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Subtropical Estuarine Ecosystems Display Both Long-term Stability and Change

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Subtropical Estuarine Ecosystems Display Both Long-term Stability and Change

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
with a concentration in Marine Resource Assessment
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University of South Florida

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ABSTRACT

Subtropical estuaries often support abundant and diverse faunal assemblages, but it is unclear how these productive ecosystems are responding to climate change. In the eastern Gulf of Mexico, estuarine faunal assemblages have been sampled for decades as part of a fisheries-independent long-term monitoring program. I assessed trends in submerged aquatic vegetation, water temperature, and the abundance, richness, and structure of faunal assemblages over more than two decades in four estuarine systems using this dataset. I used both univariate and multivariate analyses to quantify and describe the dynamics of these habitat and faunal variables. Further, I separated my analyses for summer and winter seasons since the latter has been observed to experience stronger responses to climate change in other systems. Submerged aquatic vegetation was generally stable, although I observed both decreasing and increasing cover in different systems. In contrast, water temperature increased in all systems during summer and winter. The rate of water temperature increase in winter was more than three times greater than in summer. Although faunal abundance and richness was generally stable over time, most systems exhibited slow, but significant, changes in assemblage structure consistent with ecological drift. Further, some faunal changes were indicative of tropicalization, where nearly 30% of the species that increased in abundance had distributions centered at lower latitudes. Moreover, there was a reduction in abundance of a temperate-centered taxon across all study systems in the winter. These results reflected a combination of both stability and change in habitat and the faunal assemblages it supports over the past two decades. These ecosystems

should continue to be monitored in the face of chronic and acute disturbances of climate change that have the potential to induce profound ecological shifts.

CHAPTER ONE: SUBTROPICAL ESTUARINE ECOSYSTEMS DISPLAY BOTH LONG-TERM STABILITY AND CHANGE

Introduction

Global climate change is having strong effects on biodiversity and associated ecosystem structure and functions (Doney et al. 2012, Poloczanska et al. 2016, Murphy et al. 2020). Shifts in species distributions (McCarty 2001), changes in phenology (Stenseth and Mysterud 2002), and changes in biodiversity (Dornelas et al. 2019) have been observed globally. However, the direction and magnitude of change varies. For example, species richness is declining around the equator and increasing at midlatitudes (Chaudhary et al. 2021). Some taxa are migrating poleward while others remain unchanged in distribution (Parmesan et al. 1999, Perry et al. 2005, Chivers et al. 2017). Given that changes in biodiversity can affect ecosystem stability (Hautier et al. 2015), there has been increased concern about how climate change will alter ecosystems, including rainforests (Levine et al. 2016), coral reefs (Toth et al. 2019), and estuaries (Erickson et al. 2021). Yet, our understanding of changes in ecosystem stability has been limited by a paucity of long-term time series data (but see Dornelas et al. 2018). Further, many ecosystems at lower latitudes have received comparatively less attention than those at higher latitudes. Understanding stability in these lower latitude ecosystems can shed light on their responses to climate change and broaden our understanding about generalities.

Temperature is known to affect population-level demographics in several ways, including the sex ratio of offspring (Ospina-Álvarez and Piferrer 2008), growth rates of young (Raventos et al. 2021), and individual survivorship (Stevens et al. 2016). However, the effects of shifting

temperatures are more nuanced at the community level. Studies have highlighted such influences as changes in seasonal weather extremes (Easterling et al. 2000, Miner et al. 2021), shifts in season duration (Cooper 2014), and variation in disturbance frequency, intensity, and duration (Dale et al. 2001). Such factors can drive community-level change in different magnitudes and directions. For example, as distributions of taxa shift in response to warming temperature, the invasion of predators and new pathogens can lead to the extirpation of native species (Sax et al. 2007). Although average temperatures are increasing globally, the magnitude of these changes may not be consistent among seasons, with warming expected to occur more quickly in the winter than the summer for many ecosystems (Clark et al. 2020). This seasonal imbalance in temperature change has already contributed to the global poleward expansion of mangroves and is linked to a reduction in frequency and intensity of cold weather events (Saintilan et al. 2014). Given the importance of season on biota globally (Forrest and Miller-Rushing 2010), asymmetric changes in temperature may have complex effects. For example, the intensity of a preceding winter is associated with the structure of estuarine fish assemblages the following spring (Curran and Wilber 2019). In addition, the concurrent increase in temperature variability due to climate change has been demonstrated to directly influence species richness and community stability (Zhang et al. 2018). Within marine systems, there is evidence that regions at lower latitude have become less stable compared to their higher latitude counterparts due to their responses to temperature (Miner et al. 2021).

The eastern Gulf of Mexico (eGOM) is a productive subtropical region that supports diverse communities including mangrove- and salt marsh-dominated estuaries, seagrass systems, and hardbottom reefs. The region is bisected by the Northern Gulf of Mexico ecoregion to the north and Floridian to the south, which are characterized by compositionally different marine

assemblages (Spalding et al. 2007). Seagrass systems throughout the eGOM act as important juvenile habitats for many fishes and exhibit high regional variability in the populations and communities they support (Schrandt et al. 2018, Faletti et al. 2019, Peake et al. 2022). Globally, temperate ecosystems are undergoing tropicalization, with previously rare or absent tropically associated taxa increasing in abundance through time (Nakamura et al. 2013, Osland et al. 2021). The effects of these new taxa are profound and can lead to regime drift or shifts (Vergés et al. 2014, Wernberg et al. 2016). Yet, there is evidence that some subtropical ecosystems are resilient to tropicalization due to additional factors, such as dispersal limitations of new taxa (Mizerek et al. 2021). In the eGOM, a reduced frequency of extreme cold events has been linked to the expansion of three co-occurring mangrove species in Florida estuaries (Cavanaugh et al. 2014). This is already creating novel mangrove-marsh assemblages (Cook-Patton et al. 2015) and shifts in faunal communities are predicted to follow (Scheffel et al. 2018). Indeed, warmer winter temperatures have been associated with the poleward expansion of a mangrove-associated fish species in this region (Purtlebaugh et al. 2020) and has affected community stability in other estuarine systems in North America (Miner et al. 2021).

Increased abundance of tropically associated taxa had already been observed in northern Gulf of Mexico seagrass systems as early as 2006, potentially indicating tropicalization by taxa from the Floridian ecoregion (Fodrie et al. 2010). However, Fodrie et al. (2010) was restricted to the northernmost edge of the eGOM as well as only the summer and fall seasons. Further, assemblages commonly differ between summer and winter in subtropical and temperate estuaries (Hagan and Able 2003, Strydom 2015, Schrandt and MacDonald 2020). Thus, it is unclear how estuarine systems across the broader eGOM may be responding to climate change, especially in the context of imbalanced changes in average seasonal temperatures. Long-term data collected

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consistently within and across multiple eGOM estuaries that span temperate and subtropical latitudes can improve our ability to evaluate the stability of these assemblages and establish a timeline of tropicalization in this region. Long-term time series data are available in the eGOM, where estuarine fish composition and abundance surveys have been conducted monthly since 1997 and followed consistent study designs and methods. Using these data, I investigated whether fish assemblages in estuaries within the eGOM changed over a 23-year period and if there was a potential response to climate change. Specifically, I addressed the following questions: 1) Has submerged aquatic vegetation coverage and water temperature changed in eGOM estuaries over a 23-year period? 2) Has the abundance and richness of fishes within eGOM estuarine fish assemblages changed over this same time period and, if so, are these changes related to submerged aquatic vegetation coverage or water temperature? 3) Has the composition and stability of eGOM estuarine fish assemblages changed over time and what were the relative roles of submerged aquatic vegetation coverage or water temperature on these multivariate outcomes?

Methods

Data Collection

I used data collected by the Florida Fish and Wildlife Research Institute's (FWRI) Fisheries Independent Monitoring (FIM) program. The program follows a monthly stratified random sampling design in estuaries across Florida, including four in the eastern Gulf of Mexico (from north to south: Apalachicola Bay (AB), Cedar Key (CK), Tampa Bay (TB), and Charlotte Harbor (CH); Figure 1). Apalachicola Bay is a shallow, semi-enclosed estuary located on the northern coast of the GOM in the panhandle of Florida, USA and is within the Northern Gulf of Mexico ecoregion (Spalding et al. 2007). Cedar Key is located within the Suwannee River open

estuary system and is also in the Northern Gulf of Mexico ecoregion. Tampa Bay is Florida's largest open water estuary and lies within the Floridian ecoregion (Spalding et al. 2007). Charlotte Harbor, a drowned river estuary system, is within the Floridian ecoregion (FWRI 2017). All systems are dominated by seagrass vegetation in shallow waters, except for Apalachicola Bay, where seagrass is less than 7% of bottom coverage (FWRI 2017). Finally, salt marsh and oyster beds are dominant along shorelines in Apalachicola Bay and Cedar Key, while mangroves dominate in Charlotte Harbor, and Tampa Bay is characterized by a mix of salt marsh, oyster beds, and mangroves (FWRI 2017).
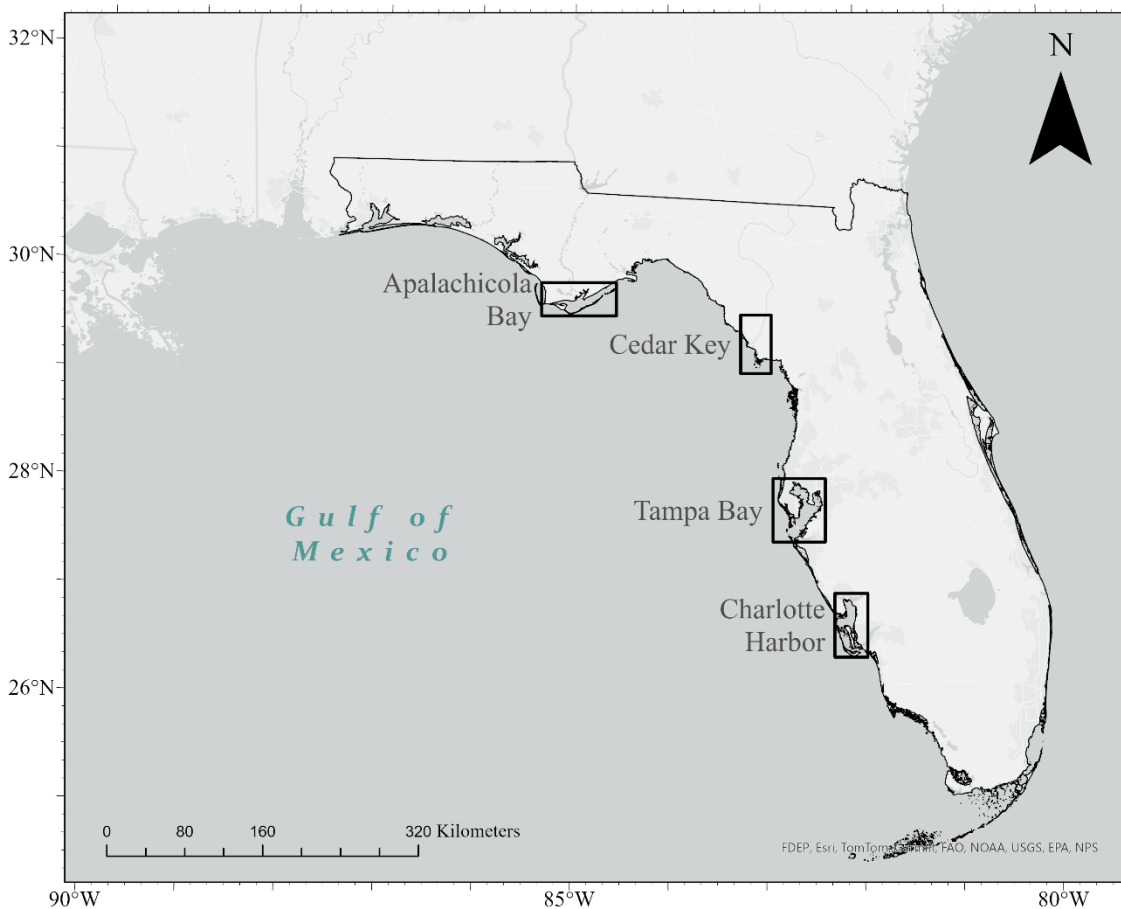
Figure 1: Locations of all estuarine systems in this study. Generated using ArcGIS Pro software.

Sampling was divided into zones (subdivided into 1-nm^2 grids) within each estuarine system based on geographic, habitat, and depth criteria (FWRI 2024). These criteria defined which of three different types of gear were used to collect organisms. For this study, I used data from the 21.3-m seine sampling gear because it was used the longest and most consistently throughout the study period. This gear targeted young-of-year and juvenile fishes in shallow habitats (≤1.8-m deep). Further, seines in bays and open estuarine habitats were pre-stratified by the presence of submerged aquatic vegetation (SAV) in all systems except Cedar Key. Seines were also pre-stratified by the presence of a shoreline in all systems. Additionally, the number of seine nets pulled was relative to the amount of available sampling habitat (*i.e.*, if a particular zone contained 20% SAV habitat, 20% of the SAV samples for the entire system were collected from that zone, see FWRI 2024). Depending on shoreline presence, the seine was either hauled parallel to the shore with one wing set on the shoreline or set off the shoreline and hauled the same distance (9.1-m) before collection. In either case, the area sampled was approximately 140-m^2. For every seine haul (hereafter referred to as "sampling event"), all vertebrates and select commercially important invertebrates were counted and identified to the lowest practical taxonomic level (typically species). I used all available summer and winter seine net data from 1998 to 2020 that occurred in bays or open estuarine habitats. I filtered each sampling event by season, with summer defined as June-September and winter as December-March, following Schrandt and MacDonald (2020). To reduce potential effects of *in situ* species-level misidentification, I aggregated certain taxa to the genus level due to similarity in appearance (Table 1). A visual estimate of the SAV coverage was recorded for each sampling event. Finally, a YSI sonde was used to record water temperature at the surface of the water and every meter thereafter to the bottom during each sampling event. For my analyses, I calculated the average of

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all measured water temperature values to produce a mean water column temperature for each sampling event.

Table 1: Taxa that were difficult to identify in the field and subsequently aggregated at the genus level to reduce misidentification effects.

Genus	Species
Anchoa	A. cayorum
	A. cubana
	A. hepsetus
	A. lamprotaenia
	A. lyolepis
	A. mitchilli
Eucinostomus	E. argenteus
	E. gula
	E. harengulus
	E. havana
	E. jonesii
	E. lefroyi
	E. melanopterus
Farfantepenaeus	F. aztecus
	F. duorarum

In total, 17,492 sampling events occurred where at least one taxon was caught and counted during summer and winter in any of the four systems. For seven sampling events, water temperature data were unavailable and thus excluded from the analyses. Further, I removed hauls composed solely of rare species (taxa found in ≤5% of all samples for that system and season)

which reduced the sample count to 17,260. Overall, the dataset contained 297 taxa recorded over 23 years of collections.

Data Analyses

I conducted all analyses using the R Statistical Computing Environment v4.3.0 with an alpha of 0.05 for all significance testing (R Core Team 2023). Unless otherwise indicated, I reported values from all analyses as mean ± SE and generated plots with R packages *ggplot2* and *patchwork* (Wickham 2016, Pedersen 2022). To address if SAV coverage and water temperature have changed over time in eGOM estuarine systems, I used Analysis of Covariance (ANCOVA) models, with Year as a continuous predictor (fixed) and estuarine System as a categorical predictor (fixed, 4 levels: Apalachicola Bay, Cedar Key, Tampa Bay, Charlotte Harbor) plus their interaction. Given the well-documented seasonal differences in estuarine systems (see Hagan and Able 2003, Strydom 2015, Schrandt and MacDonald 2020), in this and all subsequent analyses, I separately analyzed summer and winter. The formula used for each ANCOVA was:

response ~ Year + System + Year:System

where response was either mean annual percent SAV coverage or mean annual water temperature. When the interaction between Year and System was not significant, I dropped the term and reran the test as an additive model. For significant interactions between Year and System, I ran independent linear models by Year for each system within each season. Prior to this analysis, I removed any outlier data from years in which temperatures were anomalously higher or lower (>2.5 standard deviations) than the long-term average (*e.g.*, winter of 2010, see also Stevens et al. 2016). I performed post-hoc contrasts for any significant terms in these models to determine the magnitude of differences in means across systems using the *emmeans* package and used the Tukey method for *p*-value correction (Lenth 2023).

I tested whether the abundance and richness of fishes from the four estuaries changed over the study period and examined the relationships between faunal dynamics and both SAV coverage and water temperature. Specifically, I modeled total abundance and total richness per sampling event across all systems for both the summer and winter seasons using generalized linear mixed models (GLMMs) from the R package *glmmTMB* (Brooks et al. 2017). For each sampling event, I calculated the total abundance as the sum of all enumerated individuals and richness as the number of distinct taxa present. In this and all subsequent analyses, I fourth-root transformed the abundance data prior to summation to reduce the effects of highly abundant taxa. For each model, the predictors were Year (fixed, continuous), System (fixed, categorical with four levels: Apalachicola Bay, Cedar Key, Tampa Bay, Charlotte Harbor), SAV Coverage (fixed, continuous), and Water Temperature (fixed, continuous). I also included an interaction term between Year and System and treated it the same as in the above-described models. I applied a z-score transformation to SAV Coverage and Water Temperature to enable comparison of relative effect sizes. Since sampling events were conducted in consecutive months, I included a first-order autoregressive covariance term in each model based on sampling month to account for temporal autocorrelation (Brooks et al. 2017). This covariance term included within-system zone as a random grouping effect to further address spatial autocorrelation. Given that species richness is strongly affected by sampling effort (Mittelbach and McGill 2019), I included an offset term to account for variation in the number of sampling events. Thus, I used the following formula for each model:

response ~ Year + System + Year:System + Temp_Z + SAV_Z + offset(log(n_hauls)) + ar1(yearMonth + 0|systemZone)

where response was either fourth-root transformed total abundance or total richness per haul. I again used the *emmeans* package for post-hoc contrasts of means and the Tukey method for *p*-value correction (Lenth 2023).

To examine the composition and stability of eGOM estuarine fish assemblages over time, I started with a univariate approach to examine beta diversity with Bray-Curtis dissimilarity over time. I first calculated the mean annual abundance of each taxon for each system within each season. I used the R package *betapart* to then calculate Bray-Curtis dissimilarity annually with respect to the first year of available data (Baselga et al. 2023). I modeled this dissimilarity index over time with ANCOVA using the formula:

beta diversity index ~ Year + System + Year:System

I treated the interaction term the same as described above. Further, I decomposed the annual dissimilarity index into the elements of turnover and nestedness. I then used permutational multivariate analysis of variance (PERMANOVA) from the R package *vegan* to evaluate the effect of Year (fixed, categorical) and System (fixed, four levels), plus their interaction, within season on square-root transformed Bray-Curtis dissimilarities of the fourth-root transformed assemblage data (Oksanen et al. 2022). I used square-root transformed Bray-Curtis dissimilarity matrices to provide a more conservative estimate of the variance explained by the subsequent PERMANOVAs (Legendre and Andersson 1999). The resultant models used were thus:

$(Bray\text{-}Curtis\ matrix)^{0.5}$ ~ Year + System + Year:System

I handled the interaction term in the same manner as described above. I generated canonical analysis of principal coordinates (CAP) ordinations using the R package *BiodiversityR* to visualize patterns across Years for all PERMANOVAs that indicated a significant effect of Year within each System and season (Kindt and Coe 2005, *sensu* Peake et al. 2022). In addition, I

included taxon biplot correlation vectors in these CAP ordinations to visualize which taxa contributed to any observed differences in groups. I applied the Pythagorean theorem to the first two axis scores of each taxon vector to evaluate its relative magnitude. To explore the effects of SAV coverage and water temperature on the assemblages, I performed distance-based redundancy analysis (dbRDA) with the R package *vegan* using the same square-root transformed Bray-Curtis dissimilarities stated above (Oksanen et al. 2022). The resultant formula was thus: (Bray-Curtis matrix)0.5 ~ Year + Temp_Z + SAV_Z

Finally, I followed methods described in Dornelas et al. (2019) to assess whether the abundance of individual taxa had changed over time. Within each system and season, I ran a linear model on the average annual fourth-root transformed abundance for each taxon against time to calculate both the magnitude and direction of change. I binned the model coefficients to construct histograms that displayed the distribution and magnitude of rates of change for each system within season. I then assessed the balance of how many taxa increased or decreased significantly in abundance for each system within season. Finally, I pulled climatological association data from FishBase (Froese and Pauly 2000) using the R package *rfishbase* and examined whether there were distribution patterns of any taxa that underwent significant change (Boettiger et al. 2012).

Results

Overview

Throughout the 23-year study period, submerged aquatic vegetation (SAV) displayed nuanced dynamics, with no observed change in Apalachicola Bay for either season, a decrease in Cedar Key during summer only, an increase in Tampa Bay during winter only, and increases observed in Charlotte Harbor (both seasons; Figure 2). Water temperature increased during

summer and winter for all estuary systems, but the rate of change in winter was more than triple

that observed during the summer (Figure 3). Both total abundance and richness remained

relatively stable throughout the study period. Of the 297 total taxa examined, 91 (31%) changed

significantly in abundance over time across all systems and seasons, nearly equally balanced

between increases and decreases in abundances. These changes were further reflected in the

slow, but significant, changes in the assemblage structure, indicative of ecological drift.

Habitat Dynamics

Submerged Aquatic Vegetation

The dynamics of SAV differed across systems within each season (Year:System

interaction term for summer $p <0.001$ and winter $p <0.001$). Therefore, I used independent

models for each system and season combination. The northernmost system in this study,

Apalachicola Bay, did not have any significant change in SAV over the sampling period for

either season (Figure 2; Table 2). Significant changes in SAV coverage occurred in Cedar Key

(decreased in summer; $p <0.05$; Table 2), in Tampa Bay (increased in winter; $p <0.05$; Table 2),

and in Charlotte Harbor (increased for both seasons; $p <0.05$; Table 2). In addition, mean annual

percent SAV differed across all systems within each season with lower coverage in northern

systems than southern ones for both seasons ($p <0.05$ for all pairwise comparisons; Table 3; see

also Table S3).

Table 2: Slopes of SAV change over time for all independent linear models. Bold rows highlight terms where $p < 0.05$.

Season	System	Slope	Standard error	t-statistic	p-value
Summer	AB	0.235	0.146	1.61	0.126
	CK	**-0.441**	**0.146**	**-3.02**	**0.007**
	TB	0.065	0.098	0.66	0.518
	CH	**0.348**	**0.118**	**2.96**	**0.008**
Winter	AB	-0.155	0.171	-0.91	0.377
	CK	-0.217	0.129	-1.69	0.109
	TB	**0.404**	**0.101**	**4.01**	**<0.001**
	CH	**0.486**	**0.117**	**4.17**	**<0.001**

Table 3: Least square means of SAV in each system for both seasonal linear models.

Season	System	Estimated mean	Standard error	DF
Summer	AB	32.0	0.81	78
	CK	13.6	0.81	78
	TB	39.5	0.76	78
	CH	49.7	0.76	78
Winter	AB	26.5	0.83	78
	CK	9.1	0.83	78
	TB	41.2	0.77	78
	CH	46.4	0.77	78
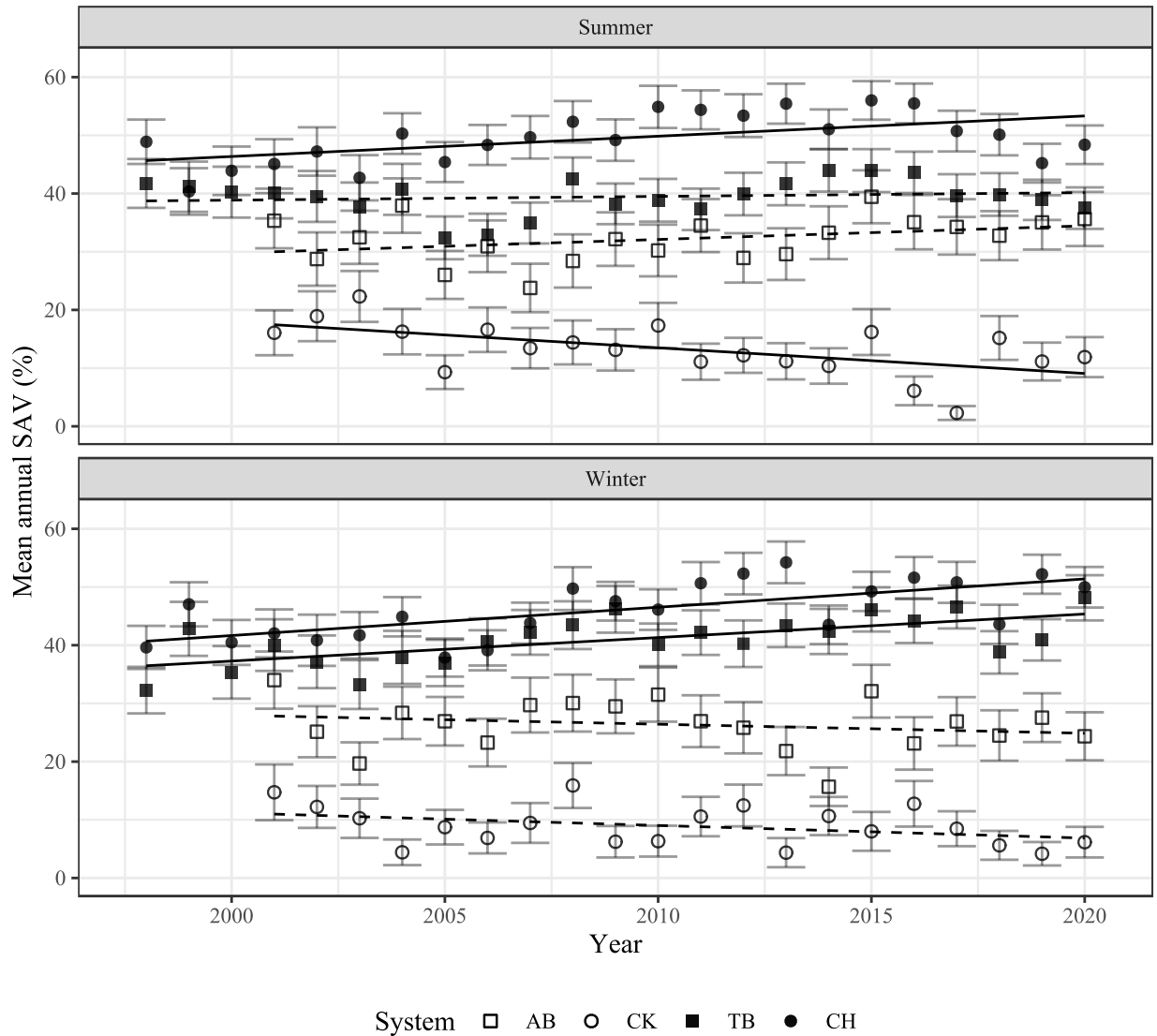
Figure 2: Annually averaged SAV coverage over time. Error bars represent ± 1 standard error. Solid lines indicate significant modeled trends and dashed lines indicate non-significant trends, per each independent linear model.

Water Temperature

During the 23-year study period, water temperature increased consistently across all systems (Year:System interaction term for summer $p = 0.627$ and winter $p = 0.915$). Summer water temperature increased at a rate of $0.018°Cyr^{-1} \pm 0.007$ and winter water temperature increased more than three times as quickly at a rate of $0.063°Cyr^{-1} \pm 0.015$ (Figure 3).
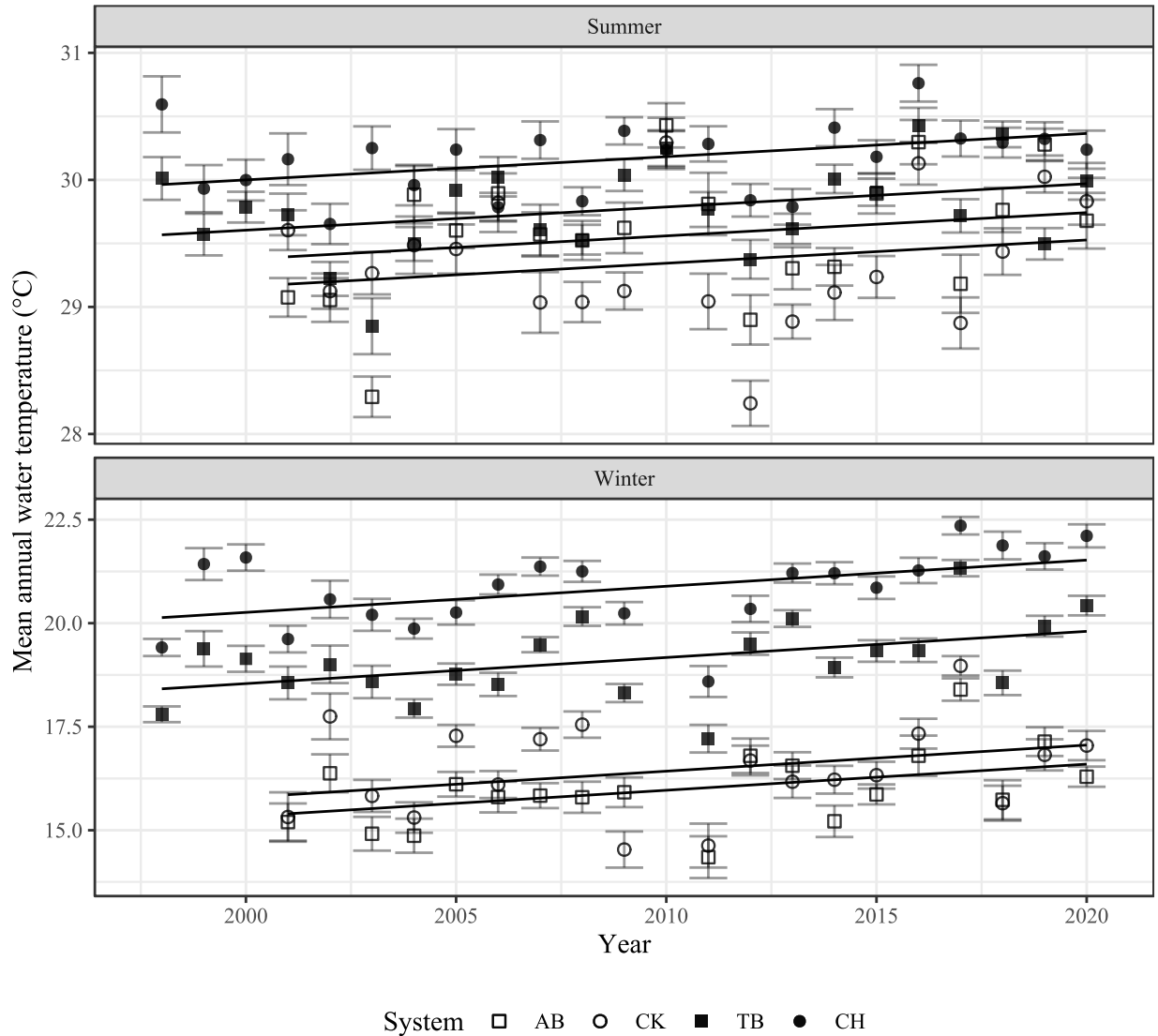
Figure 3: Annually averaged water temperature over time. Error bars represent ± 1 standard error. Slopes of lines are derived from ANCOVA models.

Despite the consistency in the rates of increase, post-hoc contrasts revealed the long-term mean water temperatures differed among most systems, with Charlotte Harbor consistently warmer than all other estuaries in both seasons ($p < 0.05$ for 9 out of 12 pairwise comparisons; Table 4).

Table 4: Least square means of water temperature in each system for both seasonal linear models.

Season	System	Estimated mean	Standard error	DF
Summer	AB	29.6	0.09	81
	CK	29.3	0.09	81
	TB	29.8	0.08	81
	CH	30.2	0.08	81
Winter	AB	15.9	0.21	77
	CK	16.4	0.21	77
	TB	19.2	0.19	77
	CH	20.9	0.19	77

Assemblage Structure: Patterns and Dynamics

Abundance and Richness

Total abundance of fauna was generally higher (mean total abundance 418 ±19) for all systems in the summer season compared to winter (mean total abundance 275 ±14; Figure 4). The Year:System interaction terms were significant in the GLMMs for abundance ($p < 0.05$ for both seasons), therefore, I separated the models for each system and season combination. Within these independent GLMMs, total abundance decreased for Apalachicola Bay in winter ($p < 0.001$; Table 5), increased for Tampa Bay in summer ($p = 0.026$; Table 5), and remained stable for all other systems (Table 5). Summer abundances were positively related to SAV coverage for all systems ($p < 0.001$) except Cedar Key ($p = 0.119$; Table 5). Further, I did not detect a relationship between summer abundances and water temperature ($p = 0.529 - 0.941$; Table 5). The relationship between abundance and SAV coverage was more nuanced in the winter than during the summer. Winter abundance was negatively related to SAV coverage in Apalachicola Bay (p

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<0.001; Table 5) and was not related with SAV coverage in Cedar Key (p >0.05; Table 5).

However, in Tampa Bay and Charlotte Harbor, winter abundance was positively related to SAV

coverage (p <0.05; Table 5). In addition, winter abundances were positively related to water

temperature for all systems (p <0.001) except Cedar Key (p = 0.729; Table 5).
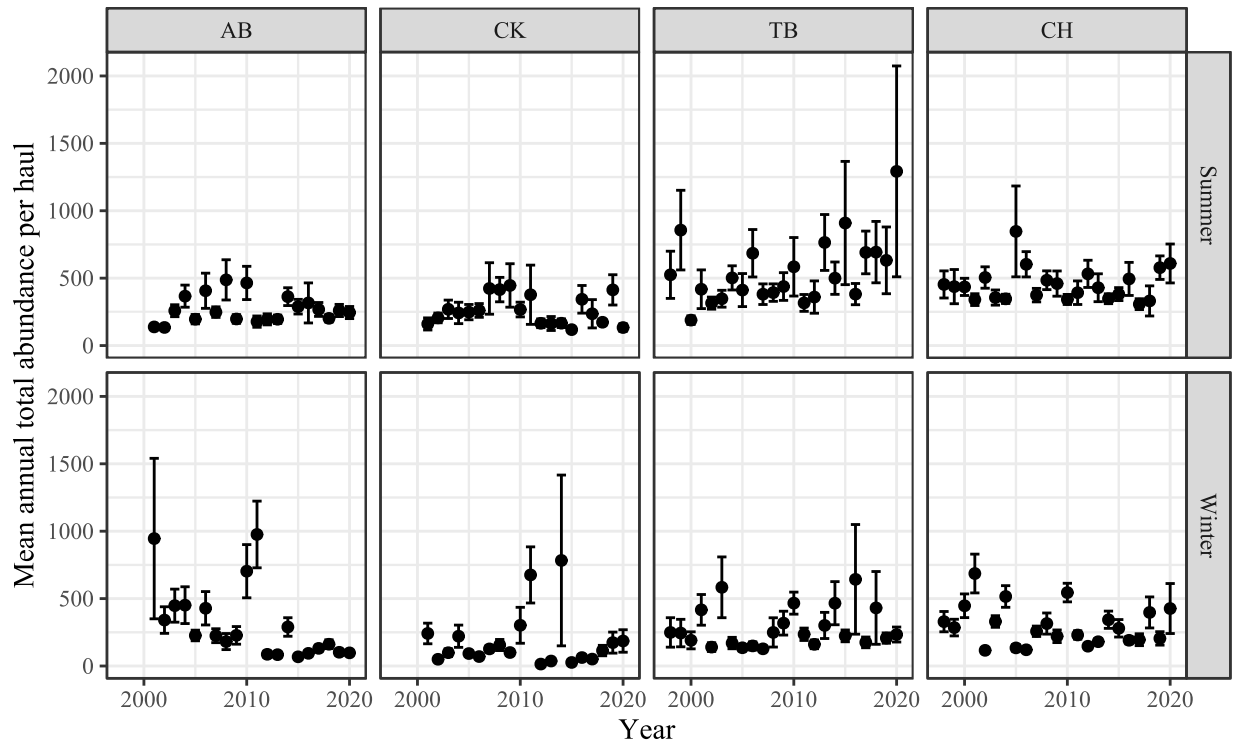
Figure 4: Mean total faunal abundance (fourth-root transformed) per haul over time. Error bars represent ± 1 standard error.

Table 5: Coefficients of terms in total faunal abundance GLMMs. Bold rows highlight terms where $p < 0.05$.

Season	System	Term	Coefficient	Standard error	*t*-statistic	*p*-value
Summer	AB	Year	1.108	4.828	0.23	0.819
		Temp_Z	-6.933	17.260	-0.40	0.688
		SAV_Z	**91.130**	**16.396**	**5.56**	**<0.001**
	CK	Year	-2.228	3.723	-0.60	0.550
		Temp_Z	-1.604	21.497	-0.07	0.941
		SAV_Z	-33.589	21.557	-1.56	0.119
	TB	**Year**	**18.257**	**8.199**	**2.23**	**0.026**
		Temp_Z	-33.255	52.819	-0.63	0.529
		SAV_Z	**132.835**	**52.679**	**2.52**	**0.012**
	CH	Year	-0.933	3.695	-0.25	0.801
		Temp_Z	-9.156	23.645	-0.39	0.699
		SAV_Z	**72.756**	**23.644**	**3.08**	**0.002**
Winter	AB	**Year**	**-26.851**	**5.836**	**-4.60**	**<0.001**
		Temp_Z	**100.240**	**33.454**	**3.00**	**0.003**
		SAV_Z	**-73.846**	**33.167**	**-2.23**	**0.026**
	CK	Year	2.370	6.542	0.36	0.717
		Temp_Z	-12.954	37.420	-0.35	0.729
		SAV_Z	-27.792	37.361	-0.74	0.457
	TB	Year	1.811	4.588	0.39	0.693
		Temp_Z	**67.465**	**29.553**	**2.28**	**0.022**
		SAV_Z	**79.617**	**29.342**	**2.71**	**0.007**
	CH	Year	-6.225	3.546	-1.76	0.079
		Temp_Z	**99.256**	**17.225**	**5.76**	**<0.001**
		SAV_Z	**83.063**	**16.404**	**5.06**	**<0.001**

Mean richness per haul in summer (8.7 ±0.046) was consistently higher for each system than in the winter (5.8 ±0.038; Figure 5). The Year:System interaction terms for the richness GLMMs were not significant in either seasonal model (p = 0.156 - 0.912), therefore, I used additive models for each system. The revised GLMMs revealed that richness did not change during either summer or winter for any system (summer p = 0.154 and winter p = 0.535; Table 6). Further, richness in summer was positively related to SAV coverage for all systems (p <0.001; Table 6) and not related to water temperature (p = 0.092; Table 6). In contrast, richness in winter was positively related to both SAV coverage (p <0.001; Table 6) and water temperature for all systems (p <0.001; Table 6).
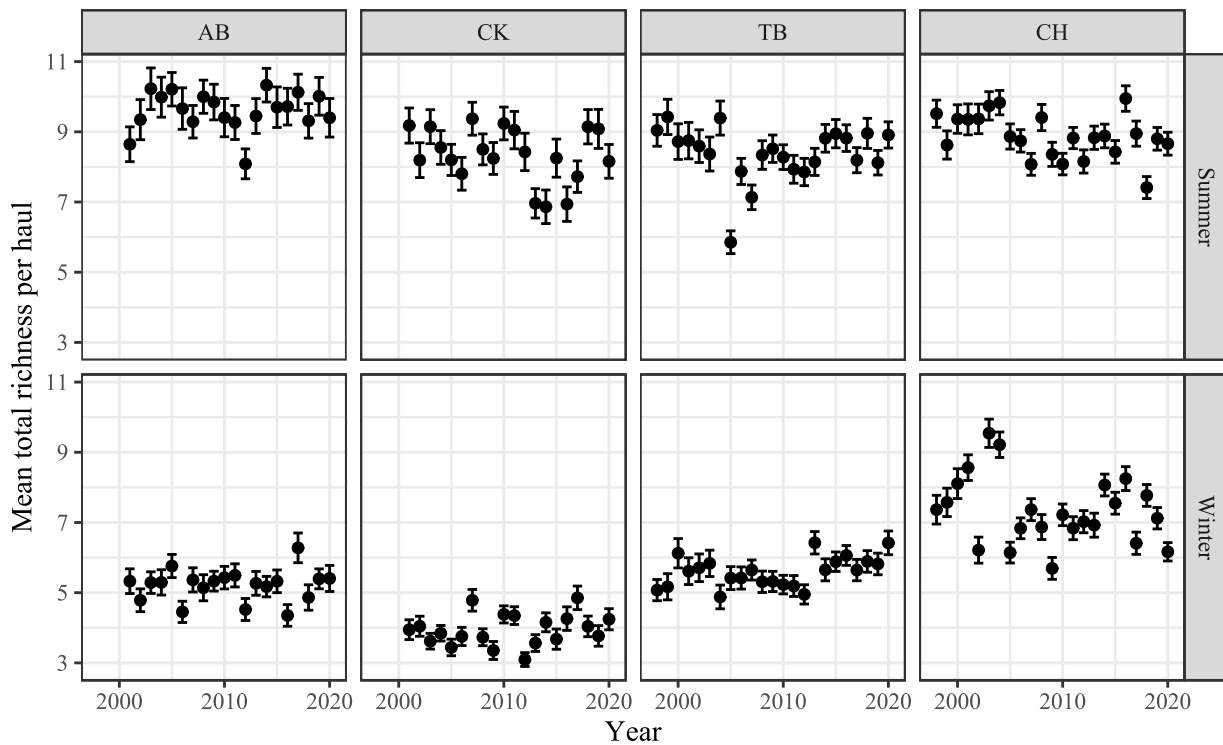
Figure 5: Mean total richness averaged annually. Error bars represent ± 1 standard error.

Table 6: Coefficients of terms in total faunal richness GLMMs. Bold rows highlight terms where *p* <0.05.

Season	Term	Coefficient	Standard error	*t*-statistic	*p*-value
Summer	**(Intercept)**	**2.364**	**0.302**	**7.84**	**<0.001**
	Year	-0.020	0.014	-1.42	0.154
	systemCK	**-1.188**	**0.343**	**-3.47**	**<0.001**
	systemTB	**-1.706**	**0.287**	**-5.94**	**<0.001**
	systemCH	**-1.262**	**0.296**	**-4.27**	**<0.001**
	SAV_Z	**1.497**	**0.045**	**33.60**	**<0.001**
	Temp_Z	0.075	0.045	1.69	0.092
Winter	**(Intercept)**	**-2.056**	**0.325**	**-6.32**	**<0.001**
	Year	-0.009	0.015	-0.62	0.535
	systemCK	**-1.161**	**0.377**	**-3.08**	**0.002**
	systemTB	-0.072	0.313	-0.23	0.818
	systemCH	**1.555**	**0.323**	**4.81**	**<0.001**
	SAV_Z	**0.657**	**0.036**	**18.27**	**<0.001**
	Temp_Z	**0.469**	**0.037**	**12.80**	**<0.001**

Beta Diversity
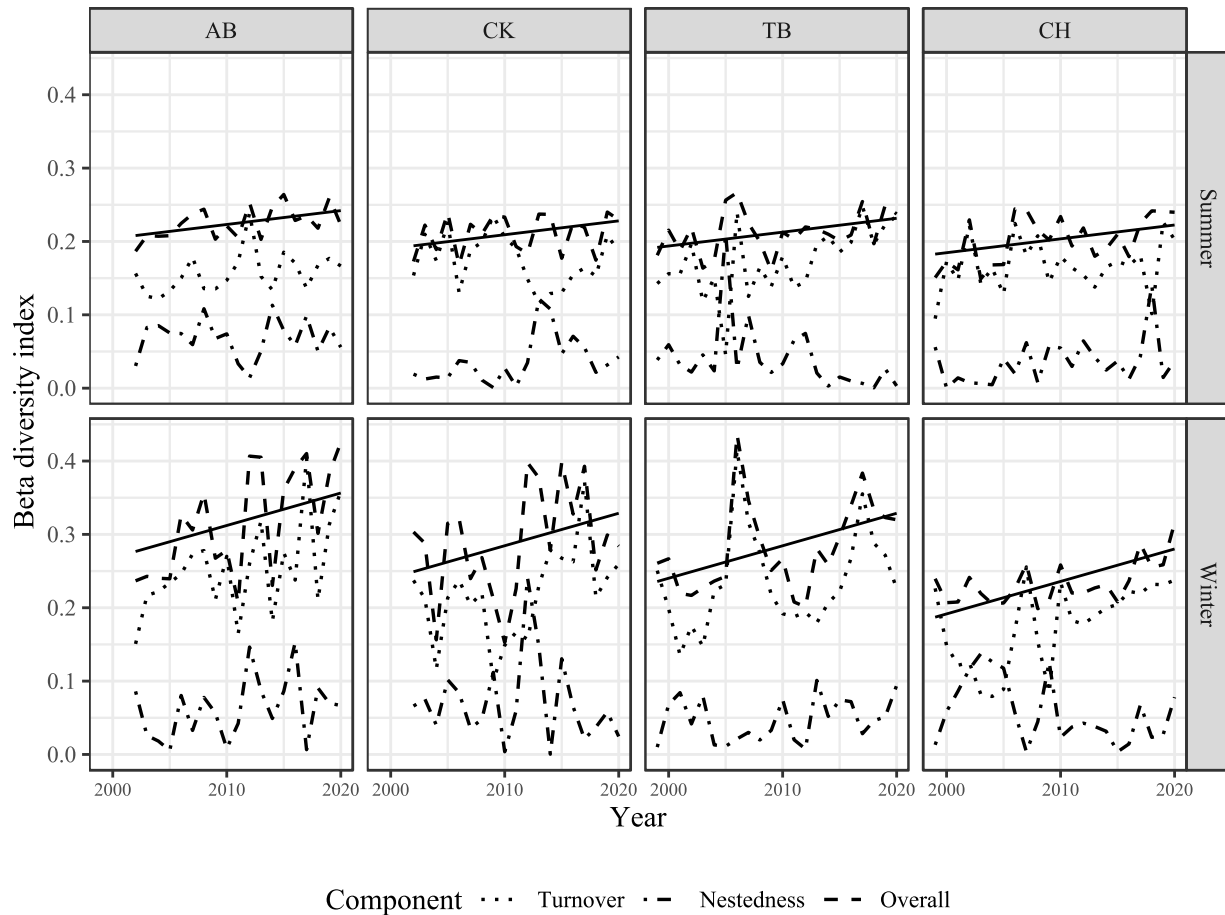
Figure 6: Partitioned beta diversity calculated pairwise with respect to the first year of available data. Trend lines (solid) calculated using seasonal ANCOVA models.

Bray-Curtis dissimilarity of species composition increased consistently across all systems within each season (Year:System interaction term for summer $p = 0.243$ and winter $p = 0.218$). The rate of increase in dissimilarity during summer was $0.002\text{yr}^{-1} \pm 0.0005$, with a winter rate twice that of summer ($0.005\text{yr}^{-1} \pm 0.001$; Table 7; Figure 6). In summer, the variability of dissimilarity was lower than in the winter for all systems except Charlotte Harbor (Table 8). Within dissimilarity overall, there were clear variations in the underlying components of beta diversity (turnover and nestedness), although they were not modeled here.

Table 7: ANCOVA model outputs for betadiversity indices over time. Bold values are statistically significant at alpha 0.05.

Season	Term	Estimate	Standard error	*t*-statistic	*p*-value
Summer	**(Intercept)**	**0.207**	**0.008**	**25.64**	**<0.001**
	Year	**0.002**	**0.000**	**5.29**	**<0.001**
	systemCK	-0.005	0.008	-0.66	0.510
	systemTB	**-0.021**	**0.008**	**-2.63**	**0.010**
	systemCH	**-0.030**	**0.008**	**-3.78**	**<0.001**
Winter	**(Intercept)**	**0.269**	**0.018**	**15.32**	**<0.001**
	Year	**0.005**	**0.001**	**4.44**	**<0.001**
	systemCK	-0.033	0.018	-1.83	0.071
	systemTB	**-0.034**	**0.017**	**-1.99**	**0.050**
	systemCH	**-0.083**	**0.017**	**-4.80**	**<0.001**

Table 8: Coefficients of variation in the Bray-Curtis dissimilarity index for each season and system.

Season	System	Coefficient of Variation
Summer	AP	8.86
	CK	14.04
	TB	13.71
	CH	16.08
Winter	AP	22.95
	CK	25.43
	TB	21.44
	CH	12.55

PERMANOVAs indicated assemblage composition and abundance varied differently over time among systems (Year:System interaction term for summer $p = 0.001$ and winter $p = 0.001$; Table 9). I therefore conducted separate PEMANOVAs and CAP ordinations for each system within each season (*sensu* Peake et al. 2022). From the individual PERMANOVA models, assemblage composition changed significantly over time in each estuary and each season (all $p = 0.001$; Table 10).

Table 9: Summary outputs from assemblage composition and abundance PERMANOVAs conducted for each season. Values in bold are statistically significant at alpha 0.05.

Season	Term	DF	Sum of squares	R^2	Pseudo F-value	p-value
	Year	**22**	**13.80**	**0.01**	**5.08**	**0.001**
	System	**3**	**48.23**	**0.04**	**130.29**	**0.001**
Summer	**Year:System**	**60**	**16.59**	**0.01**	**2.24**	**0.001**
	Residual	8,833	1,089.98	0.93		
	Total	8,918	1,168.61	1.00		
	Year	**22**	**60.07**	**0.02**	**6.99**	**0.001**
	System	**3**	**159.80**	**0.05**	**136.32**	**0.001**
Winter	**Year:System**	**60**	**58.32**	**0.02**	**2.49**	**0.001**
	Residual	8,255	3,225.64	0.92		
	Total	8,340	3,503.83	1.00		

Table 10: Outputs from assemblage composition and abundance PERMANOVAs conducted for each system and season combination. Values in bold are statistically significant at alpha 0.05.

Season	System	Term	DF	Sum of squares	R^2	Pseudo F-value	p-value
Summer	AB	**Year**	**19**	**13.94**	**0.02**	**1.91**	**0.001**
		Residual	1,563	600.52	0.98		
		Total	1,582	614.47	1.00		
	CK	**Year**	**19**	**16.41**	**0.03**	**2.22**	**0.001**
		Residual	1,625	632.01	0.97		
		Total	1,644	648.42	1.00		
	TB	**Year**	**22**	**21.57**	**0.02**	**2.58**	**0.001**
		Residual	2,796	1,064.60	0.98		
		Total	2,818	1,086.17	1.00		
	CH	**Year**	**22**	**24.18**	**0.02**	**3.29**	**0.001**
		Residual	2,849	950.80	0.98		
		Total	2,871	974.98	1.00		
Winter	AB	**Year**	**19**	**20.87**	**0.04**	**2.89**	**0.001**
		Residual	1,428	542.04	0.96		
		Total	1,447	562.91	1.00		
	CK	**Year**	**19**	**19.94**	**0.03**	**2.65**	**0.001**
		Residual	1,427	565.59	0.97		
		Total	1,446	585.52	1.00		
	TB	**Year**	**22**	**33.83**	**0.03**	**3.72**	**0.001**
		Residual	2,621	1,084.62	0.97		
		Total	2,643	1,118.46	1.00		
	CH	**Year**	**22**	**39.56**	**0.04**	**4.84**	**0.001**
		Residual	2,779	1,033.39	0.96		
		Total	2,801	1,072.95	1.00		

CAP ordinations revealed that in most systems and seasons, there was a slow drift from the earlier years of assemblage composition to the more recent years, as evidenced by the minimal overlap among earlier and recent year centroids (Figure 7). However, notable exceptions included Cedar Key in the summer, which had stronger separation into two groups transitioning around the year 2010, and Charlotte Harbor, which, for both seasons, had considerably more overlap among earlier and recent year centroids (Figure 7). In winter, *Leiostomous xanthurus* was consistently identified as the taxa most associated with yearly assemblage differences and was most associated with the centroids of earlier year groups in the dataset (Table 11; Figure 7). For Cedar Key in summer, pre-2010 years were most aligned with *L. xanthurus* and the more recent years with *Eucinostomus* fishes (Figure 7). Overall, the CAP models explained 12.24% to 20.74% of the variability, indicating a large portion was not explained by the assemblage composition and abundances alone. Looking at the assemblage most associated with yearly differences, only five taxa were selected as the top associated with yearly separation on the first two canonical axes for all system and season combinations (Table 11). Specifically, each system in summer had a different taxon associated with the greatest yearly separation, but in the winter, all systems are best separated on a yearly basis by *L. xanthurus* (Table 11).

Table 11: Taxon with the greatest magnitude vector as measured on the first two axes of variation for each system and season.

Season	System	Scientific name
Summer	AB	*Microgobius thalassinus*
	CK	*Eucinostomus* spp.
	TB	*Eucinostomus* spp.
	CH	*Lagodon rhomboides*
Winter	AB	*Leiostomus xanthurus*
	CK	*Leiostomus xanthurus*
	TB	*Leiostomus xanthurus*
	CH	*Leiostomus xanthurus*

SAV and water temperature were significantly related to assemblage structure across all systems and seasons (Figure 8). However, there were no clear temporal patterns in most of the ordinations (Figure 8). Across systems, Tampa Bay had the most tightly clustered group of yearly centroids, particularly in winter (Figure 8). In all systems, both SAV coverage and water temperature had strong correlations with the first canonical axis as indicated by their direction and magnitude. Further, the relative magnitude of SAV coverage was generally greater than water temperature in all cases, suggesting a stronger influence on assemblage variability among years.
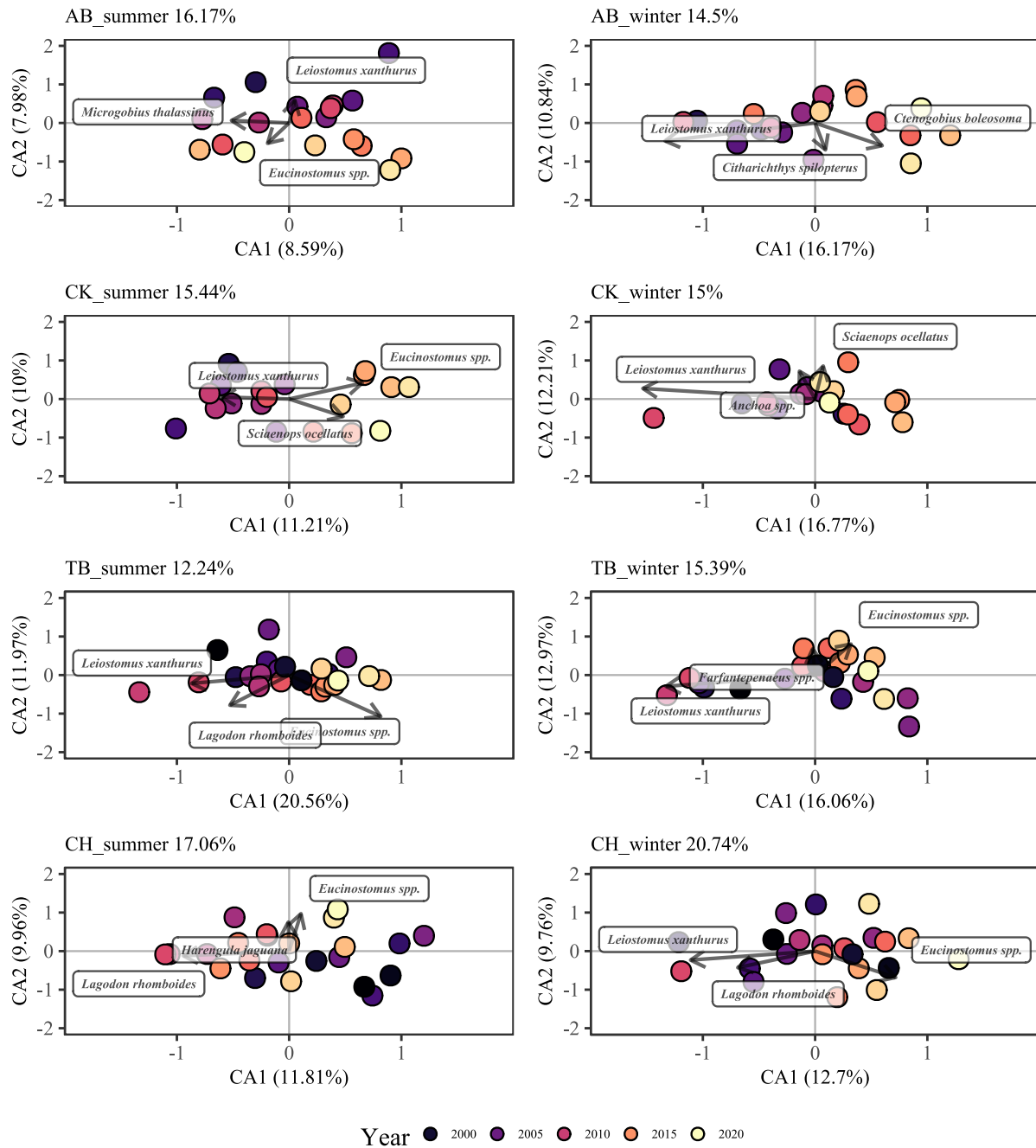
Figure 7: Canonical analysis of principal coordinates ordinations of assemblage composition and abundance. Shading of markers indicates year for that group, with darker colors indicating centroids of the oldest years in the data and lighter colors indicating the most recent years. Percentages next to subplot title indicate total variability captured by the model. Top three taxa associated with canonical axes scores plotted as vectors. Canonical axis (CA) percentages indicate the among-group variation captured in each axis.
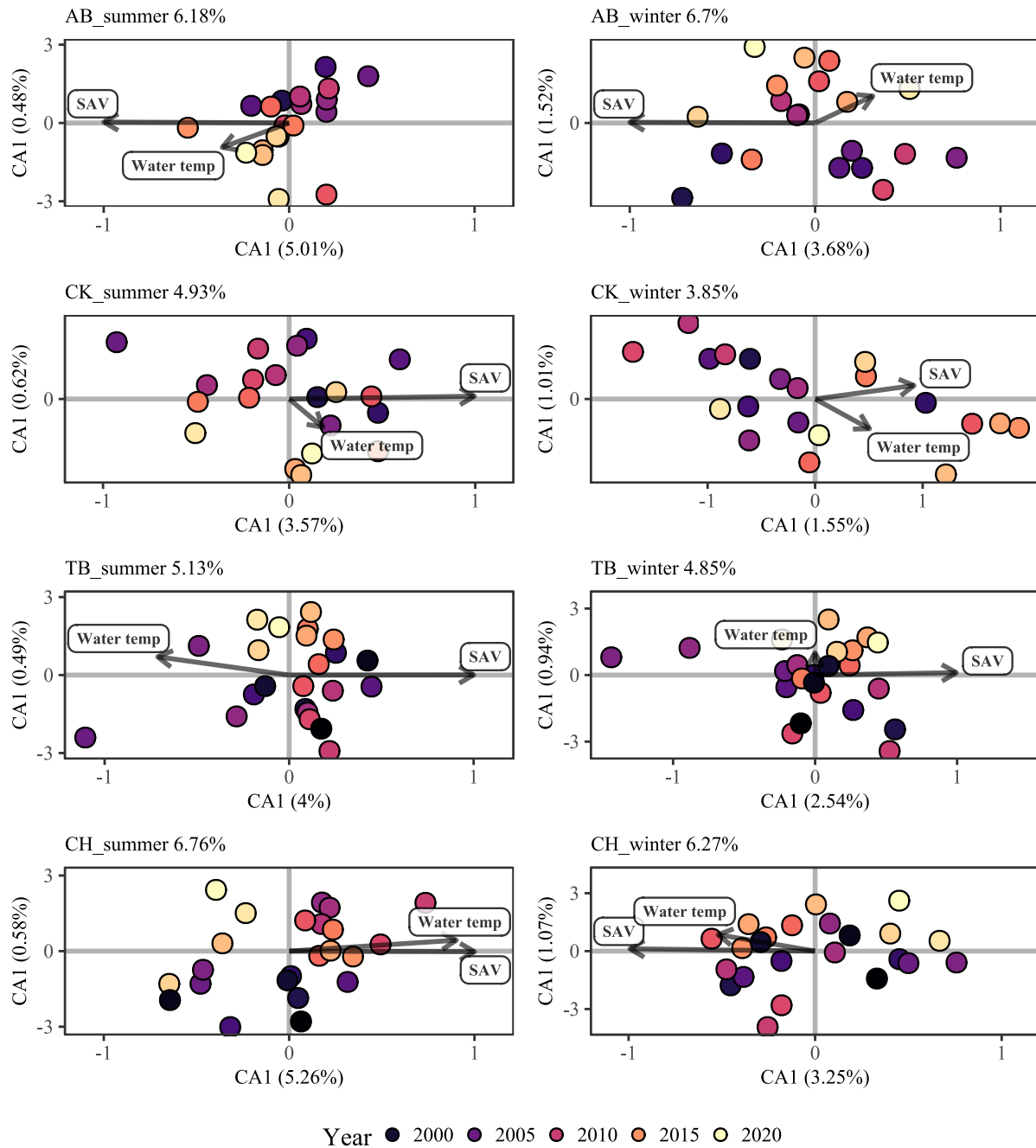
Figure 8: Distance-based redundancy analysis (dbRDA) ordination to visualize effects of habitat parameters. Shading of markers indicates year for that group, with darker colors indicating centroids of the oldest years in the data and lighter colors indicating the most recent years. Canonical axis (CA) percentages indicate the total variation in estuarine communities explained by that axis. Each habitat variable is represented by vectors and centroids of taxa groups are calculated using weighted average scores.

Individual Taxon Analyses
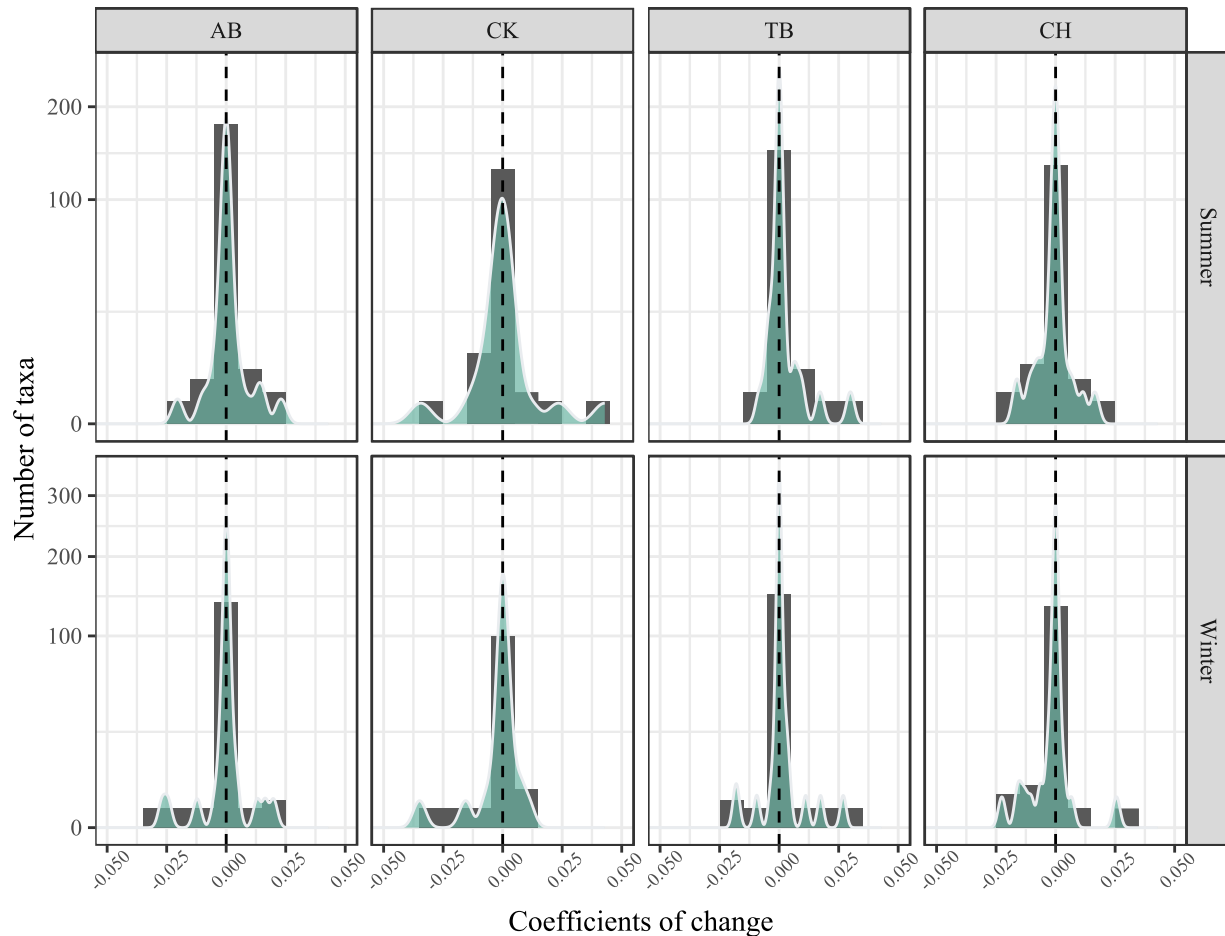
Figure 9: Density plots of slopes of all mean annual taxa abundances over time. Dashed line indicates a slope of 0. Includes slopes of no statistical significance.

The majority of taxa (69%) did not exhibit significant changes in abundance over time (206 out of 297 taxa), with a large group centered around zero rate of abundance change in both summer and winter for all systems (Figure 9). There was no difference in the overall percentage of taxa changing between systems ($t = 0.70$; $p = 0.599$) or seasons ($t = 1.32$; $p = 0.241$). The percentage of taxa undergoing population declines was greater in the summer than in the winter ($t = 2.65$; $p = 0.019$; Table 12), and there was no difference between seasons in the percentage of taxa that increased ($t = -1.76$; $p = 0.929$; Table 12). Overall, most taxa that had significant changes in abundance were either tropical-associated or ubiquitous in distribution and

experienced rather modest changes, yet, a few taxa had rates of change an order of magnitude greater than the rest (Table 13; Figure 10).

Table 12: Percent of observed taxa with statistically significant changes in abundance over time as well as the split between positive and negative change within.

Season	System	Change overall	Positive change	Negative change
Summer	AB	10.5%	50.0%	50.0%
	CK	17.4%	44.0%	56.0%
	TB	15.1%	50.0%	50.0%
	CH	17.0%	48.0%	52.0%
Winter	AB	13.1%	68.4%	31.6%
	CK	10.3%	72.7%	27.3%
	TB	11.0%	82.4%	17.6%
	CH	15.3%	54.5%	45.5%

Table 13: Climatological associations of taxa that significantly changed over time. Percentages listed are calculated with respect to number of taxa with available climate data.

| Season	System	Climatology	Positive change	Negative change
Summer	AB	Tropical	27.3%	9.1%
		Ubiquitous	18.2%	45.5%
	CK	Ubiquitous	35.7%	64.3%
	TB	Tropical	14.3%	23.8%
		Ubiquitous	33.3%	28.6%
	CH	Tropical	20.0%	15.0%
		Ubiquitous	25.0%	40.0%
Winter	AB	Tropical	33.3%	8.3%
		Ubiquitous	25.0%	16.7%
		Subtropical	8.3%	0.0%
		Temperate	8.3%	0.0%
	CK	Tropical	16.7%	0.0%
		Ubiquitous	66.7%	16.7%
	TB	Tropical	33.3%	8.3%
		Ubiquitous	58.3%	0.0%
	CH	Tropical	28.6%	21.4%
		Ubiquitous	28.6%	21.4%
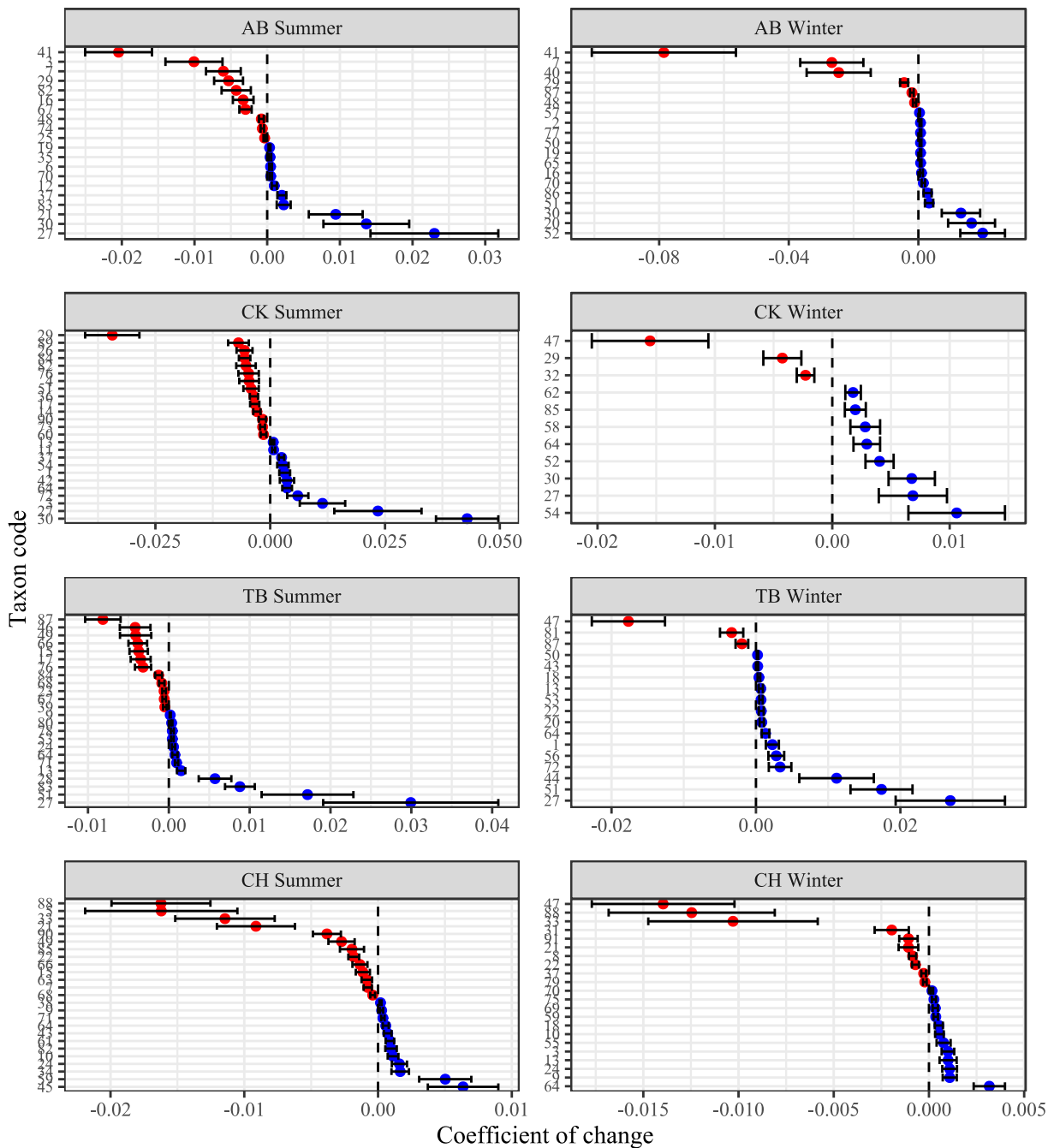
Figure 10: Coefficients of change of transformed mean annual taxa abundance over time plotted per system and season. Red indicates a negative change over time and blue indicates a positive change. The dashed line represents a slope of 0. Error bars represent ± 1 standard error. Numbers on *y*-axis correspond to individual taxa, see Table 14 for key.

Table 14: Key to taxa in univariate analyses plots.

ID key	Scientific name	ID key	Scientific name
1	*Achirus lineatus*	29	*Fundulus similis*
2	*Archosargus probatocephalus*	30	*Gobiosoma bosc*
3	*Ariopsis felis*	31	*Gobiosoma robustum*
4	*Bagre marinus*	32	*Haemulon plumierii*
5	*Bairdiella chrysoura*	33	*Hippocampus zosterae*
6	*Bathygobius soporator*	34	*Hyporhamphus meeki*
7	*Brevoortia* spp.	35	*Hyporhamphus* spp.
8	*Calamus arctifrons*	36	*Hyporhamphus unifasciatus*
9	*Calamus penna*	37	*Hypsoblennius hentz*
10	*Callinectes ornatus*	38	*Lagodon rhomboides*
11	*Callinectes similis*	39	*Leiostomus xanthurus*
12	*Caranx latus*	40	*Litopenaeus setiferus*
13	*Centropomus undecimalis*	41	*Lophogobius cyprinoides*
14	*Centropristis striata*	42	*Lucania parva*
15	*Chaetodipterus faber*	43	*Lutjanus griseus*
16	*Chasmodes saburrae*	44	*Membras martinica*
17	*Chilomycterus schoepfii*	45	*Menidia* spp.
18	*Citharichthys macrops*	46	*Menippe* spp.
19	*Citharichthys* spp.	47	*Menticirrhus americanus*
20	*Ctenogobius boleosoma*	48	*Menticirrhus littoralis*
21	*Cynoscion nebulosus*	49	*Microgobius gulosus*
22	*Dasyatis sabina*	50	*Micropogonias undulatus*
23	*Dasyatis say*	51	*Monacanthus ciliatus*
24	*Diapterus auratus*	52	*Mugil cephalus*
25	*Echeneis naucrates*	53	*Mugil curema*
26	*Etropus crossotus*	54	*Mugil trichodon*
27	*Eucinostomus* spp.	55	*Notropis petersoni*
28	*Eugerres plumieri*	56	*Ogcocephalus cubifrons*

Table 14: (Continued)

ID key	Scientific name	ID key	Scientific name
57	*Opisthonema oglinum*	74	*Sphoeroides nephelus*
58	*Opsanus beta*	75	*Sphoeroides* spp.
59	*Oreochromis/Sarotherodon* spp.	76	*Sphyraena barracuda*
60	*Orthopristis chrysoptera*	77	*Sphyraena guachancho*
61	*Paralichthys albigutta*	78	*Sphyrna tiburo*
62	*Portunus* spp.	79	*Stephanolepis hispidus*
63	*Prionotus longispinosus*	80	*Strongylura marina*
64	*Prionotus scitulus*	81	*Strongylura notata*
65	*Prionotus tribulus*	82	*Strongylura timucu*
66	*Rhinoptera bonasus*	83	*Symphurus plagiusa*
67	*Rimapenaeus constrictus*	84	*Syngnathus floridae*
68	*Rimapenaeus* spp.	85	*Syngnathus louisianae*
69	*Sarotherodon melanotheron*	86	*Syngnathus scovelli*
70	*Sciaenops ocellatus*	87	*Synodus foetens*
71	*Scomberomorus maculatus*	88	*Trinectes maculatus*
72	*Selene vomer*	89	*Urophycis floridana*
73	*Serranus subligarius*		

Discussion

I observed varying levels of stability and change in estuarine habitats and the fauna they supported. Long-term dynamics of SAV cover varied across estuaries and seasons, displaying system-specific increases, decreases, or no change. In contrast, water temperature increased for all systems and seasons at rates similar to previous work that characterized estuarine warming (Bashevkin et al. 2022). Estuarine faunal assemblages in the eGOM were generally stable in both abundance and richness over the study period despite stressors such as major storms (Greenwood et al. 2006), harmful algal blooms (Flaherty and Landsberg 2011), and climate change (Erickson

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et al. 2021). Specifically, long-term population dynamics were relatively stable for most taxa. Among taxa that changed in abundance, there were similar numbers of populations that increased or decreased in the summer (*i.e*., balanced "winners" and "losers"), a result consistent with global findings (Dornelas et al. 2019). In the winter, there were relatively fewer taxa that decreased in abundance than in the summer (*i.e*., more "winners" than "losers"), possibly in line with expectations from Clark et al. (2020). However, the assemblage structure in all systems displayed slow, but significant, change (*i.e*., ecological drift). In sum, the findings of my study indicated eGOM estuaries displayed changes in SAV and water temperature, and their associated fauna had relatively stable abundance and diversity, yet a drifting assemblage structure during the study period.

Variable dynamics in the cover of SAV suggested system-specific factors may have occurred. The most common observation was that SAV cover did not change for most estuaries in most seasons. However, SAV cover in the southernmost estuaries increased over the study period, especially during winter. Seasonal variability in SAV is well-documented, with changes in biomass (Duarte 1989), isotopic composition (Fourqurean et al. 2005), and growth rates (Tussenbroek 1995), among other responses. Seagrasses located at temperate and subtropical latitudes often undergo leaf necrosis in the winter particularly as water temperatures decrease below 20°C (Zieman 1975, Iverson and Bittaker 1986). However, net seagrass growth persists through all seasons at lower subtropical and tropical latitudes, due to milder winter temperatures (Zieman 1975). Given the rapid increase of winter water temperature observed in this study, Tampa Bay and Charlotte Harbor may now be warm enough year-round to mitigate winter leaf necrosis. In addition, decades of intensive seagrass recovery efforts in Tampa Bay resulted in a coverage peak in 2016 (Sherwood et al. 2017). This major recovery effort is still active and has

led to management changes focused on reducing the nutrient loading of the estuary at multiple regulatory levels as well as the establishment of various monitoring programs (Sherwood et al. 2017). However, SAV has declined in recent years in Tampa Bay, partly due to hotter and fresher conditions (Beck et al. in review) as well as following high biomass harmful algal blooms (Beck et al. 2023). In addition, my study indicated SAV cover decreased over time in Cedar Key. Major declines in SAV were observed over a similar period on the east coast of Florida, largely due to harmful algal blooms, eutrophication, and subsequent light limitation (Lapointe et al. 2020). Cedar Key and surrounding SAV are located near the outflow of the Suwannee River, where management plans have recently been established to reduce nutrient loading across the river basin (FDEP 2018). Eutrophication from excess nutrients in the water column can promote high biomass of phytoplankton, which can reduce the amount of light that reaches the benthically-located SAV and lead to seagrass loss (Lapointe et al. 2020).

Water temperature consistently increased through time across estuaries within each season. Similar rates of increase in sea surface temperature were observed over the same period at several ocean observing buoys across the West Florida Shelf, including a similar rapid rise in winter temperatures compared to summer (Nickerson et al. 2023). The first winter in the life of many fishes is a critical period due to intense physiological demands, morphological changes, and habitat requirements (Hurst 2007, Stallings et al. 2010). Thus, the warming water I observed may explain the positive relationship between temperature and abundance in the winter as has been described for some fauna in other North American estuaries (Lankford and Targett 2001). In some marine systems, taxa ranges have shifted poleward in response to warming water temperatures (Hastings et al. 2020). In the latitude-limited system of the eGOM, this may lead to the greatest changes over time in the ecology of these systems as there is no potential for

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poleward migration of fishes to thermal refugia. Although increased water temperatures in the winter appear to have had positive effects on SAV (with associated positive effects on fauna), elevated temperatures during the summer may ultimately have negative effects on SAV cover. The two dominant seagrasses that contribute to SAV in the region (*Syringodium filiforme* and *Thalassia testudinum*) tend to have productivity optima at or below 30°C (Barber and Behrens 1985) and temperatures over 35°C can result in leaf death (Thorhaug et al. 1973). Long-term mean water temperatures in the summer have recently exceeded 30°C with some measurements higher than 35°C, so it will be important for future work to continue to measure how SAV responds to additional increases in water temperatures.

Despite variable SAV dynamics and consistent increases in water temperature across systems, the total abundance and richness of fauna were relatively stable over time. The only exceptions to the observed stability were the total abundance decrease in winter in Apalachicola Bay and increase in Tampa Bay in summer. Altered river flow due to upstream municipal and agricultural water withdrawals has been demonstrated to affect various faunal patterns and processes in Apalachicola Bay (Kimbro et al. 2017, Pusack et al. 2019, Peterson et al. 2023) and may partly explain the observed declining trends in my analyses. In addition, the substantial loss of oyster habitat in Apalachicola Bay (Kimbro et al. 2020) may have also contributed to overall changes in the nektonic communities therein (however see Love et al. 2024). In contrast, the increasing total abundance of fauna in Tampa Bay may have been due to improved water quality, reduction in excess nutrients (Karlen et al. 2023), and associated long-term increase in SAV coverage (Sherwood et al. 2017). The general trend of stability suggests the study estuaries were at community-level carrying capacity (*sensu* Storch and Okie 2019) to maintain high total abundance and richness. These trends further suggest that the systems were resilient and resistant

to changes due to various disturbances (*e.g*., tropical cyclones, harmful algal blooms) that affected the region during the study period (Wilson et al. 2006, Flaherty and Landsberg 2011, Weisberg et al. 2019). However, both theoretical and empirical work suggests disturbances will become more frequent and intense in the face of climate change (Stott 2016), which may erode the stability I observed. These perturbations, when severe enough, can alter ecosystems and potentially trigger shifts to alternative stable states (Nolting and Abbott 2016).

All estuaries exhibited significant changes in assemblage structure during both seasons over the study period. These changes were identified in both multivariate analyses, although more variation was captured by the CAP plots. The general trend was a gradual drift in structure from the early to recent years. This trend was further reflected in the significant change in beta diversity over time. For both seasons, the heterogeneity in structure appears to have been due to subtle changes in relative abundances of different taxa rather than extirpations, colonizations, or strong directional population dynamics (*i.e*., ecological drift). This finding is consistent with previous work by Dornelas et al. (2019) wherein most populations did not strongly change and the ones that did had similar numbers of taxa that increased or decreased (*i.e*., balanced "winners" and "losers"). However, the rate of change was approximately twice as fast during the winter compared to the summer, indicating the systems became increasingly dissimilar more rapidly during the winter. I observed some evidence of tropicalization, where nearly 30% of the species that increased in abundance had distributions centered at lower latitudes. Of note, only two species of scarids were observed, but they were found infrequently over the entire period and not indicative of tropicalization in this study in contrast to findings by Fodrie et al. (2010). Moreover, I observed decreasing population trends in some species that have higher latitude distribution centers. For example, one of the more temperate-centered species (*Leiostomus*

xanthurus) had a strong influence on the structure of the assemblages in all estuaries during winter in the early years, whereas species with distributions centered at lower latitudes (*e.g.*, gerreids) contributed to the structure in more recent years. However, SAV tended to have a stronger relationship with assemblage structure compared to water temperature, perhaps an indirect effect of warming conditions supporting year-round seagrass growth. The strong relationships identified herein between SAV and both abundance and richness are consistent with the relationship of SAV with assemblage structure and has been found repeatedly in similar systems globally (Heck et al. 1989, Beck et al. 2001, Casares and Creed 2008).

It is important to consider limitations of my study. First, I analyzed data collected from small seine net hauls, thus any inference is limited to taxa susceptible to being caught by that gear. The fisheries independent monitoring program that provided these data also uses a larger seine net and an otter trawl and those data could be the focus of future analyses. Second, a substantial amount of variance was not explained in some of my analyses. Other variables were therefore unaccounted for in my analyses, including seascape-level parameters (*e.g.*, oyster reef proximity, shoreline vegetation type), which have been identified as important in estuarine systems (Micheli and Peterson 1999, Michaud et al. 2022). Ecosystems can also display latency and lagged effects of various abiotic properties on biotic responses (Poulakis et al. 2012, Kominoski et al. 2020, Peterson et al. 2023). At broad spatial scales, sub-decadal (*i.e.*, El Niño-Southern Oscillation Index) and decadal-scale processes (*i.e.*, North Atlantic Oscillation Index) can be related to faunal patterns in the same estuaries I analyzed (Peake et al. 2022). Such large-scale processes may partly explain interannual synchrony in faunal communities between the two systems in the Northern Gulf of Mexico ecoregion (Apalachicola Bay and Cedar Key) and between the two systems in the Floridian ecoregion (Tampa Bay and Charlotte Harbor, Faletti et

al. 2019, Peake et al. 2022). Accounting for the suite of these multi-scale effects was beyond the scope of my work but may be needed to further improve model fit. Last, sampling was pre-stratified by presence of SAV in all systems except Cedar Key. This may partly explain the relatively high mean SAV for Apalachicola Bay I observed compared to previous work (>20% vs. <7% per FWRI 2017). Similarly, the lack of SAV pre-stratification in Cedar Key likely contributed to the relatively low SAV coverage I observed compared to all other systems.

Climate change is predicted to intensify disturbances (Stott 2016), including harsher heatwaves and cold fronts (*e.g.*, winter 2010 in this study). Such events can enhance mortality in fishes (Stevens et al. 2016) or even disrupt life cycle timing (Thaxton et al. 2020) which may lead to possible phenological mismatch events throughout ontogeny (Chevillot et al. 2017). My study suggests these eGOM estuarine systems are stable in some regards but also undergoing ecological drift. Faster and more abrupt ecological shifts may occur across multiple scales when systems surpass tipping points (Monaco and Helmuth 2011), but such events are often difficult to predict (Moore 2018). Long-term ecosystem monitoring programs (typically by resource management agencies) are needed to track the complex and varied effects of climate change. These efforts should contextualize biotic sampling with abiotic parameters, as well as adjacent biotic context (*e.g.*, SAV coverage in this study). The data-rich nature of such observational schemes will likely be key to understanding the ecological consequences of climate change, particularly as computing power rapidly improves and new statistical methods are developed. Ultimately, there is a need to continue to monitor ecosystems globally and to ensure observation occurs across as much geographic and temporal spread as practicable.

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APPENDIX A: SUPPLEMENTAL MATERIAL

Habitat Dynamics ANCOVAs

Table S1: Outputs of water temperature ANCOVA models.

Season	Term	Estimate	Standard error	*t*-statistic	*p*-value
	(Intercept)	**29.340**	**0.126**	**233.63**	**<0.001**
	systemCK	-0.215	0.128	-1.69	0.096
Summer	systemTB	0.228	0.124	1.84	0.070
	systemCH	**0.623**	**0.124**	**5.03**	**<0.001**
	Year	**0.018**	**0.007**	**2.62**	**0.010**
	(Intercept)	**15.208**	**0.283**	**53.83**	**<0.001**
	systemCK	0.461	0.291	1.59	0.117
Winter	**systemTB**	**3.206**	**0.282**	**11.39**	**<0.001**
	systemCH	**4.927**	**0.282**	**17.49**	**<0.001**
	Year	**0.063**	**0.015**	**4.08**	**<0.001**

Table S2: Least square means of water temperature for each system for both seasonal linear models. *P*-values for pairwise contrasts used Tukey method for correction.

Season	Contrast	Estimate	Standard error	DF	*t*-statistic	*p*-value
Summer	CK - AB	-0.215	0.128	81	-1.69	0.338
	TB - AB	0.228	0.124	81	1.84	0.265
	TB - CK	**0.443**	**0.124**	**81**	**3.57**	**0.003**
	CH - AB	**0.623**	**0.124**	**81**	**5.03**	**<0.001**
	CH - CK	**0.839**	**0.124**	**81**	**6.76**	**<0.001**
	CH - TB	**0.396**	**0.119**	**81**	**3.32**	**0.007**
Winter	CK - AB	0.461	0.291	77	1.59	0.393
	TB - AB	**3.206**	**0.282**	**77**	**11.39**	**<0.001**
	TB - CK	**2.746**	**0.282**	**77**	**9.75**	**<0.001**
	CH - AB	**4.927**	**0.282**	**77**	**17.49**	**<0.001**
	CH - CK	**4.466**	**0.282**	**77**	**15.86**	**<0.001**
	CH - TB	**1.720**	**0.270**	**77**	**6.37**	**<0.001**

Table S3: Least square means of SAV for each system for both seasonal linear models. *P*-values for pairwise contrasts used Tukey method for correction.

Season	Contrast	Estimate	Standard error	DF	*t*-statistic	*p*-value
Summer	CK - AB	-18.412	1.150	78	-16.00	<0.001
	TB - AB	7.453	1.110	78	6.71	<0.001
	TB - CK	25.865	1.110	78	23.30	<0.001
	CH - AB	17.706	1.110	78	15.95	<0.001
	CH - CK	36.118	1.110	78	32.53	<0.001
	CH - TB	10.253	1.068	78	9.60	<0.001
Winter	CK - AB	-17.378	1.175	78	-14.80	<0.001
	TB - AB	14.726	1.133	78	12.99	<0.001
	TB - CK	32.105	1.133	78	28.32	<0.001
	CH - AB	19.910	1.133	78	17.57	<0.001
	CH - CK	37.289	1.133	78	32.90	<0.001
	CH - TB	5.184	1.091	78	4.75	<0.001

Synthesis Tables

Table S4: Summary of all trends/significances for summer. Key: AB, CK, TB, CH.

Response	Time	SAV	Temp
Abundance	0, 0, +, 0	+, 0, +, +	0, 0, 0, 0
Richness	0, 0, 0, 0	+, +, +, +	0, 0, 0, 0
Assembly			
-PERMANOVA/CAP	sig, sig, sig, sig	—	—
-RDA	sig, sig, sig, sig	sig, sig, sig, sig	sig, sig, sig, sig
Water Temp	+, +, +, +	—	—
SAV	0, -, 0, +	—	—

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Table S5: Summary of all trends/significances for winter. Key: AB, CK, TB, CH.

Response	Time	SAV	Temp
Abundance	-, 0, 0, 0	-, 0, +, +	+, 0, +, +
Richness	0, 0, 0, 0	+, +, +, +	+, +, +, +
Assembly			
-PERMANOVA/CAP	sig, sig, sig, sig	—	—
-RDA	sig, sig, sig, sig	sig, sig, sig, sig	sig, sig, sig, sig
Water Temp	+, +, +, +	—	—
SAV	0, 0, +, +	—	—