig 2, Fig 4), potentially due to overlapping of communities in different years (Fig 2, Fig 4).

When small shrimp were considered alone (dispersion weighted (DW) + square root transformed) (Fig 4), they also showed significant seriation at both BH sites (Table 2). Comparison of the Bray- Curtis similarity matrix of fish + large decapods with that of just small shrimp alone for BH sites using the RELATE test indicated weak but statistically significant relationships between the inter-annual patterns of the two groups of species (BH Lighthouse: Rho: 0.119, $p=0.002$; BH East: Rho: 0.138, $p=0.0195$).

Table 2: Spearman's Rho values showing strength of inter-annual seriation estimated by RELATE tests (with significance levels, $p = * < 0.05$, $** < 0.001$) of abundance data of fish and decapods in cobble-filled bio-collectors for both BH Lighthouse and BH East sites, using either raw data, dispersion weighted (DW), DW plus square root transformation, DW plus Log transformation, or DW plus presence/absence transformation. Rho values were calculated separately for each transformation for fish + large decapods (2007 – 2024 except 2012), fish + large decapods + small shrimp (2007 – 2011, 2014 – 2015, 2022 – 2024), and small shrimp alone (2007 – 2011, 2014 – 2015, 2022 – 2024). Small shrimp were only assessed using DW plus square root transformation to compare RELATE output to other communities.

	Fish + Large Decapods		Fish + Large Decapods + Small Shrimp		Small Shrimp	
	BH Lighthouse	BH East	BH Lighthouse	BH East	BH Lighthouse	BH East
No Transformation	0.210**	0.138**	0.200**	0.189*	N/A	N/A
Dispersion Weighting (DW)	0.241**	0.181**	0.226**	0.187**	N/A	N/A
DW + Square Root	0.269**	0.202**	0.167**	0.202**	0.194**	0.161*
DW + Log	0.259**	0.189**	0.168**	0.200**	N/A	N/A
DW + Presence/Absence	0.264**	0.203**	0.102*	0.151*	N/A	N/A

3.2.2 Sudden shifts in communities

In addition to the seriation trends described above, the fish + large decapods community in the BH region also apparently experienced two more pronounced sudden inter-annual shifts during the sampling period (Fig 2). The first apparent community shift occurred between 2011 and 2013 (2007-2011 vs 2013-2022), at both BH sites (Fig 2), seen in nmMDS plots as a relatively large distance between these two years, but more importantly, as a directional shift in the “community trajectory”, which brought communities following the shift (up until second shift, outlined below) away from those before the shift. The second apparent community shift occurred between 2022 and 2023 (2013-2022 vs 2023 and 2024), seen in nmMDS plots as a second change in direction of the community trajectory, which brought the community in these later years back to a structure more similar to those of earlier years, particularly 2007, 2010 and 2011 for BH Lighthouse and 2011 for BH East (Fig 2). No such sudden community shifts were observed at Pocologan and Deadman’s Harbour (Appendix 2), but note that these sites were not sampled when the more pronounced changes in the community were detected at BH sites (i.e., not sampled before 2013 or after 2023). These proposed community shifts are based on visual examinations, which are complicated by the absence of certain years of data that influence interpretation. However, both BH sites showed a relatively defined period of greater stability (2014-2021 for BH Lighthouse, 2016-2020 for BH East) and greater differences from the communities later and earlier in the sampling period that support the idea of sudden shifts in the community on either side of this stability (Fig 2).

When considering the fish + large decapods + small shrimp community at both BH sites (Fig 4), I did not see the two pronounced community shifts (2007-2011 vs 2013-

2022, and 2013-2022 vs 2023 and 2024) that were just described for the fish + large decapods community (Fig 2). For both BH sites, I cannot attribute the lack of sudden shifts in fish + large decapods + small shrimp to the reduced number of years of data for this more complete community, because the two sudden shifts persisted for fish + large decapods considering only years which shrimp data were available (Fig 4). The community of fish + large decapods (small shrimp years) showed clear separation between early (2007-2011) and middle (2013-2022) years, whereas the later (2023, 2024) years changed directionally back towards earlier communities (Fig 4), as described for the fish + large decapods community based on all years (i.e., including when shrimps were not processed) (Fig 2). When focusing on just small shrimp (Fig 4) the same sudden shifts were not evident, indicating these species did not follow the same sudden patterns.

3.3 Species contributing to inter-annual trends

3.3.1 Identifying focal species

The removal of single species from RELATE tests to assess their individual contribution to seriation had little impact on Spearman's Rho values (changes in Rho ranged from -0.072 to 0.037), and in no case did this removal result in the loss of significant seriation (Appendix 5), implying that seriation resulted from changes in more than one species. For the fish + large decapods community, 11/20, 9/20, 9/20 and 8/20 species caused a decrease in Rho values when individually removed from BH Lighthouse, BH East, Pocologan, and Deadman's Harbour, respectively (Appendix 5). Non statistically significant seriation in this community required grouped removal of nine of the 11 species that individually caused a decrease in Rho for BH Lighthouse, 4/9

species for BH East, 2/9 species for Pocologan, and 5/8 species for Deadman's Harbour (Table 3).

When considering fish + large decapods + small shrimp communities, the individual removal of 10/27 species for BH Lighthouse and 7/27 species for BH East caused decreases in Rho (Appendix 5). Non-significant seriation for the fish + large decapods + small shrimp community required grouped removal of 3/10 species that individually caused a decrease in Rho for BH Lighthouse, and 5/7 for BH East (Appendix 6). For fish + large decapods + small shrimp communities, fish and large decapods contributed more to seriation than small shrimp. Of the species that were removed before non significance, 2/3 at BH Lighthouse and 3/5 at BH East were fish and large decapods (Appendix 6). In addition, removal of one fish species (*Tautoglabrus adspersus*) resulted in the largest individual decrease in Rho for both BH sites (Appendix 5), indicating that this species was the largest contributor to seriation. Therefore, for simplicity, I present only species from fish + large decapods graphically hereafter to assess trends in species driving inter-annual community patterns.

Spearman's Rho decreased by different amounts when sequentially removing species for fish + large decapods and for fish + large decapods + small shrimp depending on how many species were already removed. Step-wise decreases were larger once more species had been removed, indicating non-additive effects of sequentially and cumulatively removing species (Appendix 7 and 8).

Table 3: List of species whose individual removal caused a decrease in Rho, which were then sequentially removed from the RELATE test, showing their cumulative change in Spearman's Rho values until all species that caused an individual decrease in Rho were removed, or Spearman's Rho neared 0 (within 0-0.015). Data were fish + large decapods from cobble-filled bio-collectors deployed at BH Lighthouse from 2007-2024 (except 2012), BH East from 2009-2024 (except 2010, 2012, and 2015), and Pocologan and Deadman's Harbour from 2013-2023. Spearman's Rho values are shown for the initial complete community (bolded) and all reduced communities based on dispersion weighted and square root transformed abundance data, along with associated significance level resulting from 9999 permutations of randomly-assigned rank-ordered labels to the same abundance data.

Species Removed	Spearman's Rho	Cumulative Change in Spearman's Rho	Significance Level
BH Lighthouse			
None	0.269		
<i>Cancer borealis</i>	0.242	-0.027	0.0001
<i>Ulvaria subbifurcata</i>	0.209	-0.060	0.0001
<i>Cancer irroratus</i>	0.175	-0.094	0.0001
<i>Homarus americanus</i>	0.143	-0.126	0.0001
<i>Tautogolabrus adspersus</i>	0.115	-0.154	0.0001
<i>Pholis gunnellus</i>	0.050	-0.219	0.0010
<i>Lebbeus groenlandicus</i>	0.034	-0.235	0.0151
<i>Hyas coarctatus</i>	0.028	-0.241	0.0314
<i>Myoxocephalus scorpius</i>	-0.029	-0.298	0.9386
BH East			
None	0.202		
<i>Pholis gunnellus</i>	0.165	-0.037	0.0001
<i>Tautogolabrus adspersus</i>	0.132	-0.07	0.0001
<i>Myoxocephalus scorpius</i>	0.091	-0.111	0.0010
<i>Ulvaria subbifurcata</i>	0.035	-0.167	0.1141
<i>Pagurus arcuatus</i>	0	-0.202	0.4829
Pocologan			
None	0.109		
<i>Tautogolabrus adspersus</i>	0.037	-0.072	0.0171
<i>Cancer irroratus</i>	0.021	-0.088	0.1239
<i>Myoxocephalus scorpius</i>	0.002	-0.107	0.4587
Deadman's Harbour			
None	0.107		
<i>Cancer irroratus</i>	0.069	-0.038	0.0008
<i>Tautogolabrus adspersus</i>	0.054	-0.053	0.0036
<i>Ulvaria subbifurcata</i>	0.036	-0.071	0.0187
<i>Pandalus montagui</i>	0.022	-0.085	0.0374
<i>Microgadus tomcod</i>	0.011	-0.096	0.2663

When considering the fish + large decapods community (Table 3), one species contributed to seriation at all four study sites (*Tautogolabrus adspersus*), three species at three sites (*Cancer irroratus*, *Ulvaria subbifurcata*, *Myoxocephalus scorpius*), one species at two sites (*Pholis gunnellus*), and seven species at only one site (*Cancer borealis*, *Homarus americanus*, *Lebbeus groenlandicus*, *Hyas coarctatus*, *Pagurus arcuatus*, *Pandalus montagui*, *Microgadus tomcod*). Hereafter, I refer to species identified as contributors to significant seriation trends and a value of Rho above 0 (within 0-0.015), as shown in Table 3, as focal species.

3.3.2 Focal species: trends in density across years

When considering the focal species (Table 3) from the fish + large decapods community, I found a significant monotonic change in density over time for 7/9 species from BH Lighthouse (Fig 5), 1/5 from BH East (Fig 6), 3/3 from Pocologan (Fig 7), and 4/4 (*Microgadus tomcod* not analyzed because I had less than 4 years of abundance data) from Deadman's Harbour (Fig 8). At the BH Lighthouse site, densities of *Homarus americanus*, *Tautogolabrus adspersus*, *Ulvaria subbifurcata*, *Cancer irroratus* and *Cancer borealis* significantly increased over time, and *Lebbeus groenlandicus* and *Hyas coarctatus* significantly decreased (Fig 5). At the BH East site, the density of *Pagurus arcuatus* significantly decreased over time (Fig 6). At Pocologan, the densities of *Tautogolabrus adspersus* and *Cancer irroratus* significantly increased over time, and that of *Myoxocephalus scorpius* significantly decreased (Fig 7). At Deadman's Harbour, the densities of *Cancer irroratus*, *Tautogolabrus adspersus*, *Ulvaria subbifurcata*, and *Pandalus montagui* significantly increased over time (Fig 8).

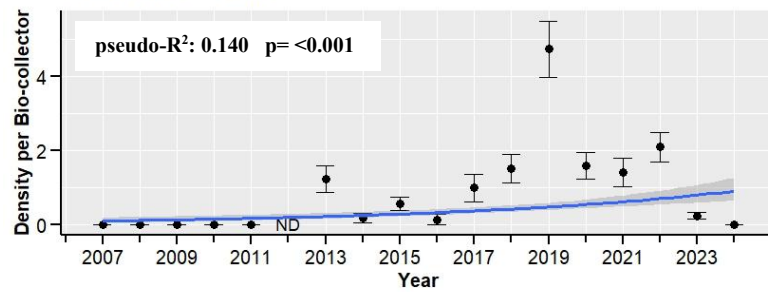
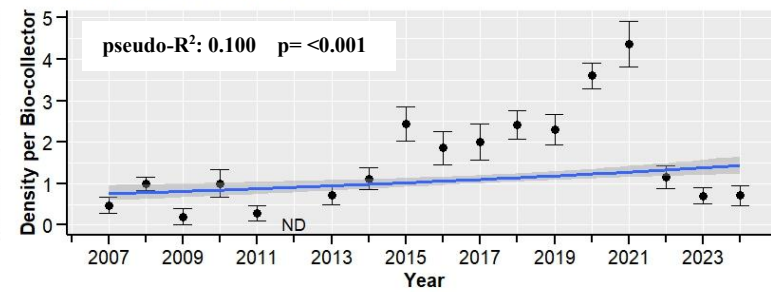
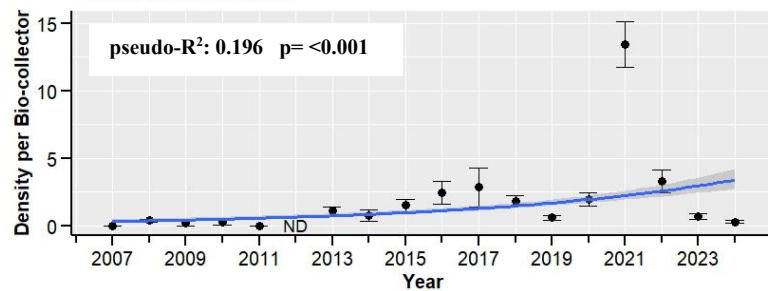
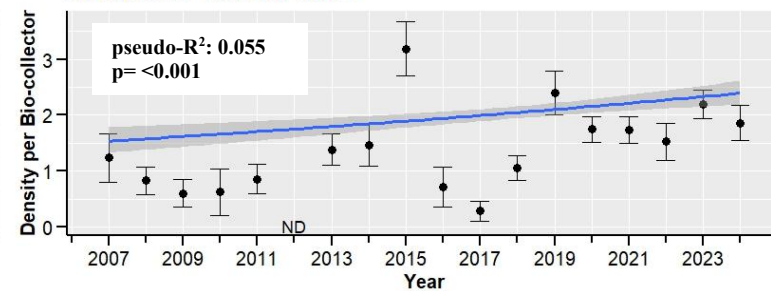
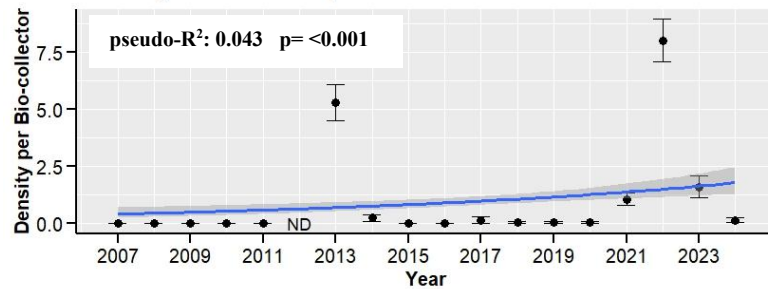
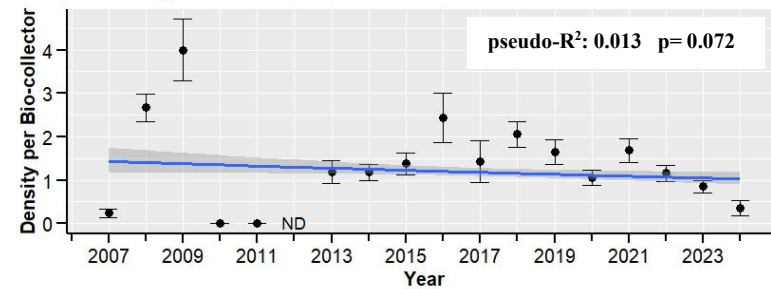
Species that contributed to seriation but did not significantly change monotonically in density were *Pholis gunnellus* and *Myoxocephalus scorpius* at both BH sites (Table 3, Fig 5, Fig 6), and *Tautogolabrus adspersus* and *Ulvaria subbifurcata* at BH East (Table 3, Fig 6). No focal species significantly changed in density at all four sites, nor even at the two more frequently sampled BH Lighthouse and BH East sites. That *Tautogolabrus adspersus* and *Ulvaria subbifurcata* showed significant temporal trends in densities at BH Lighthouse but not BH East may reflect the fact that BH East was not sampled in 2007, 2008, and 2010, potentially missing lower density levels of these species in early years. Craig and Uhler's pseudo- R^2 values for focal species density models from fish + large decapods were relatively low ($<0.001 - 0.196$) at all four sites, indicating that variability in density was not very well explained by a monotonic generalized linear relationship (Fig 5-8).

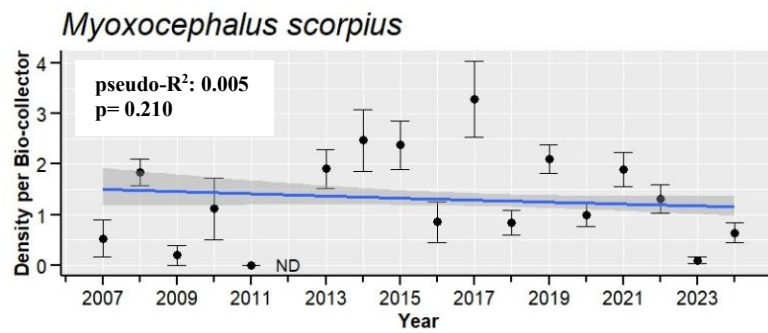
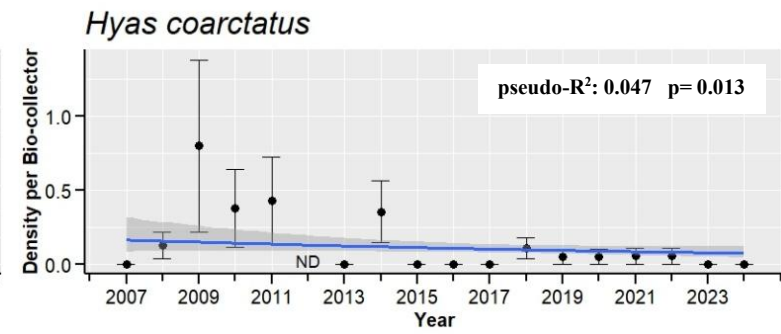
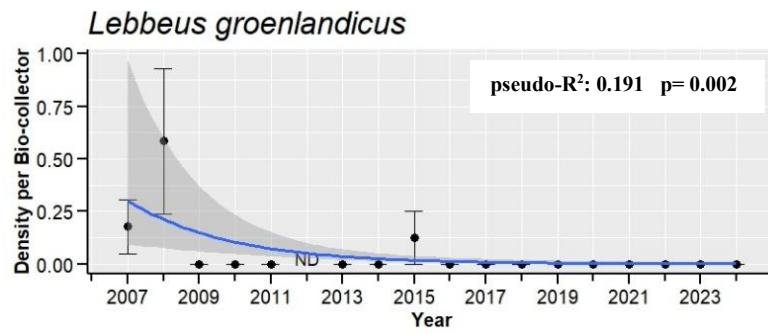
Significant inter-annual trends of fish + large decapods focal species varied, with more regular year-to-year changes in abundance in some species (e.g., *Ulvaria subbifurcata*, *Homarus americanus*, *Myoxocephalus scorpius*, *Cancer irroratus*) (Fig 5-8), in contrast to high densities of some species in only a small number of years (e.g., *Tautogolabrus adspersus*: highs in 2013 and 2022, *Pagurus arcuatus*: high in 2009) and low levels in the rest of the time series (Fig 5-8).

For focal species from the fish + large decapods + small shrimp community, I found a significant monotonic change in density over time for 5/5 species from BH Lighthouse (Appendix 9 and 11) and 4/6 species from BH East (Appendix 10 and 11). Trends for three focal species at each of BH Lighthouse and BH East were already described based on the more complete data series for the fish + large decapods

community (Fig 5, Fig 6). In addition to these three species, *Eualus pusiolus* significantly decreased at BH Lighthouse (Appendix 9), *Pandalus montagui* significantly increased at BH East (Appendix 10), and *Eualus fabricii* significantly increased at both BH sites (Appendix 9 and 10) over the course of our time series. *Pandalus montagui* was not classified as a small shrimp but shows up as a contributor to seriation when assessing the fish + large decapods + small shrimp community but not fish + large decapods in BH East (Appendix 6 and 10).

Figure 5 (next 2 pages): BH Lighthouse scatterplots showing the density ($\pm$ standard error) of each focal species (see text) of the fish + large decapods community, and sampling year, from 2007 to 2024 (except 2012; ND = no data). Also shown are negative-binomial regression lines ($\pm$ 95% Confidence Interval) through these data, and their associated pseudo- R^2 (Craig and Uhler's) and p-value. Panels are ordered from the species resulting in the greatest negative change in Rho when removed individually from the RELATE test in the top left to the least negative change in Rho at the bottom right.

Cancer borealis*Ulvaria subbifurcata**Cancer irroratus**Homarus americanus**Tautogolabrus adspersus**Pholis gunnellus*



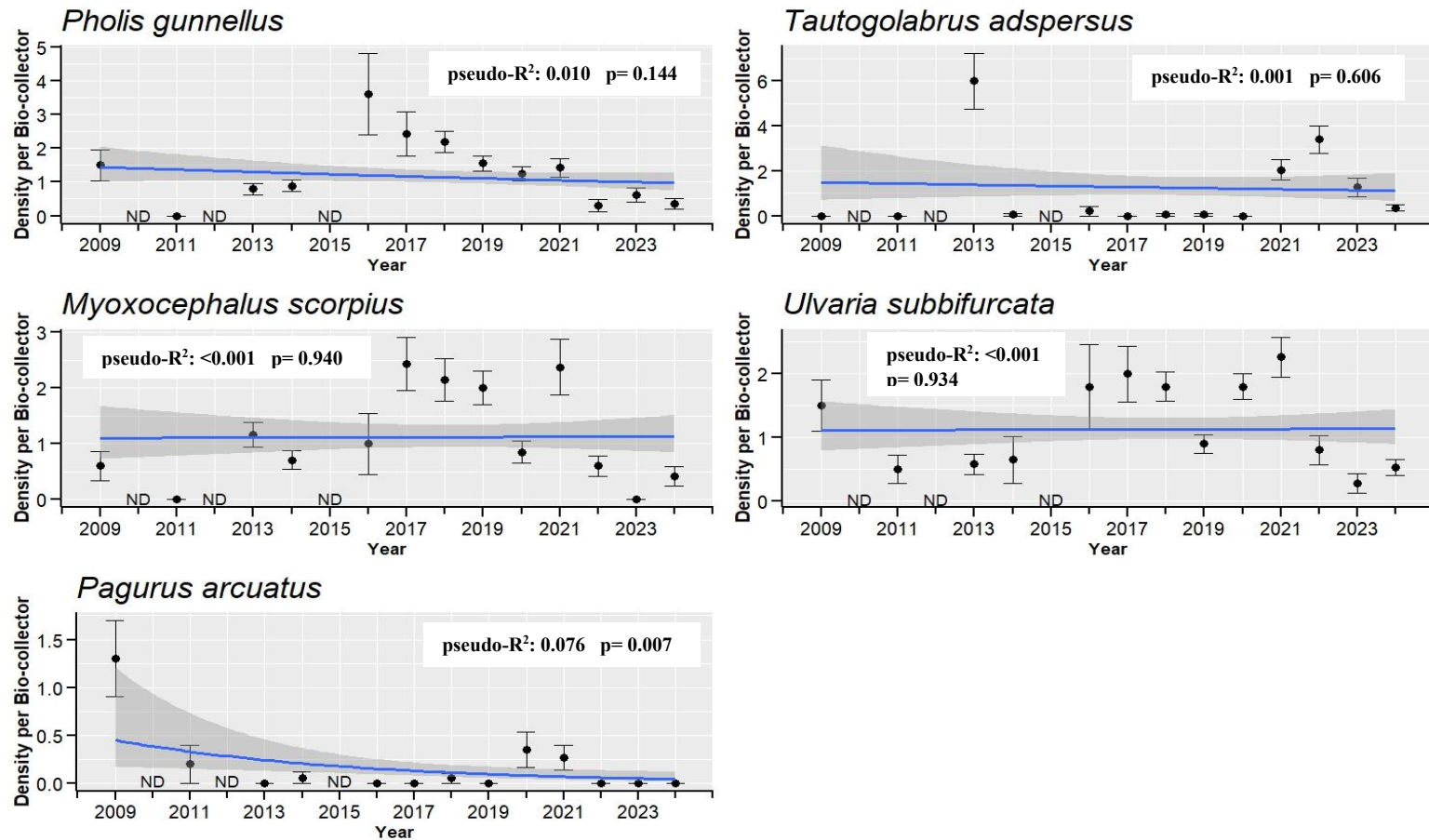


Figure 6: BH East scatterplots showing the density (±standard error) of each focal species (see text) of the fish + large decapods community and sampling year, from 2009 to 2024 (except 2010, 2012, 2015; ND = no data). Also shown are negative-binomial regression lines (± 95% Confidence Interval) through these data, and their associated pseudo-R² (Craig and Uhler's) and p-value. Panels are ordered from the species resulting in the greatest negative change in Rho when removed individually from the RELATE test in the top left to the least negative change in Rho at the bottom right.

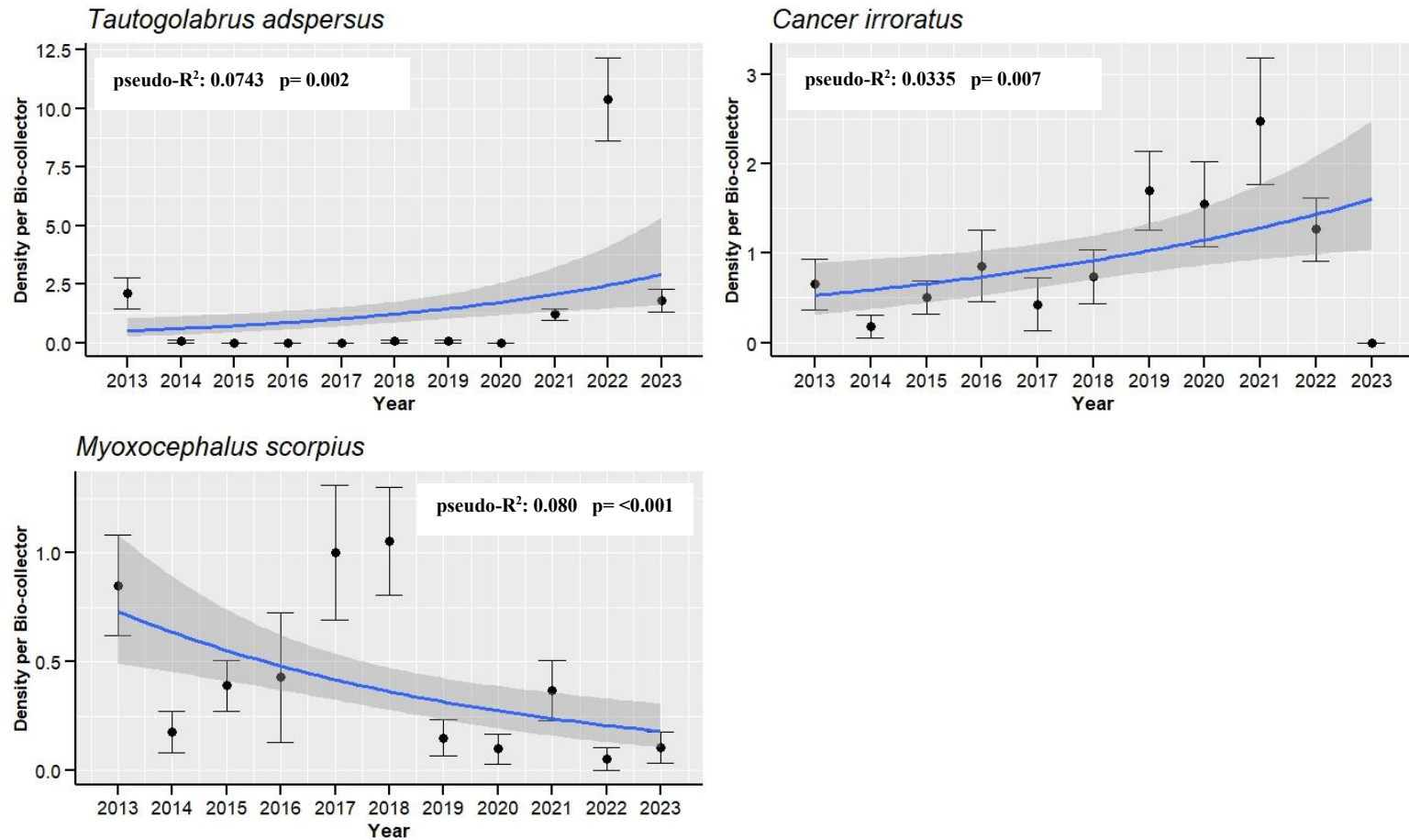


Figure 7: Pocologan scatterplots showing the density ($\pm$ standard error) of each focal species (see text) of the fish + large decapods community and sampling year, from 2013 to 2023. Also shown are negative-binomial regression lines ($\pm$ 95% Confidence Interval) through these data, and their associated pseudo-R² (Craig and Uhler's) and p-value. Panels are ordered from the species resulting in the greatest negative change in Rho when removed individually from the RELATE test in the top left to the least negative change in Rho at the bottom right.

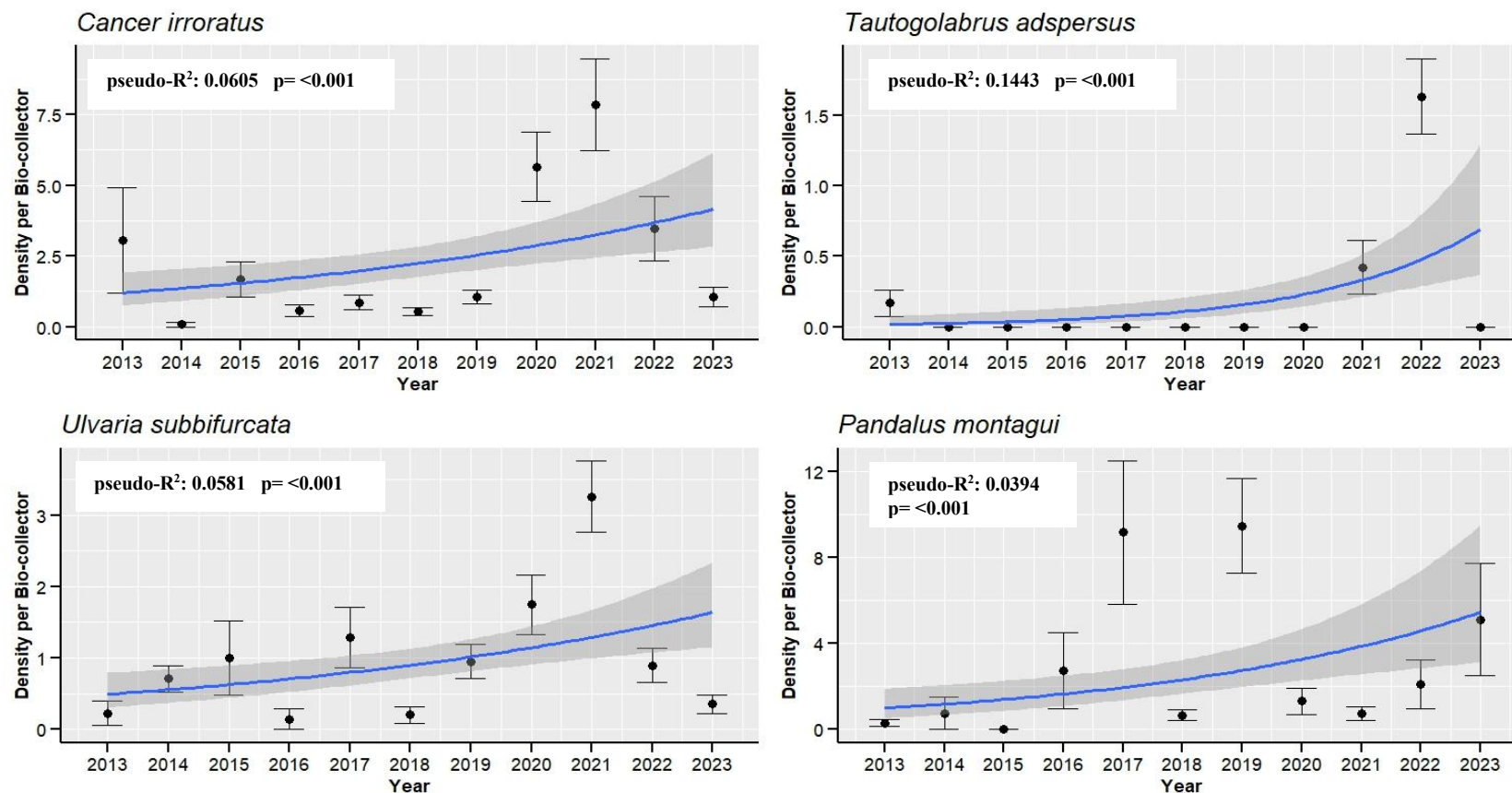


Figure 8: Deadman’s Harbour scatterplots showing the density ($\pm$ standard error) of each focal species (see text) of the fish + large decapods community and sampling year, from 2013 to 2023. Also shown are negative-binomial regression lines ($\pm$ 95% Confidence Interval) through these data, and their associated pseudo-R² (Craig and Uhler’s) and p-value. Panels are ordered from the species resulting in the greatest negative change in Rho when removed individually from the RELATE test in the top left to the least negative change in Rho at the bottom right.

3.3.3 Focal species: density comparison between time spans

At the BH Lighthouse site, most focal species of the fish + large decapods community changed in average density (Fig 9) before and after the two more sudden multivariate community shifts observed in the nmMDS figures (Fig 2). 7/9 focal species differed significantly in density between 2007-2011 and 2013-2022, six increasing and one decreasing (Fig 9, Table 4). Interestingly, 5/6 of the species that increased in density (*Cancer borealis*, *Ulvaria subbifurcata*, *Cancer irroratus*, *Tautogolabrus adspersus*, *Myoxocephalus scorpius*) between 2007-2011 and 2013-2022 decreased in density between 2013-2022 and 2023-2024, returning to levels similar to before the first community shift (not tested statistically because I had only two years in final time span), and the other species (*Homarus americanus*) showed a second smaller increase in density between 2013-2022 and 2023-2024 (Fig 9). The one species that decreased in density (*Hyas coarctatus*) between 2007-2011 and 2013-2022 was absent in 2023 or 2024 samples, thus decreasing a second time between 2013-2022 and 2023-2024 (Fig 9). *Lebbeus groenlandicus* and *Pholis gunnellus* densities did not significantly change during the first community shift, although *Pholis gunnellus* did decrease in density across the second community shift (Fig 9).

At BH East, I did not test changes in average density between time spans statistically because I had only two sampling years both before the first community shift and after the second community shift. Focal species in BH East with similar increases and subsequent decreases across time spans to those at BH Lighthouse were: *Tautogolabrus adspersus*, *Myoxocephalus scorpius*, and *Ulvaria subbifurcata* (Fig 9, Fig 10). *Pholis gunnellus* similarly increased and subsequently decreased in BH East (Fig 10)

as in BH Lighthouse (Fig 9), although I could not test this trend in the former and it was not significant in the latter. The other focal species at BH Lighthouse (*Cancer borealis*, *Cancer irroratus*, *Homarus americanus*, *Lebbeus groenlandicus*, *Hyas coarctatus*) were not focal species at BH East and I did not compare any trends.

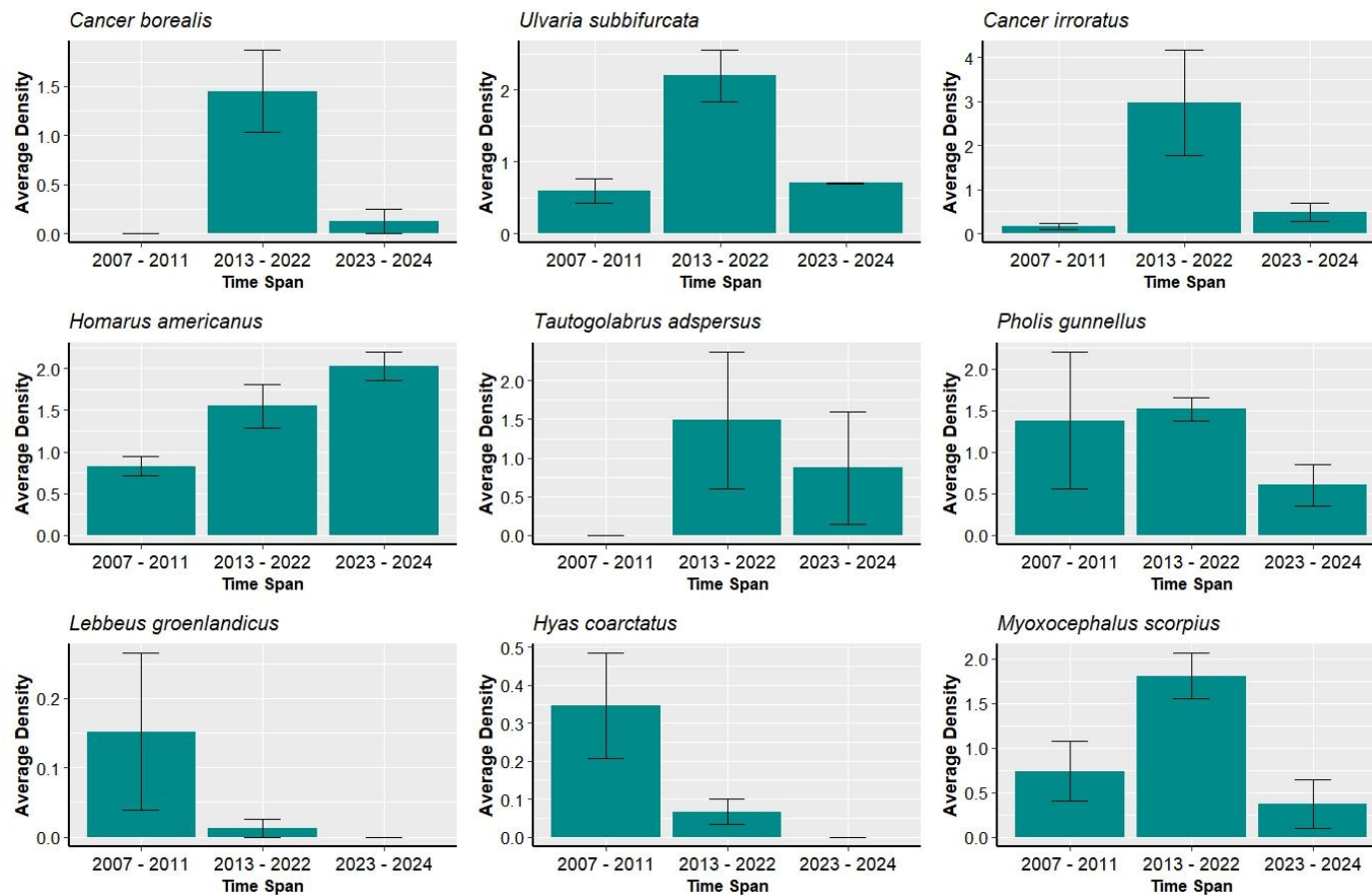


Figure 9: BH Lighthouse bar plots showing the mean ($\pm$ standard error) density of each focal species (see text) of the fish + large decapods community for three time spans associated with two community shifts identified in this study (see section 3.2.2): 2007-2011, 2013-2022, 2023-2024. Panels are ordered from the species resulting in the greatest negative change in Rho when removed individually from the RELATE test in the top left to the least negative change in Rho at the bottom right.

Table 4: Results of Kruskal-Wallis (KW) and Welch's T (WT) tests (degrees of freedom, test statistic (KW: h, WT: t), p-value) comparing, between two time spans (2007-2011 and 2013-2022), the mean density of focal species (see text) from the fish + large decapods community sampled in bio-collectors at BH Lighthouse. Welch's T was used if data was normally distributed in both time spans, Kruskal-Wallis was used if data was not normally distributed.

Species	Test type	degrees of freedom	Test statistic	p-value
<i>Cancer borealis</i>	KW	1	9.82	0.002
<i>Ulvaria subbifurcata</i>	WT	12.21	-4.061	0.002
<i>Cancer irroratus</i>	KW	1	9.392	0.002
<i>Homarus americanus</i>	WT	11.82	-2.54	0.026
<i>Tautoglabrus adspersus</i>	KW	1	6.68	0.001
<i>Pholis gunnellus</i>	WT	4.23	-0.166	0.876
<i>Lebbeus groenlandicus</i>	KW	1	2.215	0.137
<i>Myoxocephalus scorpius</i>	WT	8.66	-2.547	0.032
<i>Hyas coarctatus</i>	KW	1	3.997	0.046

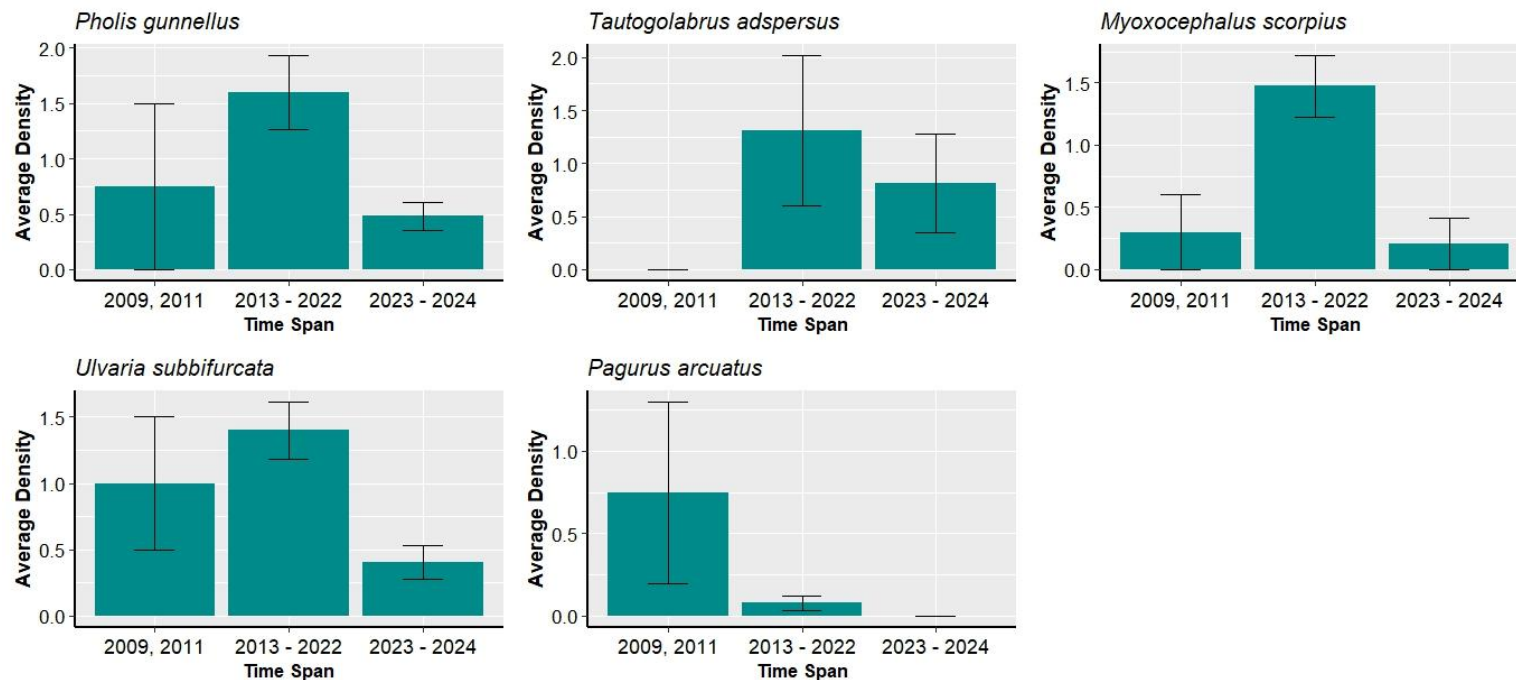


Figure 10: BH East bar plots showing the mean ($\pm$ standard error) density of each focal species (see text) of the fish + large decapods community for three time spans associated with two community shifts identified in this study (see section 3.2.2): 2009 + 2011, 2013-2022 (except 2015), 2023-2024. Panels are ordered from the species resulting in the greatest negative change in Rho when removed individually from the RELATE test in the top left to the least negative change in Rho at the bottom right.

4.0 Discussion

4.1 Overview

This study revealed two inter-annual temporal patterns in the fish and decapod crustacean cobble bottom communities in the Beaver Harbour (BH) region of the South-West Bay of Fundy (BoF) between 2007 and 2024. The first pattern, a significant seriation trend, was evident for all sites, with greater similarity in community structure in adjacent years than years farther apart. The second temporal pattern, observed at the two BH sites, was two more sudden inter-annual community shifts, one between 2011 and 2013 and the other between 2022 and 2023. Seriation trends were expected due to temporal auto-correlation (i.e., demographic persistence of individuals and lagged biotic and abiotic processes or reproduction) but also seemed to be partly driven by abiotic forcing. The two more pronounced sudden shifts in the community coincided with major changes in oceanographic conditions in the BoF related to a marine heat wave (MHW) and the beginning of a cooling period, respectively. In contrast to the fish and large decapods community, the fish, large decapods, and small shrimp community did not show inter-annual directional trends or sudden shifts, potentially because of differences in species' longevity, reproductive traits, and the fewer number of years sampled. Thus, I will focus on the community of fish and large decapods, which varied strongly inter-annually. Patterns outlined are applicable to all four study sites unless specified otherwise.

4.2. Gradual community change from 2007 – 2024: patterns

The fish and decapods community in the southwest BoF showed significant seriation over the 17-year study period (2007-2024). Significance of seriation trends

persisted with various transformations, indicating patterns were driven by both abundance and species identity. Rho values for fish + large decapods and fish + large decapods + small shrimp at BH Lighthouse and fish + large decapods at BH East were larger when analyses were based on dispersion-weighted (DW) data than with raw data, indicating stronger seriation when down weighting years of high variability in abundance of species across replicates of a given site, and hence species that appeared more consistently contributed more to trends (Rho values for raw and DW transformed were very similar for fish + large decapods + small shrimp at BH East). The opposite trend was seen in Deadman's Harbour and Pocologan, with lower Rho values for DW data than raw data, indicating greater variability in species occurrence and abundance across replicates contributed to seriation more than species with less variability across replicates. This difference may reflect the shorter timespan over which Pocologan and Deadman's Harbour were sampled (2013-2023 vs 2007-2024). More specifically, sudden changes in species identity and abundances observed at the two BH sites likely interrupted seriation, and seriation was more pronounced when I reduced the effect of these species. The same effect (of data transformation) was not observed at Pocologan and Deadman's Harbour sites because these locations did not experience the more sudden and pronounced community changes. Significant seriation at all sites persisted when I down weighted highly abundant species by square root or log transformations, indicating that trends persisted when increasing the relative contribution of less abundant species. In fact, Presence/Absence transformed community data yielded higher Rho values than raw community data for fish + large decapods for BH East and Deadman's Harbour indicating that species identity may play a larger role in seriation patterns than changes in

abundance at these two sites, potentially because fewer species had longer term trends in abundance.

4.3: Gradual community change from 2007 – 2024: processes

One underlying cause of seriation is that community composition in any one year likely exhibits temporal auto-correlation with adjacent years, given that community structure in one year constrains that in subsequent years (Warwick et al. 2002; Vindenes & Engen, 2017), in other words, the abundance levels of species will likely resemble adjacent years, given that many individuals present in year x will also occur in year $x+1$ (and so on). Such linkages can cause the seriation I observed in our bio-collectors which allowed manifestation of temporal auto-correlation because many species could enter the bio-collectors in more than one year of their life, resulting in non-independence of the communities sampled in adjacent years, although the effect of this was not investigated in the present study. Based on their size, brachyuran crab species sampled in this study could enter the bio-collectors as new recruits up to several years in life. Hermit crab species could enter for most if not all of their life span, although there is no information on the total lifespan of the two hermit crab species observed in the present study (*Pagurus arcuatus*, *Pagurus acadianus*). American Lobsters (*Homarus americanus*) could enter bio-collectors as settlers up to perhaps 4-5 years of life, when they are considered juveniles, after which point they become adolescents and begin undertaking seasonal migrations with adults. Studied fish species varied in how many years they may have entered the bio-collectors because of differences in body size and shape: Cunner (*Tautoglabrus adspersus*) and Shorthorn Sculpin (*Myoxocephalus scorpius*) were likely able to enter as young of year up to a few years of life, and Rock Gunnel (*Pholis*

gunnellus) for most if not all of its life span, of approximately five years (Altman & Dittmer, 1962). Radiated Shanny (*Ulvaria subbifurcata*) could presumably enter for most if not all its life span of approximately 6-10 years (LeDrew & Green, 1975). All small (in the fish + large decapods + small shrimp community) and large (in the fish + large decapods community) shrimp species could likely enter the bio-collectors in all years of their life, or approximately 2-3 years for “small shrimp” (Squires, 2000) and up to 5-6 years for “large shrimp” (Squires, 1996). Nevertheless, the mesh of the bio-collectors prevented access to larger individuals of some species (e.g., Cunner, brachyuran crabs), which presumably constrained seriation trends to some extent. Note that the habitat sampled serves as nursery grounds for many species that occupy it only for a portion of their life given life stage-specific habitat preference (e.g., American Lobster).

That temporal auto-correlation may have been promoted by individuals of species able to enter the bio-collectors in more than one year of life may explain why community similarity values showed a relatively gradual decreasing trend in communities sampled one to ~6-7 years apart (See Fig 4 in results), and then showed less of a clear trend or no further decrease for communities separated by more years, because this time frame (6-7 years) represents the approximate time period over which I expect that individuals of the initial cohort of many species could enter the bio-collectors given their size or life history restrictions. After this time, probability of sampling individuals from the initial cohort decreases greatly, with new individuals from cohorts that settled in later years potentially responding differently to the environment and resulting in less of a decrease in similarity between later years.

Biotic interactions, reproductive success, and abiotic conditions can also cause seriation, through (i) increased temporal auto-correlation caused by “memory” of communities and conditions, and (ii) biotic/abiotic “forcing” causing directional change in conditions and communities. “Memory” causes greater impact on each year’s community by greater similarity in biotic (e.g., reproductive success, predation, competition) and abiotic (e.g., temperature) conditions in adjacent years (Warwick et al. 2002; Vindenes & Engen, 2017; Postuma et al. 2020). Biotic forcing, through gradual changes in factors such as predation and competition, can cause directional changes in community structure (Voje et al. 2015). Similarly, abiotic forcing on communities can come from directional and persistent changes in oceanographic conditions, such as warming temperatures, with communities responding to abiotic forcing through gradual changes in species and their abundance in a specific direction (Drinkwater et al. 2010). Abiotic forcing can also indirectly drive change in communities through its influence on patterns of biotic forcing.

As a first investigation of this complex community dataset, I did not attempt to discriminate the processes contributing to seriation in this study due to time constraints, but evidence suggests that auto-correlation was not solely at play. More specifically, the number of species contributing to seriation, trends in individual species abundances, low seriation Rho values, and sudden shifts in communities (observed in nmMDS plots) all suggested that biotic/abiotic forcing also contributed to seriation. First, I had to remove a relatively small number of fish and large decapod species as a group to cause non significant seriation (4/20 for BH East, 2/20 for Pocologan, 5/20 for Deadman’s Harbour), and less than half at the fourth site (9/20 for BH Lighthouse), suggesting that

forcing contributed to seriation trends, given that auto-correlation alone would likely result in a gradual loss of seriation involving a greater proportion of the community. Second, most species that contributed to seriation (a Rho above 0) were similar across all sites, with significant monotonic changes in abundance over the 17-year time series (7/9 for BH Lighthouse, 1/5 for BH East, 3/3 for Pocologan, and 4/4 (*Microgadus tomcod* not analyzed due to less than four years of abundance) for Deadman's Harbour), strongly suggesting process-driven changes in these species may be at play, given no expectation that auto-correlation would result in directional abundance trends. Thirdly, a low seriation Rho indicates a weak monotonic temporal structuring of the community, leaving greater scope for a contribution of forcing to trends, although non-monotonic auto-correlation (e.g., cyclic) could also produce such a pattern. Lastly, the sudden community shifts shown in nmMDS plots also indicate that auto-correlation was not solely at play, because it would not be expected to cause large differences in community similarity between adjacent years or cause large directional changes in the community trajectory.

4.3.1 Seriation in literature

Seriation studies have previously focused on subtidal benthic fish (Collie et al. 2008) and invertebrate communities (Warwick et al. 2002; Franz et al. 2019), but few have involved cobble-bottom communities. The few studies on this habitat have addressed spatial seriation (Cranfield et al. 2004; Smale et al. 2008), assessing seriation along a spatial or depth gradient for fish or invertebrate communities in the intertidal zone (Staglicic et al. 2011; Trott, 2016), or invertebrate communities associated with kelp on cobble bottom (Winkler et al. 2017). Therefore, the present study is the first to

investigate seriation in fish and invertebrate species living on/around subtidal cobble bottom.

Warwick et al. (2002) reported significant seriation in soft-bottom subtidal macroinvertebrate communities over 24 years in the North Sea associated with changes in total number of species and total abundance. Collie et al. (2008) identified seriation of benthic fish and invertebrate species over 47 years in Narragansett Bay, associated with increased taxonomic distinctness, the pelagic:demersal ratio, and changes in abundance of individual fish species. Stagličić et al. (2011) reported seriation in littoral fish communities on the eastern Adriatic coast over 16 years associated with increases in total abundance, total biomass, and Shannon's diversity. Franz et al. (2019) identified seriation in sub-tidal hard bottom sessile communities over 10 years in the South-West Baltic coast associated with changes in dominant species and community structure.

All the studies described above attributed community seriation to abiotic or biotic forcing, without quantifying or even acknowledging the potential role of temporal autocorrelation. Some studies suggested abiotic forcing but did not test for statistical associations. For example, Warwick et al. (2002) attributed trends to decreased oxygen and increased temperature, and Stagličić et al. (2011) attributed seriation at all study sites driven by increased catches of four indicator species to recovery of the littoral fish community after legislative changes to fishing regulations. Nonetheless, some studies tested for associations of abiotic forcing. Collie et al. (2008) found community changes strongly correlated with changes in sea surface temperature, chlorophyll-*a* concentration, and winter NAO (North Atlantic Oscillation), although they did not discuss the amount of community variability explained by these variables. Franz et al. (2019) found community

trends to be most strongly correlated with changes in sea surface temperature, current speed, and chlorophyll-*a* concentration, with fixed effects of the model explaining 32% of the deviance. Although the changes in ocean conditions described above likely explain some of the community trends in these studies, temporal auto-correlation likely also explains a portion of variability. Future studies should make greater efforts to discriminate the contributions of forcing versus temporal auto-correlation to community seriation to increase our understanding of temporal changes in marine communities. This goal is no easy task, but one approach would be to use the RELATE test to compare community similarity matrices to: (i) matrices reflecting temporal distance between samples (e.g., year, month), and (ii) matrices reflecting temporal changes in environmental variables, with the relative strength of these associations providing an estimate of the relative contribution of these different processes to community seriation. Due to time constraints this was not done in the present study.

Some studies found no evidence of seriation, which they generally attributed to more sudden and frequent changes in ocean conditions. Wahl et al. (2013) detected no seriation in hard bottom filter feeders in the South-West Baltic Sea over six years, which they attributed to high inter-annual variability in temperature and salinity causing an almost cyclical pattern of dominant species. Stobart et al. (2009) reported insignificant seriation in fish communities over eight years in areas surrounding a marine reserve on the Mediterranean coast, which they attributed to increased and consistent fishing pressure outside the reserve after the reserve's implementation. James et al. (2008) found no seriation for a temperate estuarine fish community in South Africa over nine years, which they associated with drastic changes in ocean conditions following cyclical

changes to the sandbar at the mouth of the estuary (open/closed). Notably, however, although these studies generally attributed the absence of seriation to abrupt changes or high variability in ocean conditions, all were carried out over fewer sampling years than the studies discussed earlier (including the present one) that detected significant seriation, suggesting that study length may be a major contributor to differences in detection of seriation among studies.

4.3.2 Species contributing to gradual change in the community

Five species in the present study were the most important contributors to seriation trends based on the result of sequential removal from the RELATE test in one or more sites, significant changes in abundance over the sampling period in one or more sites, and also changes in density across the two community shifts in BH sites. Four of these species increased significantly in abundance (Cunner, Atlantic Rock Crab, Radiated Shanny, Jonah Crab), and one decreased significantly in abundance (Shorthorn Sculpin), at one or more of the four sites over the study period. These species may be the main contributors to seriation because they were present in most years sampled and changed directionally in abundance. The initial and continued presence in bio-collectors of Cunner and Jonah Crab, as of 2012 and 2013, respectively, caused a change in species composition in the community, which contributed to seriation separate from overall abundance trends. Note that Rock Gunnel contributed to seriation for both BH sites, but with no significant abundance trend in either site.

The present study did not investigate the causes of significant changes in abundance over time for the five important species discussed above, but documented changes in ocean conditions in the region may have contributed through abiotic forcing.

In particular, ocean temperatures in the BoF and greater Gulf of Maine (GoM) have exhibited a warming trend since the 1980s (0.47°C per decade), with this region experiencing one of the highest rates of warming globally (Hebert et al. 2024; Gulf of Maine Research Institute, 2025). Regime shift analysis done by the Department of Fisheries and Oceans has also found three distinct and increasing warmer climatological regimes from 1981-2024 for the GoM and BoF, with the current regime beginning in 2010 showing a positive anomaly compared to the 1991-2020 climatological mean (Layton et al. 2025). Many studies looking at benthic fish and invertebrate species in the last 50 years in the BoF/GoM and broader North-East Shelf have linked shifts in median distributions and changes in abundance to warming or other changes in ocean conditions (Nye et al. 2009; Nye et al. 2010; Fredston-Hermann et al. 2020; Fredston et al. 2021; Williams, 2025). Some studies of fish and invertebrate species have also documented range expansions in the GoM (Mills et al. 2013; Wade et al. 2024; Pershing et al. 2021) and northern GoM (Woodard, 2014; Quinn 2018). This observation suggests that the community and abundance changes I saw in the present study may also have been driven by changing ocean conditions.

Some species important to seriation that changed in abundance, i.e., Cunner, Jonah Crab, Atlantic Rock Crab, have shown similar changes in other areas of the GoM and Northeast Shelf. The BoF is within the range of adult Cunner (Chesapeake Bay, Maryland to Conception Bay, Newfoundland (Bigelow et al. 1953)), but historically the species has had very low recruitment levels in the region. The increasing numbers of juvenile Cunner in bio-collectors may result from increases in summer water temperatures causing increased recruitment in the BoF, based on increased development

success of embryos with increasing temperature in a laboratory study, as well as correlations between presence and density of young-of-year Cunner in bio-collectors and bottom temperature (Woodard, 2018). The increasing abundance of Jonah Crab may similarly result from increasing temperatures that enable an expansion of thermally preferred habitat. Jonah Crabs span a wide geographic range (Newfoundland to Florida and the Bermudas (Wade et al. 2024)) but have increased in abundance on Georges Bank and the Mid Atlantic-Bight since the 1970s, potentially because of increasing temperatures (Wade et al. 2024). Atlantic Rock Crab also span a wide geographic distribution (Labrador to South Carolina (Wade et al. 2024)), with the temperature in the BoF falling within its preferred temperature range (0-14° C) (Wade et al. 2024). Increases in abundance since the 1990s on George's Bank and the northern Mid-Atlantic Bight, potentially result from changing ocean conditions (Wade et al. 2024).

In contrast to the three aforementioned species, no studies have documented trends in abundance for the other two species important to seriation, i.e., Shorthorn Sculpin, Radiated Shanny, in the BoF or GoM. Shorthorn Sculpin, a colder-water species with a more northerly range (Arctic to New England (Bigelow et al. 1953)), occurs in higher abundances at summer temperatures lower than 12-15°C (Bigelow et al. 1953). I cannot confidently attribute the decreasing trend in Pocologan to increasing temperature, because BH sites do not show significant decreasing trends with a longer sampling period. Although the temperature preference of Radiated Shanny is not well known, this species has a more northerly southern limit of their range than other fish species in the present study (Newfoundland to Massachusetts (LeDrew & Green, 1975)), suggesting

temperature may not be responsible for the increasing abundance of this species over the course of our study.

4.4 Sudden shifts between 2011 and 2013 and between 2022 and 2023

In addition to the significant seriation trends, fish and large decapod communities in both BH sites appeared to undergo two more pronounced shifts over shorter time intervals. The first sudden shift on the nmMDS plots occurred between 2011 and 2013 (2007-2011 vs 2013-2022), and the second between 2022 and 2023 (2013-2022 vs 2023 and 2024). Interestingly, the second sudden shift appeared to increase the similarity of the community to communities observed earlier in the time series (before 2012). These two shifts were not evident at the Pocologan and Deadman's Harbour sites because sampling at these sites occurred over a narrower time period (2013-2023) that did not capture either the first (2007-2011 vs 2013-2022) or the second (2013-2022 vs 2023 and 2024) shift.

Similar to the present study, some previous seriation studies also detected more pronounced and sudden temporal shifts of communities in addition to seriation (Warwick et al. 2002; Collie et al. 2008; Trott, 2016). Warwick et al. (2002) reported a sudden shift in a subtidal soft-bottom macroinvertebrate community from 1993-1994 (1980-1993 vs 1994-1999) associated with increases in the number of species, Shannon diversity, and average taxonomic distinctness. Collie et al. (2008) identified a sudden shift in species abundance and community composition of a subtidal fish and invertebrate community from 1984-1985 (1959-1984 vs 1985-2005), resulting in a community dominated by species with higher temperature preferences than the earlier time period. Trott (2016) reported a significant shift in the intertidal macroinvertebrate community of Cobscook Bay in the GoM from the late 1900s to the 2000s associated with the loss of core

assemblage species. The sudden shifts described above were attributed to changes in ocean conditions or human impacts. Warwick et al. (2002) hypothesized that the temporal shift in the macroinvertebrate community was associated with construction of a barrage within the estuary. Collie et al. (2008) linked the community shift in their study to increases in ocean temperature. Trott (2016) associated the community shift to warming temperatures and increased diversification and intensity of commercial exploitation.

4.4.1 Species contributing to sudden community shifts

The five species that contributed to the two more sudden community shifts, (between 2011 and 2013 and between 2022 and 2023), i.e., Cunner, Atlantic Rock Crab, Radiated Shanny, Jonah Crab, and Shorthorn Sculpin, were the same species that primarily contributed to seriation trends. All five of these species increased significantly in density across the first sudden shift in BH Lighthouse and returned to lower density levels after the second sudden shift at this site. I could not test these changes statistically at BH East, but three of the aforementioned five species (Shorthorn Sculpin, Cunner, and Radiated Shanny) showed very similar patterns at this site. The other two species (Jonah Crab, Atlantic Rock Crab) were not focal species at BH East therefore I did not compare trends.

The sudden changes in density of the five species discussed above may result from similarly sudden changes in oceanographic conditions. Since an increased rate of warming began around 2010, the BoF/GoM has experienced multiple marine heatwaves (MHWs), with the most extreme occurring from 2012-2013, with temperatures more than 2°C above the 1982-2011 mean (Mills et al. 2013; Pershing et al. 2018; Townsend et al. 2023; Record et al. 2024). The BoF harbours a sub-Arctic ecosystem at a temperate

latitude, because strong tidal mixing prevents summer stratification, with temperatures normally not exceeding 12°C in summer in years prior to 2011/2012 (Wilkinson et al. 2009; Wahle et al. 2013). The extreme MHW in 2012 coincided with the first sudden community shift observed for fish and large decapods in both BH sites. Since the early fall of 2023, the GoM and BoF have experienced cooler bottom temperatures and lower salinities because of the southward movement of the eastern portion of the Gulf Stream and an increased influx of Labrador and Scotian Shelf Slope Waters into the system (Record et al. 2024; Hebert et al. 2024; Galbraith et al. 2025). This influx caused cooler temperatures in 2023 compared to the record highs of the two prior years (Hebert et al. 2024; Galbraith et al. 2025), and temperature and salinity profiles in 2024 similar to the pre-2010 period, indicating a shift to a new period of cooler temperatures (Townsend et al. 2023; Record et al. 2024; Hebert et al. 2024; Koul et al. 2024; Galbraith et al. 2025). This shift to cooler temperatures coincided with the second sudden community shift observed for fish and large decapods in both BH sites between 2022 and 2023, with 2023 and 2024 appearing to shift back towards early years on the nmMDS plots.

The 2012 MHW may be linked to the first and continued presence of juvenile Cunner and Jonah Crab in our bio-collectors beginning in 2012 and 2013, respectively. A study on effects of temperature on hatch success of Cunner reported markedly greater hatch at temperatures >13°C (Woodard, 2018), implying increased temperatures from the 2012 MHW may have caused an expansion of thermally preferred habitat for successful reproduction. Fisher observations in the upper BoF's Minas Basin also reported the initial and continued presence of Cunnners beginning in 2012 (Quinn, 2018). The initial and continued presence of Jonah Crabs in our bio-collectors beginning in 2013 may similarly

result from increasing temperatures expanding thermal habitat, coinciding with increased abundance indices along the United States Atlantic coast since 2010 (Wade et al. 2024) and a new fishery opening in New England in 2015 (Truesdale et al. 2019). The decrease in density of Cunner and Jonah Crab across the second shift (2013-2022 vs 2023 and 2024) between 2013-2022 and 2023, 2024, may result from decreasing temperatures in the BoF at this time, potentially reducing thermally preferred habitat for Jonah Crab, and available thermal habitat for reproduction ($> \sim 13^{\circ}\text{C}$) for Cunner.

Three of the five species contributing to the sudden community shifts, i.e., Shorthorn Sculpin, Atlantic Rock Crab, and Radiated Shanny, show similar patterns to the species discussed above (Cunner, Jonah Crab). Atlantic Rock Crabs may have increased in density due to increasing temperatures from the 2012 MHW, because gradual increases in abundance in the Mid-Atlantic Bight and Georges Bank have been linked mainly to temperature increases (Wade et al. 2024). The decrease in density in the present study in the later cooler years may result from decreasing temperatures causing lower density levels. Finally, Shorthorn Sculpin and Radiated Shanny also increased in density after the 2012 MHW, and decreased in density after the more recent cooler period (2023, 2024), but I found little information in the literature to explore the cause of these trends.

4.4.2 Similar sudden shifts in species within the BoF/GoM

In the present study, the first sudden shift of the community coincided with the 2012 MHW. Other studies on similar fish and/or invertebrates in the BoF/GoM have not explicitly tested the impacts of the MHW on overall communities, although there is literature on the effects on individual species that show similar trends to those of the focal

species in the present study. Increased temperatures associated with the 2012 MHW apparently enabled Blue Crab (*Callinectes sapidus*) to enter the GoM (Pershing et al. 2018) and have been proposed to be responsible for the first recorded observations of Longfin Squid (*Doryteuthis pealeii*) and Black Sea Bass (*Centropristis striata*) in the GoM (Mills et al. 2013; Pershing et al. 2013). This MHW also caused changes in activity and catches of American Lobster, resulting in higher recruitment to the fishery in the GoM, and spikes in landings and abundance levels in 2012 (Mills et al. 2013; Pershing et al. 2013). Abrupt drops in abundance of the invasive Green Crab (*Carcinus maenas*) and the polychaete *Alitta virens* in the upper BoF's Minas Basin shortly after 2012 (Quinn, 2018), and decreases in abundance of Cod (*Gadus morhua*) in the GoM starting in 2012 (Pershing et al. 2013), were also linked to this heatwave. The recency of the second sudden community shift I observed between 2022 and 2023, contributes to the absence of published studies addressing how communities and species have changed after 2023 in the region.

4.5 Small shrimp species not contributing to trends

Small shrimp species (n=7) were not the largest contributors to seriation and did not show similar sudden community shifts as fish and larger decapods. Their lesser contribution to seriation may partly relate to the shorter lifespan of these species, reducing temporal auto-correlation over the time span of this study. Note that the smaller number of sampling years for small shrimp (BH Lighthouse: 2007-2011, 2014-2015, 2022-2024, BH East: 2009, 2011, 2014, 2022-2024) resulted in incomplete trends with discontinuous data, reducing my confidence in shrimp species' trends and their contribution to community changes. Limited literature exists on the lifespan of the shrimp

species observed in this study, although Squires et al. (2000) reported a lifespan of two years for males and three years for females for *Eualus pusiolus*, which is shorter than the age up to which many other fish and large decapods can enter the bio-collectors. That small shrimp species having shorter lifespans and faster turnover in bio-collectors may cause higher variability in densities year to year, reducing temporal auto-correlation. That these species also did not show sudden community shifts potentially indicates that they did not respond to the same external forces (e.g., temperature) as the fish and larger decapod species, but I acknowledge that the small number of years sampled between the first and second community shift (2014-2015 for BH Lighthouse, 2014 only for BH East) may also have contributed to the absence of visible shifts.

The two most abundant species of small shrimp, i.e., *Eualus fabricii* and *Eualus pusiolus* contributed to seriation of the fish + large decapods + small shrimp community and increased significantly in density over time. *Eualus fabricii* has a boreal-arctic distribution (Sokolov, 2006), and the large increases in abundance of this species at the end of the time series may reflect decreasing temperatures in the BoF after 2022, though I note similarly high abundances were not seen in earlier cooler years (2007-2011). Interestingly, *Eualus pusiolus* has a more temperate distribution, does not inhabit the Canadian Arctic coast (Sokolov, 2006), and increased markedly in abundance in the middle of the time series, when temperatures were warmer, and then noticeably decreased in 2024 when temperatures cooled.

4.6 Conclusion

This study used bio-collectors to sample communities inhabiting subtidal cobble bottom, offering rare insight into understudied and difficult to sample cryptic species,

including early life stages and smaller taxa. I successfully documented through significant seriation and assessment of changes in abundance, changes in a community of 27 fish and decapod crustaceans in the BH region of the South-West BoF over 17 years. This study also captured two more pronounced sudden community shifts, including one after the well known 2012 MHW. Five species were the main drivers of seriation in one or more site and underpinned sudden shifts at our two main study sites: Cunner, Jonah Crab, Atlantic Rock Crab, Radiated Shanny, and Shorthorn Sculpin.

The geographic scope of our study was limited, by the capacity to sample only a few sites consistently over the 17-year sampling period. Future studies could continue this long-term monitoring in sites with the most complete datasets, to further contribute to our understanding of temporal trends in the region, noting that the value of the data increases as more years are added. Future investigations should also aim to disentangle the contribution of temporal auto-correlation and forcing to seriation trends, and the contributions of different biotic and abiotic factors. Continuation of this monitoring program and research associated with it is of increased importance in a rapidly changing ocean climate.

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Appendix A: Additional figures and tables

Table A1 (current and next page): Record of presence in bio-collectors of the 27 fish and decapod species sampled from 2007-2024 (except 2012) at 4 study sites in the Beaver Harbour region of the South-West Bay of Fundy. An x is denoted if a species was present in bio-collectors in the fish + large decapods + small shrimp community in the BH Lighthouse and BH East sites, as well as if a species was present in bio-collectors in the fish + large decapods community in each of the 4 sites. Fish + large decapods + small shrimp were sampled from 2007-2011, 2014-2015, and 2022-2024 in BH Lighthouse and 2009, 2011, 2014, and 2022-2024 in BH East. Fish + large decapods were sampled from 2007-2024 (except 2012) in BH Lighthouse, 2009-2024 (except 2010, 2012, 2015) in BH East and 2013-2023 in Pocologan and Deadman's Harbour. Small shrimp species that were only processed in certain years are denoted with an asterisk by the species name and by "np" for not processed under fish + large decapods. Species found to be contributing to significant seriation within a site and dataset have bolded capital Xs.

	Fish + Large Decapods + Small Shrimp		Fish + Large Decapods			
Species	BH Lighthouse	BH East	BH Lighthouse	BH East	Pocologan	Deadman's Harbour
<i>Cancer borealis</i>	X	x	X	x	x	x
<i>Cancer irroratus</i>	X	X	X	x	X	X
<i>Carcinus maenas</i>	x	x	x	x	x	x
<i>Caridion gordonii</i> *	x	X	np	np	np	np
<i>Crangon septemspinosa</i> *	x		np	np	np	np
<i>Cyclopterus lumpus</i>			x	x	x	x
<i>Eualus fabricii</i> *	X	X	np	np	np	np
<i>Eualus gaimardii</i> *	x	x	np	np	np	np
<i>Eualus pusiolus</i> *	X	x	np	np	np	np
<i>Homarus americanus</i>	x	x	X	x	x	x

<i>Hyas coarctatus</i>	x	x	X	x	x	x
<i>Lebbeus groenlandicus</i>	x	x	X	x	x	x
<i>Lebbeus microceros*</i>	x		np	np	np	np
<i>Lebbeus polaris*</i>	x	x	np	np	np	np
<i>Liparis sp.</i>	x		x	x	x	x
<i>Microgadus tomcod</i>	x	x	x	x	x	X
<i>Myoxocephalus octodecemspinosus</i>	x		x	x	x	x
<i>Myoxocephalus scorpius</i>	x	x	X	X	X	x
<i>Pagurus acadianus</i>		x		x	x	x
<i>Pagurus arcuatus</i>	x	X	x	X	x	x
<i>Pandalus montagui</i>	x	X	x	x	x	X
<i>Pholis gunnellus</i>	x	x	X	X	x	x
<i>Stichaeus punctatus</i>	x	x	x	x	x	x
<i>Tautoglabrus adspersus</i>	X	X	X	X	X	X
<i>Ulvaria subbifurcata</i>	x	x	X	X	x	X
<i>Urophycis tenuis</i>	x		x	x		x
<i>Zoarces americanus</i>	x		x	x	x	x

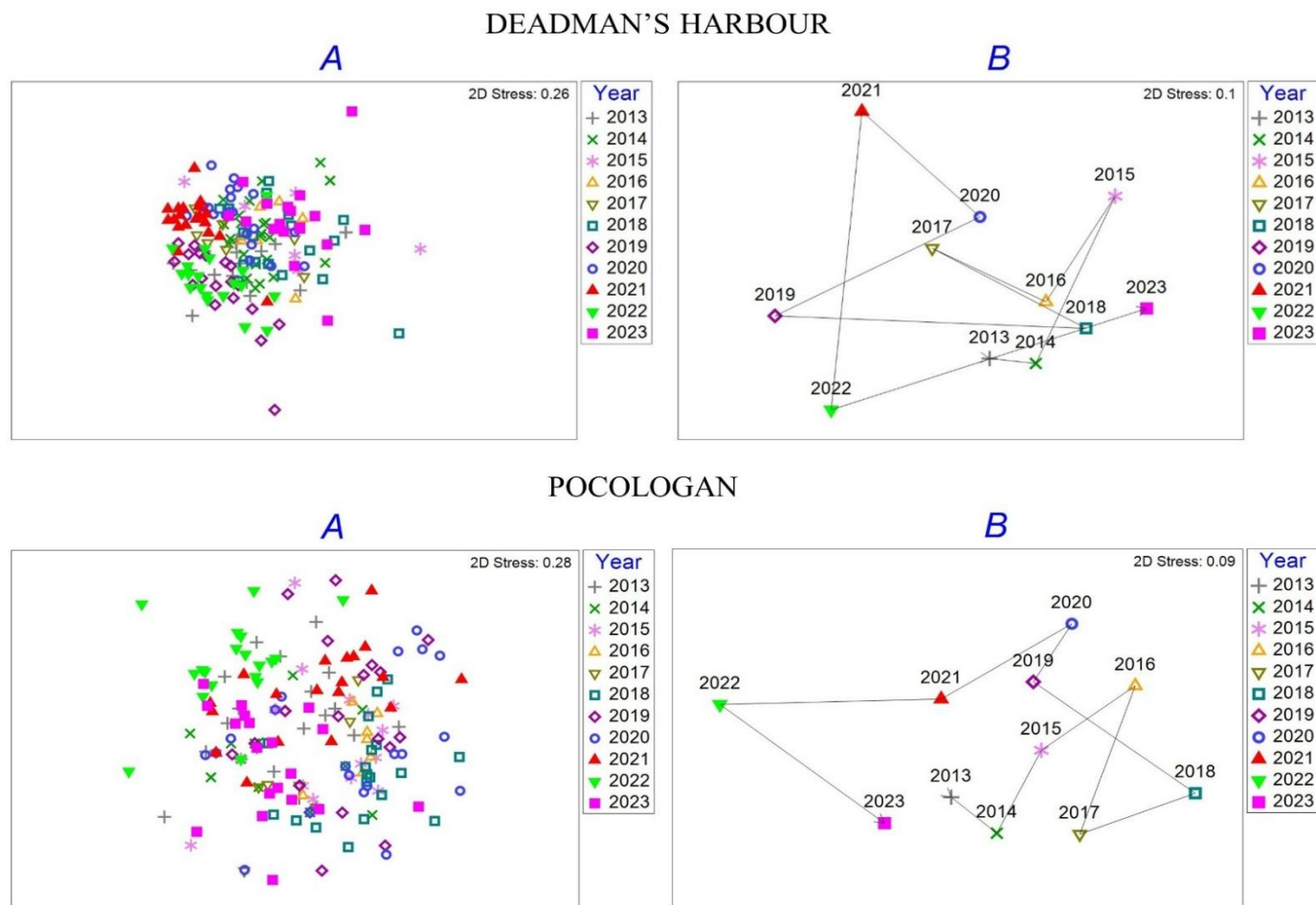


Figure A1: nmMDS plots created from dispersion weighted, square root transformed abundance data of fish + large decapods from cobble filled bio-collectors deployed at Pocologan and Deadman's Harbour in 2013-2023, showing similarity of (A) each bio-collector and (B) the centroids of similarity among bio-collectors deployed in a same year; lines are used to connect consecutive years to help visualize "community trajectory" over time.

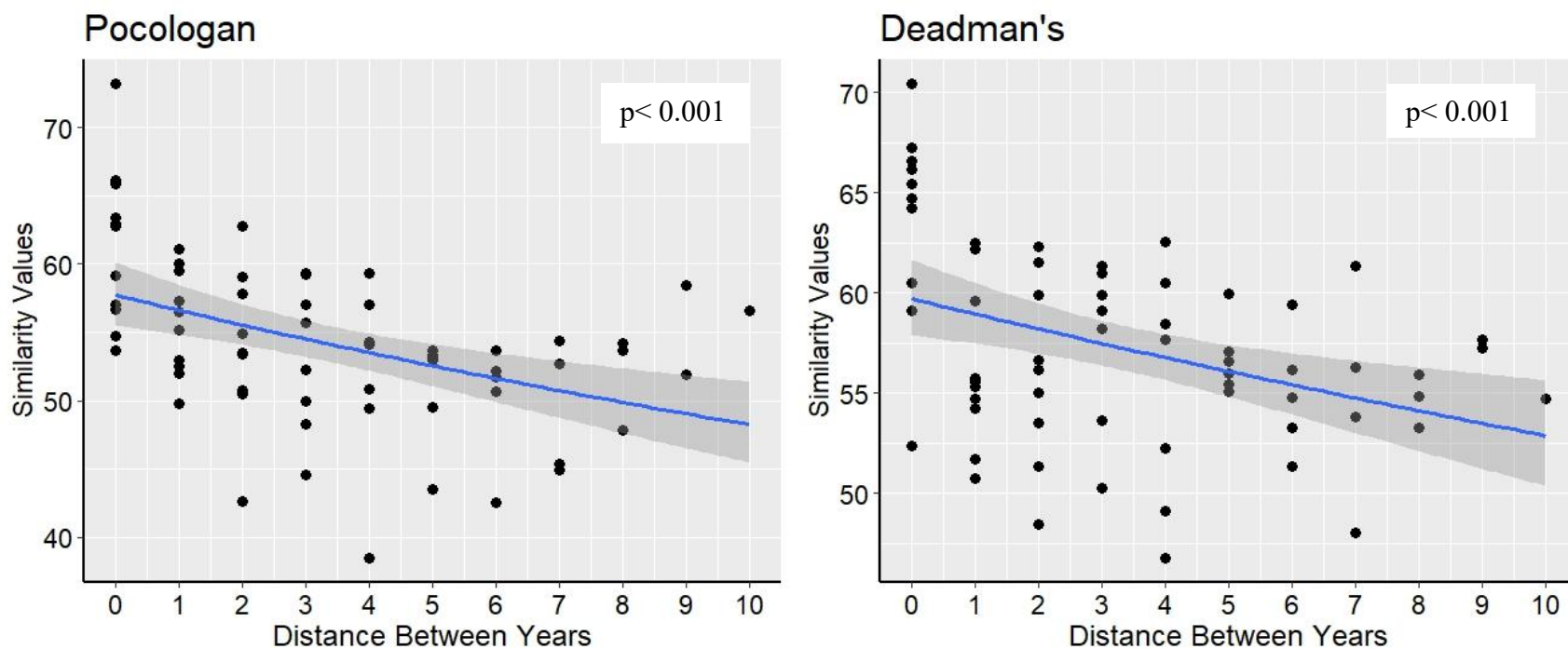


Figure A2: Scatter plots showing the relationship between pair-wise community similarity values between years and distance between the two years being compared. Similarity values are estimated based on PERMANOVAs of dispersion weighted and square root transformed abundance data for fish + large decapods at Pocologan and Deadman's Harbour from 2012-2023. Also shown are Gamma regression lines ($\pm$ 95% Confidence Interval) and their associated p-value.

Table A2: Spearman's Rho values showing strength of inter-annual seriation estimated by RELATE tests (with significance levels, $p = * < 0.05$, $** < 0.001$) of abundance data of fish + large decapods in cobble-filled bio-collectors for both Pocologan and Deadman's Harbour sites from 2013-2023, using either raw data, dispersion weighted (DW), DW plus square root transformation, DW plus Log transformation, or DW plus presence/absence transformation.

	Fish + Large Decapods	
	Pocologan	Deadman's Harbour
No Transformation	0.139**	0.111**
Dispersion Weighting (DW)	0.108**	0.070**
DW + Square Root	0.109**	0.107**
DW + Log	0.103**	0.082**
DW + Presence/Absence	0.099**	0.162**

Table A3 (current and next page): Spearman’s Rho from RELATE tests results for the 27 fish and decapod crustacean species sampled in bio-collectors at the 4 study sites. Each species was removed individually from either the fish + large decapods dataset or the fish + large decapods + small shrimp dataset before running a RELATE test. Change in Rho was calculated by comparing to the test output with all species of that site and dataset included. Change in Rho values were found for each species for the dispersion weighted + square root transformed fish + large decapods dataset for Beaver Harbour Lighthouse, and Beaver Harbour East from 2007 to 2024 (except 2012), and Pocologan, and Deadman’s Harbour from 2013 to 2023, as well as the DW + square root transformed fish + large decapods + small shrimp dataset for Beaver Harbour Lighthouse from and Beaver Harbour East from 2007 – 2011, 2014 – 2015, 2022 – 2024.

[illegible]

<i>Lebbeus polaris</i>	0.169	0.002	0.202	0.000	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>Liparis sp</i>	0.166	-0.001	0.202	0.000	0.108	-0.001	0.107	0.000	0.269	0.000	0.207	0.005
<i>Microgadus tomcod</i>	0.165	-0.002	0.203	0.001	0.109	0.000	0.099	-0.008	0.269	0.000	0.203	0.001
<i>M. octodecemspinosus</i>	0.173	0.006	0.202	0.000	0.112	0.003	0.108	0.001	0.271	0.002	0.205	0.003
<i>M. scorpius</i>	0.18	0.013	0.21	0.008	0.097	-0.012	0.103	-0.004	0.267	-0.002	0.175	-0.027
<i>Pagurus acadianus</i>	0.167	0.000	0.202	0.000	0.110	0.001	0.110	0.004	0.269	0.000	0.203	0.001
<i>Pagurus arcuatus</i>	0.182	0.015	0.172	-0.030	0.112	0.003	0.104	-0.003	0.269	0.000	0.184	-0.018
<i>Pandalus montagui</i>	0.162	-0.005	0.187	-0.015	0.107	-0.002	0.095	-0.012	0.268	-0.001	0.201	-0.001
<i>Pholis gunnellus</i>	0.18	0.013	0.205	0.003	0.107	-0.002	0.128	0.011	0.264	-0.005	0.165	-0.037
<i>Stichaeus punctatus</i>	0.171	0.004	0.204	0.002	0.107	-0.002	0.107	0.000	0.268	-0.001	0.200	-0.002
<i>Tautoglabrus adspersus</i>	0.119	-0.048	0.169	-0.033	0.037	-0.072	0.092	-0.015	0.253	-0.016	0.173	-0.029
<i>Ulvaria subbifurcata</i>	0.189	0.022	0.207	0.005	0.106	-0.003	0.093	-0.014	0.244	-0.025	0.182	-0.020
<i>Urophycis tenuis</i>	0.169	0.002	0.202	0.000	0.109	0.000	0.107	0.000	0.269	0.000	0.206	0.004
<i>Zoarces americanus</i>	0.168	0.001	0.202	0.000	0.109	0.000	0.110	0.003	0.269	0.000	0.204	0.002

Table A4: List of species whose individual removal caused a decrease in Rho, which were then sequentially removed from the RELATE test, showing their cumulative change in Spearman's Rho values until all species that caused an individual decrease in Rho were removed, or Spearman's Rho neared 0. Data were fish + large decapods + small shrimp from cobble-filled bio-collectors deployed at BH Lighthouse from 2007-2011, 2014-2015, 2022-2024, and BH East from 2009, 2011, 2014, 2022-2024. Spearman's Rho values are shown for the initial complete community (bolded) and all reduced communities based on dispersion weighted and square root transformed abundance data, along with associated significance level resulting from 9999 permutations of randomly-assigned rank-ordered labels to the same abundance data.

Species Removed	Spearman's Rho	Cumulative Change in Spearman's Rho	Significance Level
BH Lighthouse Fish + Large Decapods + Small Shrimp			
None	0.176		
<i>Tautogolabrus adspersus</i>	0.119	-0.057	0.0064
<i>Eualus fabricii</i>	0.074	-0.102	0.0474
<i>Cancer borealis</i>	0.056	-0.12	0.0992
<i>Cancer irroratus</i>	0.033	-0.143	0.2070
<i>Eualus pusiolus</i>	-0.007	-0.183	0.5296
BH East Fish + Large Decapods + Small Shrimp			
None	0.202		
<i>Tautogolabrus adspersus</i>	0.169	-0.033	0.0008
<i>Eualus fabricii</i>	0.136	-0.066	0.0036
<i>Pagurus arcuatus</i>	0.096	-0.106	0.0187
<i>Pandalus montagui</i>	0.068	-0.134	0.0374
<i>Caridion gordonii</i>	0.048	-0.154	0.1139
<i>Cancer irroratus</i>	0.044	-0.158	0.1325

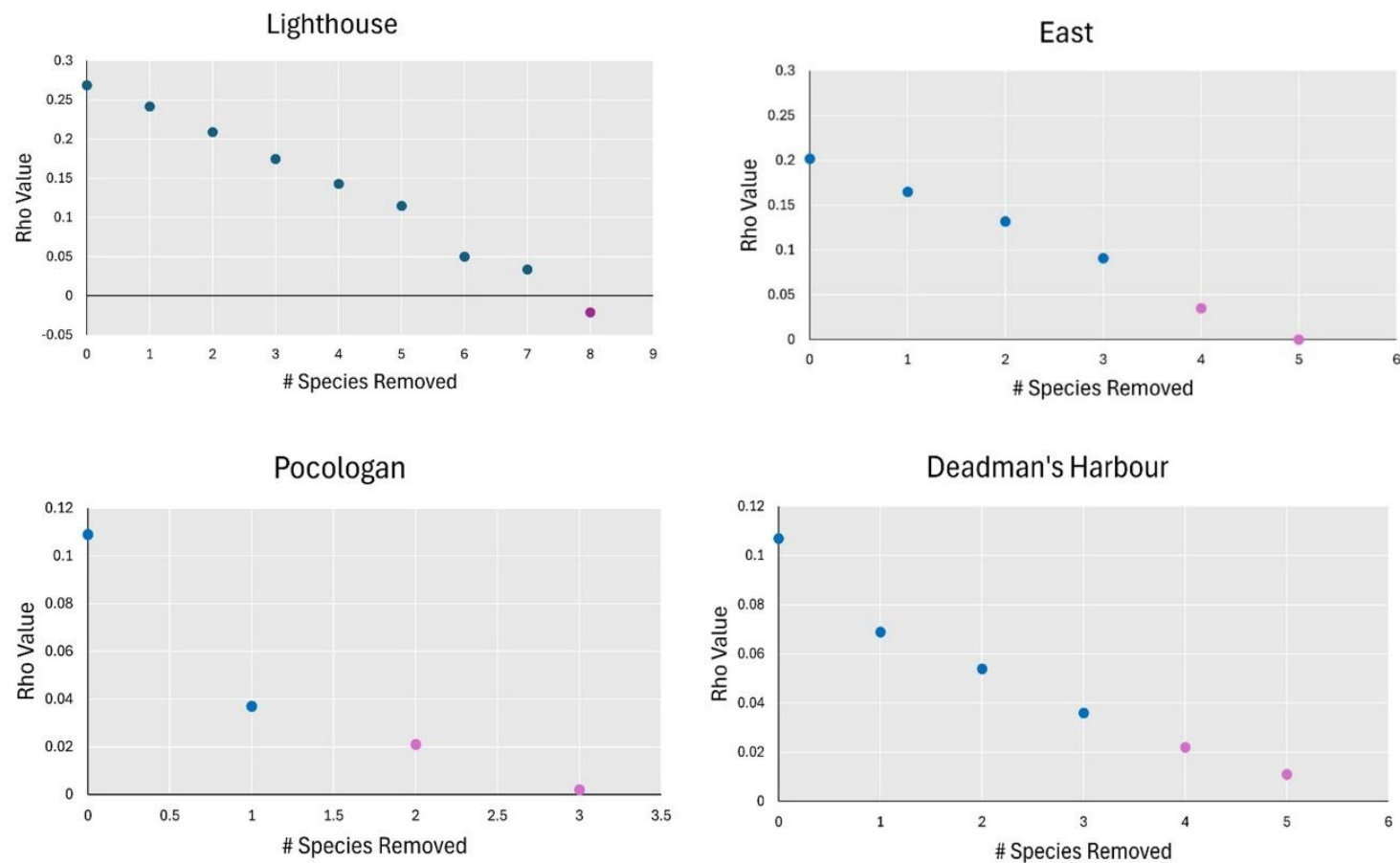


Figure A3: Scatter plots showing the relationship between Spearman's Rho values from the RELATE test and number of species removed based on sequential removals (Table 2) from the RELATE test, for fish + large decapods found in cobble filled bio-collectors from BH Lighthouse from 2007 – 2024, (except 2012), BH East from 2009 – 2024 (except 2010, 2012, 2015), and Pocologan and Deadman's Harbour from 2013 - 2023. Loss of significance of the RELATE test (sig level >0.05) is shown by the change in data point color from blue to purple.

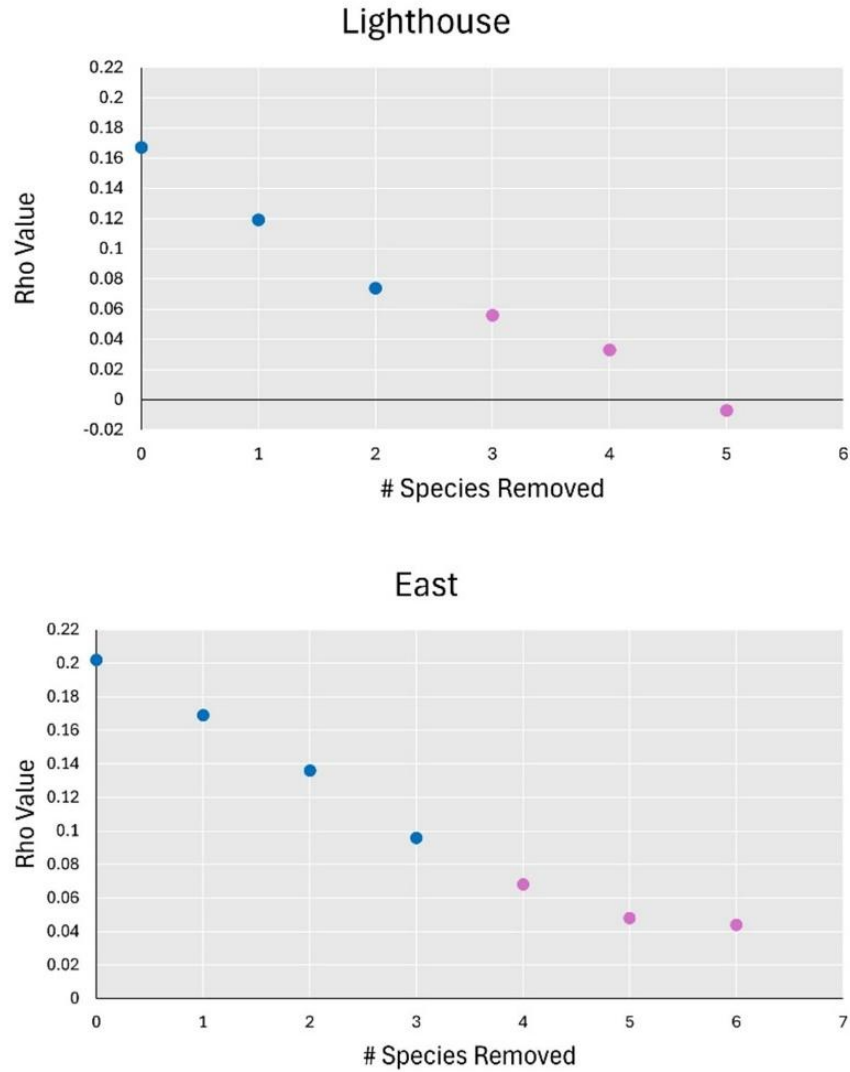


Figure A4: Scatter plots showing the relationship between Spearman's Rho values from the RELATE test and number of species removed based on sequential removals (Appendix 6) from the RELATE test, for fish + large decapods + small shrimp found in cobble filled bio-collectors from BH Lighthouse from 2007 – 2011, 2014 – 2015, 2022 – 2024, and BH East from 2009, 2011, 2014, 2022 - 2024. Loss of significance of the RELATE test (sig level >0.05) is shown by the change in data point color from blue to purple.

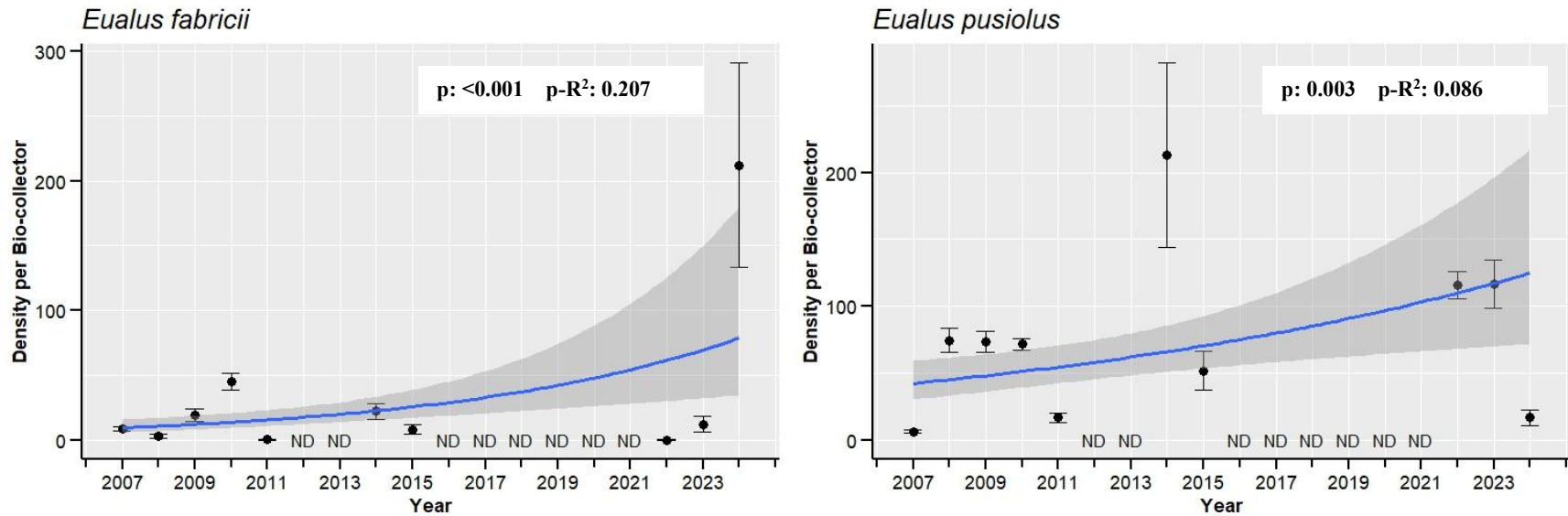


Figure A5: BH Lighthouse scatterplots showing the density ($\pm$ standard error) of each focal species (see Appendix 6) of the fish + large decapods + small shrimp community and sampling year from 2007-2011, 2014-2015, 2022-2024 (ND = no data). Also shown are regression lines ($\pm$ 95% Confidence Interval) (distribution in Appendix 11) through these data, and their associated pseudo- R^2 (Craig and Uhler's) and p-value. Panels are ordered from the species resulting in the greatest negative change in Rho when removed individually from the RELATE test in the top left to the least negative change in Rho at the bottom right.

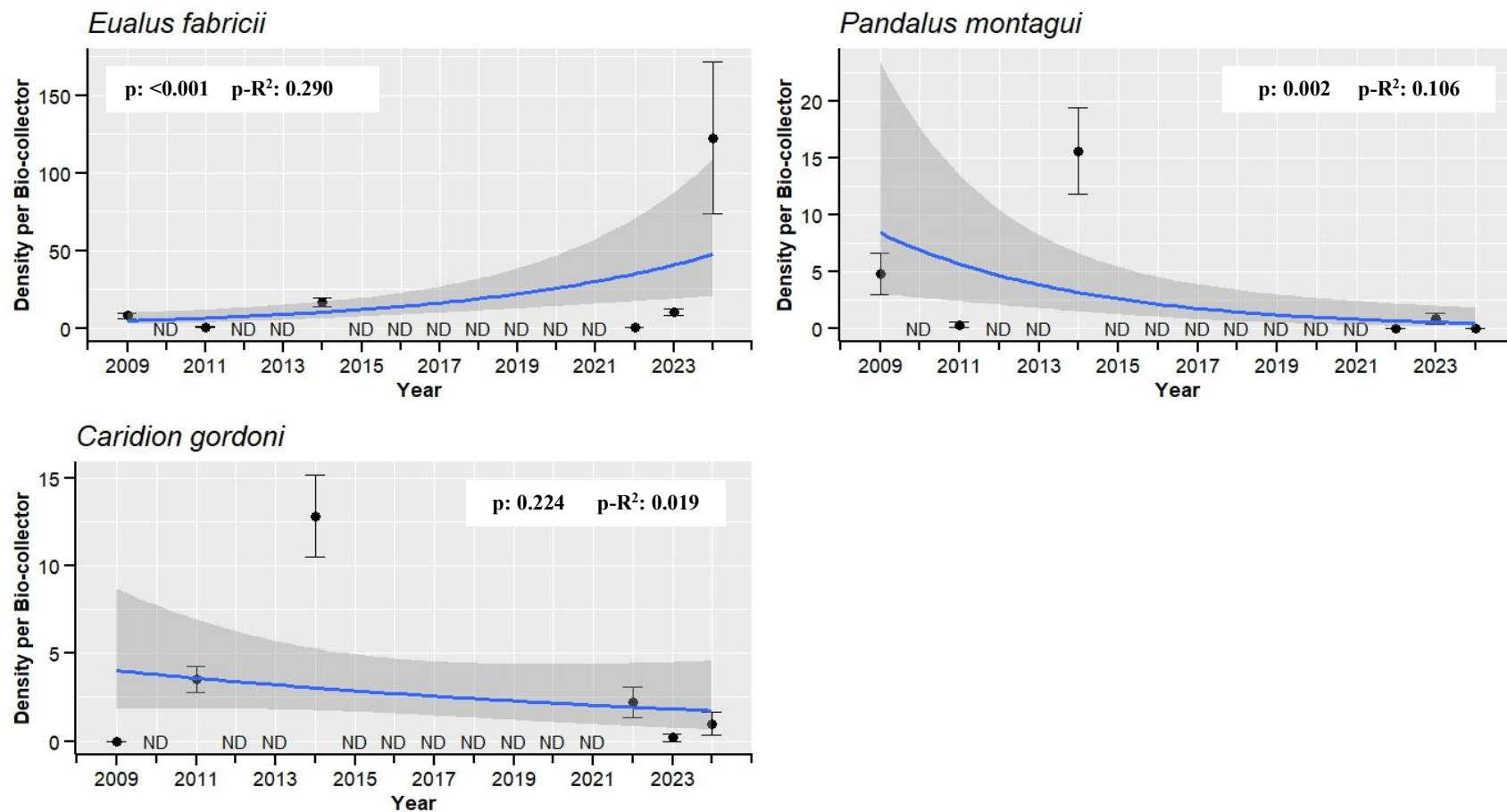


Figure A6: BH East scatterplots showing the density (±standard error) of each focal species (see Appendix 6) of the fish + large decapods + small shrimp community and sampling year from 2009, 2011, 2014, 2022-2024 (ND = no data). Also shown are regression lines (± 95% Confidence Interval) (distribution in Appendix 11) through these data, and their associated pseudo-R² (Craig and Uhler's) and p-value. Panels are ordered from the species resulting in the greatest negative change in Rho when removed individually from the RELATE test in the top left to the least negative change in Rho at the bottom right.

Table A5: Generalized linear model distribution and results (p-value and Pseudo-R² value) for relationship of species abundance to year for fish + large decapods + small shrimp collected in cobble bio-collectors at BH Lighthouse from 2007-2011, 2014-2015, 2022-2024, and BH East from 2009-2011, 2015, 2022-2024. Year is used as a continuous variable.

Species	Distribution	Trend	p-value	Craig + Uhlers pseudo-R ²
Lighthouse Fish + Large Decapods + Small Shrimp				
<i>Tautogolabrus adspersus</i>	poisson	pos	<0.001	0.824
<i>Eualus fabricii</i>	neg-binomial	pos	<0.001	0.207
<i>Cancer borealis</i>	poisson	pos	<0.001	0.285
<i>Cancer irroratus</i>	neg-binomial	pos	0.001	0.125
<i>Eualus pusiolus</i>	neg-binomial	pos	0.003	0.086
East Fish + Large Decapods + Small Shrimp				
<i>Tautogolabrus adspersus</i>	poisson	pos	0.001	0.524
<i>Eualus fabricii</i>	neg-binomial	pos	<0.001	0.290
<i>Pagurus arcuatus</i>	poisson	neg	0.011	0.546
<i>Caridion gordonii</i>	neg-binomial	neg	0.224	0.019
<i>Pandalus montagui</i>	neg-binomial	neg	0.002	0.106
<i>Cancer irroratus</i>	neg-binomial	pos	0.234	0.026

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Publications: None

Conference Presentations:

Brown, M.J., Rochette, R., and Hunt, H. "Investigating temporal variation in cobble-bottom assemblages of fish and decapod crustaceans in the Beaver Harbour region of the Bay of Fundy over the last 17 years." Atlantic Canada Coastal and Estuarine Science Society (ACCESS) Conference. Wolfville, NS. May 28 – 30, 2025. Oral presentation.

Brown, M.J., Rochette, R., and Hunt, H. "Investigating temporal variation in cobble-bottom assemblages of fish and decapod crustaceans in the Beaver Harbour region of the Bay of Fundy over the last 17 years." Benthic Ecology Meeting. Mobile, AL. April 1 – 4, 2025. Oral presentation.

Brown, M.J., Rochette, R., and Hunt, H. "Investigating temporal variation in cobble-bottom assemblages of fish and decapod crustaceans in the Beaver Harbour region of the Bay of Fundy over the last 17 years." Atlantic Canada Coastal and Estuarine Science Society (ACCESS) / Bay of Fundy Ecosystem Partnership (BOFEP) Joint Conference. Saint Andrews, NB. June 4 – 7, 2024. Poster presentation.

Brown, M.J., and Duston, J. "Growth and shell shape of Eastern oysters (*Crassostrea virginica*) cultured in a new design of cages." Science Atlantic Aquaculture & Fisheries and Biology Conference. Saint John, NB. March 3 – 5, 2023. Oral presentation.

Brown, M.J. and Duston, J. "Growth and shell shape of Eastern oysters (*Crassostrea virginica*) cultured in a new design of cages." Cameron Conference for Biology & Marine Biology Honours Student Research. Halifax, NS. Feb 11, 2023. Poster presentation.