Tropicalization of mid-western Atlantic coastal bays by pinfish *Lagodon rhomboides*: a combined ecological and oceanographic perspective

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ABSTRACT: As climate change continues to shift the distributions of species worldwide, understanding where, why, and how organisms move beyond their historical ranges is of critical importance. Here, we report on the expansion of pinfish *Lagodon rhomboides* poleward along the mid-western Atlantic in response to rising temperatures. Pinfish are a key interactor in nearshore subtidal habitats like seagrasses in the southwestern Atlantic and Gulf of Mexico, but they have been historically sparse north of the ecotone at Cape Hatteras, North Carolina, USA. Using multidecadal trawl surveys, we show that while pinfish have been present both below (North Carolina) and above (Virginia and Maryland) this ecotone for many years, they have increasingly intruded into restored eelgrass (*Zostera marina*) meadows in the coastal bays of Virginia over the past decade. In 2022, for instance, pinfish abundances in Virginia equaled those observed historically in North Carolina. To understand the factors promoting these changes in abundance, we used a passive drifter model to show that these increases are not necessarily tied to changes in offshore currents. Instead, linear models revealed that the local abundance of pinfish in Virginia correlates most with inshore summertime water temperatures. Thus, favorable environmental conditions of the recipient bays appear to encourage greater recruitment and therefore greater abundance of pinfish. Given their outsized ecological role in subtropical ecosystems, and that the climate will continue to warm, our findings suggest that pinfish may soon come to dominate the structure and functioning of temperate seagrass meadows in Virginia and beyond.

KEY WORDS: Range shift · Range expansion · Seagrass · Eelgrass · Restoration · Passive drifter model

1. INTRODUCTION

Global climate change is altering the abundance and distribution of countless organisms across the planet (Poloczanska et al. 2013). In aquatic environments, such shifts generally occur as a consequence of water temperatures increasing beyond the thermal tolerance of resident species, who must therefore emigrate poleward from their historical ranges and colonize new habitable areas or go locally extinct (Sunday et al. 2012). At the same time, emerging conditions may encourage the immigration of more heat-tolerant species from warmer tropical and subtropical areas to the point where they outnumber resident cooler-affinity species, a process referred to as 'tropicalization' (Wernberg et al. 2013). This process can occur rapidly or take many years, depending on the life history of the organisms and the rate of change in

the local and regional environments (Bates et al. 2014). Tropicalization is of particular concern because, once present and established, range expanders can exert significant influence on the ecosystem by outcompeting endemic species, threatening biodiversity and endangered species, and altering the energy flow through the ecosystem via novel trophic interactions (Vergés et al. 2014, Pecl et al. 2017). These outcomes make managing natural systems increasingly difficult, particularly from the perspective of preserving the reliable delivery of ecosystem services such as fisheries (Pecl et al. 2017).

By virtue of their relatively high dispersal capacity, marine organisms tend to more frequently occupy the fringes of their ranges, and so extensions or contractions are especially evident in the world's oceans (Sunday et al. 2012, Pinsky et al. 2020). As a result, tropicalization has been well documented across a range of marine habitats: e.g. in Australia, warming has encouraged the intrusion of subtropical fish grazers, which have consumed temperate kelps and contributed to the rise of algal-dominated turfs on both the eastern (Vergés et al. 2016) and western coasts (Wernberg et al. 2013). Similarly, in Japan, the expansion of subtropical herbivores has cleared formerly macroalgal-dominated substrate, paving the way for colonization by tropical corals (Kumagai et al. 2018). In the eastern US, warmer-than-average wintertime temperatures have encouraged the northward migration of subtropical mangroves which are actively replacing large swathes of temperate salt marshes in Florida (Cavanaugh et al. 2014). The implications of turnover in these foundation species — and associated faunal communities — are likely to be significant, not just ecologically but societally and economically as well (Hensel et al. 2023).

Seagrasses have received increasing attention from the scientific community and from managers seeking to mitigate the impacts of climate change and prepare shorelines against future threats such as storms and erosion (Dunic et al. 2021, Turschwell et al. 2021). Because of their widespread distribution across both temperate and tropical realms, seagrass habitats are increasingly investigated for signals of tropicalization (Hyndes et al. 2016). An early demonstration of the phenomenon highlighted the role of seagrass beds as recipients for northward-migrating fishes in the Gulf of Mexico (Fodrie et al. 2010), many of whom directly consume seagrass and may therefore threaten the future persistence of meadows in the region (Heck et al. 2015). Seagrass meadows in the mid-Atlantic straddle an historical ecotone at Cape Hatteras, North Carolina (see our Fig. 1), that separates 2 distinct biogeo-graphic regions for seagrasses, the Temperate North Atlantic and the Tropical Atlantic (Short et al. 2007). This ecotone generally constitutes the lower limit of the cool-affinity eelgrass *Zostera marina* as well as numerous species of shallow water fishes (Robertson & Cramer 2014) and invertebrates (Pappalardo et al. 2015). Below this ecotone, seagrass meadows can still include eelgrass but are increasingly dominated by subtropical seagrasses such as *Halodule wrightii* and, farther south, by *Thalassia testudinum* and *Syringo-dium filiforme* (Bartenfelder et al. 2022).

These subtropical seagrass communities are frequently characterized by very high abundances of pinfish *Lagodon rhomboides*. In North Carolina and areas south through Florida and into the Gulf of Mexico, pinfish are the most dominant members of the nearshore fish community and are often associated with structured habitats, such as seagrasses (Adams 1976b, Fodrie & Heck 2011, Faletti et al. 2019). These mesopredators are a key link in the food web, transferring energy and nutrients acquired from foraging in seagrass meadows (and other nearshore benthic habitats) to higher predators and along the coast in quantities unparalleled by other organisms (Nelson et al. 2013). Furthermore, pinfish change their diet preferences throughout their ontogeny: as juveniles, they are strictly carnivorous, feeding primarily on small crustaceans, transitioning to omnivory as they grow, even feeding directly on the seagrass itself as mature adults (Stoner 1980). Their presence is therefore integral to the functioning of shallow water ecosystems throughout the southern US and Gulf of Mexico. North of the historical ecotone, however, pinfish have been historically sparse and, in the estuarine Chesapeake Bay, are reported to have declined in abundance since the 1970s (Sobocinski et al. 2013). Yet, as global climate change has raised temperatures by 1–2°C along the mid-Atlantic in the past 4 decades (Wallace et al. 2018) and is projected to increase temperature by another 2–6°C in the coming half century (Najjar et al. 2010), abiotic conditions in the bay and other nearby bodies of water may increasingly resemble those found in subtropical North Carolina and provide an optimal environment for pinfish.

As pinfish have complex life histories, climate change could influence their abundance and distribution at multiple points throughout their ontogeny. Like many fishes that use subtropical or temperate estuaries (including many sciaenids, paralichthyids, and lutjanids), pinfish make ontogenetic migrations between nearshore bays and estuaries and the ocean environments as part of their core life history. Within our study region, juvenile pinfish typically enter the

coastal zone in the spring (Warlen & Burke 1990), and (sub-)adults exit nearshore systems and travel to the ocean by late fall to spawn (Baillie et al. 2015). These egressing individuals appear to distribute broadly from the coast to the deeper continental shelf (Hildebrand & Cable 1938, Caldwell 1957). The exact behaviors and locations associated with pinfish spawning remain poorly documented, but there is some evidence that spawning occurs >20 km from shore (Hildebrand & Cable 1938) and largely during November−March (Able & Fahay 2010), with a pelagic larval duration of ~1 mo (Checkley et al. 1988). During this time, larvae are subject to large-scale dispersal associated with the Gulf Stream. Beginning in December, larvae begin to immigrate into estuaries, with larval ingress peaking in January and February and waning in March when temperatures reach 10−16°C.

Here, we draw on multiple decades of monitoring data of inshore fish communities both north (Virginia and Maryland) and south (North Carolina) of the historical ecotone to examine whether pinfish are changing in abundance across this range through time relative to the larger fish community. We further integrate oceanographic models to explore the role of large-scale physical factors during early life stages spent in the Gulf Stream in driving subsequent patterns in pinfish abundance in the coastal zone. We hypothesize that changes in pinfish abundance just north of the ecotone in Virginia could be due to more favorable local conditions (warmer water temperatures), more favorable offshore conditions (warmer sea surface temperatures [SSTs]), changes in physical transport processes such as winds and currents from offshore to inshore, mid-Atlantic-wide recruitment events (i.e. higher-than-average abundances across both sides of the ecotone), or some combination of the above.

2. MATERIALS AND METHODS

2.1. Fish trawl surveys

Fish community surveys were conducted monthly from May to September in 3 nearshore regions along the western mid-Atlantic seaboard (from south to north): Back and Core Sounds in North Carolina (approximately 34° 41′ N, 76° 34′ W) from the years 2010−2022; South Bay in Virginia (37° 15′ N, 75° 49′ W) from 2012−2022; and Assawoman (38° 25′ N, 75° 5′ W), Chincoteague (38° 1′ N, 75° 18′ W), Isle of Wight (38° 23′ N, 75° 6′ W), and Sinepuxent Bays (38° 14′ N, 75° 8′ W) in Maryland from 1989−2022 (Fig. 1). Surveys employed a similar methodology, using a 4.9 m otter trawl (1.9 cm mesh wings and 0.6 cm cod end liner, 0.3 m × 0.7 m doors). Trawls were towed from a shallow draft vessel through predominantly seagrass habitats during daytime high tides in North Carolina and Virginia. In Maryland, trawls did not specifically target seagrass, and thus were also conducted over unvegetated bottom adjacent to — or formerly occupied by — seagrass (Maryland). The number of trawls conducted per
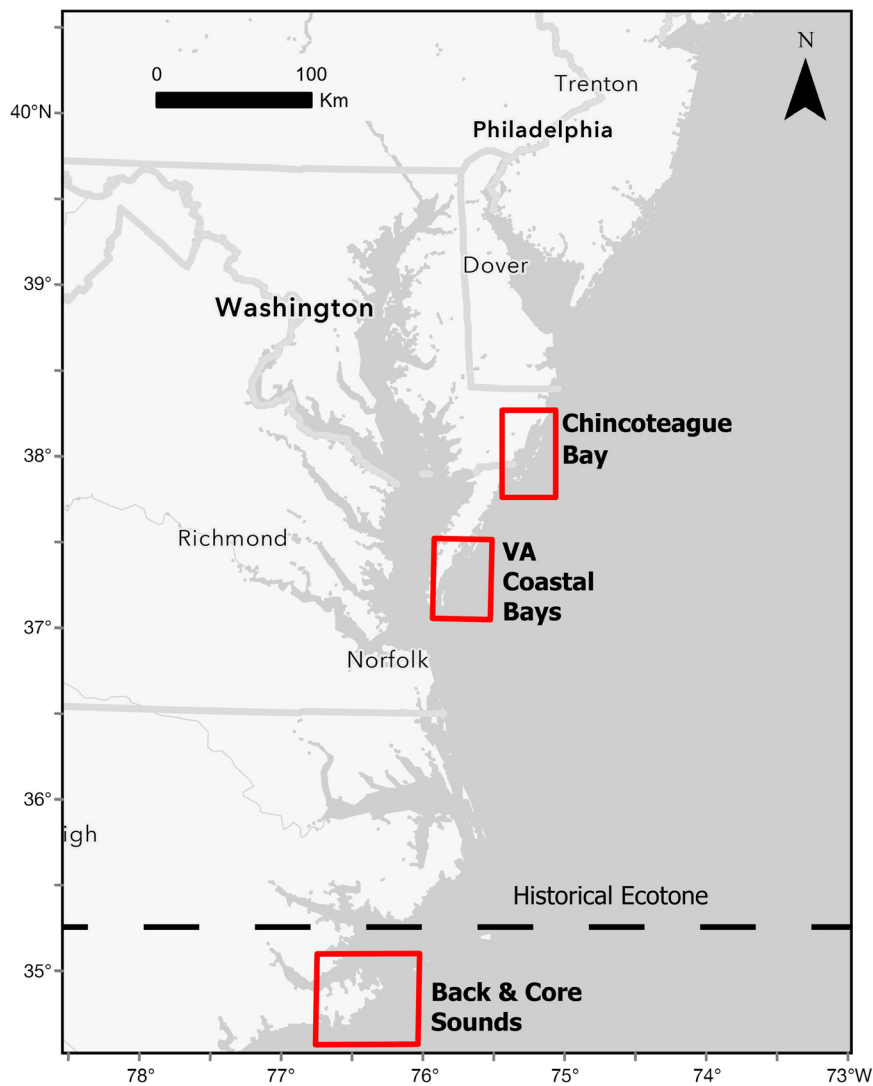

Fig. 1. The 3 study regions surveyed. VA: Virginia

sampling event varied by location (North Carolina: 2–12; Virginia: 6; Maryland: 20). Each tow was either 2 min (North Carolina and Virginia) or 6 min (Maryland) in duration. Tow length was extracted from measurements made using a hand-held GPS unit on the vessel, and all tows were nonoverlapping.

For each trawl, all fishes were brought onboard and identified to species level and enumerated. We note that full community data were not requested for Maryland, so we report only on pinfish abundances in that region. Additionally, in Virginia, up to 10 individuals of each species in each tow were randomly selected and measured for total length (TL, in cm). Handling was conducted following approved Institutional Animal Care and Use Committee protocols. We restricted our analysis to actinopterygian fishes (excluding any sharks, rays, and invertebrate species). Species with <5 individuals observed across the entire dataset within each region were removed. To account for varying effort (i.e. distance, duration) across the surveys, both within and across the regions, we expressed the measurements as the number of individuals per standardized 100 m tow expressed by (abundance of each species/total distance swept) × 100 m. To account for differences in replication across sampling dates, we averaged abundance across all tows for a given species, date, and location.

2.2. Drifter model

To investigate the physical transport processes that operate to deliver post-larvae to the coastal zone, we employed a passive drifter model based on surface and near-surface velocities from the HYbrid Coordinate Ocean Model (HYCOM). HYCOM is a global 1/12°, generalized-coordinate, data-assimilative ocean model; assimilated data includes satellite-derived SST and *in situ* temperature and salinity casts. Our passive drifter model used daily time steps with 4th-order Runge-Kutta numerical integration and inverse distance weighting interpolation to advect drifters (i.e. pinfish larvae) out of a breeding region in the Gulf Stream. The drifters were initialized at regular spacing along a line at 34° 24' N between 77° 31' W and 76° 52' W. Reanalysis data are available up to 2015, and we focus on the period 2011–2015, corresponding to the breeding seasons initiated in late fall of 2010–2014.

The HYCOM is useful for demonstrating the potential pathways of large-scale transport from pinfish breeding regions south of Cape Hatteras to the Virginia shelf. However, we note that it has not been explicitly validated against *in situ* data for our study region and period of interest, so the results of the passive drifter model are useful for characterizing the relative variability among years, rather than to estimate the absolute recruitment of larval/juvenile pinfish. Additionally, since the global model cannot resolve the fine-scale nearshore processes that deliver pinfish to very shallow water areas, we recorded the number of drifters that remain within 2 km of the coast for at least 24 h, assuming that local processes take over at this stage.

2.3. Temperature covariates

We collated data for both inshore and offshore water temperatures for the Virginia location, based on our initial hypotheses. We obtained offshore SST for Gulf Stream waters adjacent to the inshore study area from the NOAA National Centers for Environmental Information's Daily Optimum Interpolation dataset (version 2.1, https://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOisst21Agg_LonPM180.html). We obtained daily values of SST from 2011–2022 and averaged these values over the study region for the period of October to March preceding each year of survey, as this is the time period during which pinfish are spawning offshore (Caldwell 1957) and therefore most likely to respond to the temperatures observed there.

Inshore temperature data were collected from a YSI 6600 EDS Sonde moored in the shallow waters of South Bay, Virginia. The sonde was deployed from 2004–2019, with several months of interruption in 2015, before it was taken offline in 2019. To fill in these gaps, we sourced data from a nearby NOAA monitoring station at Wachapreague, Virginia (https://www.ndbc.noaa.gov/station_page.php?station=wahv2), ~35 km north of the study site. To validate this choice, we correlated the period of overlapping observations between both datasets (from 2004–2015 and 2015–2019) and found a Pearson correlation coefficient of r = 0.99. Such a high degree of correlation demonstrates strong agreement between temperatures recorded from the YSI and from the NOAA station, so we collapsed them into a single set of observations of water temperature. We then averaged inshore water temperature in the 30 d preceding each survey, assuming the catch on a given day is an accumulation of temperature effects over the period between surveys. Continuous inshore water data corresponding to the locations of the surveys in North Carolina and Maryland were not available, so we focused on the surveys in Virginia for further analysis.

2.4. Data analysis

To examine potential differences in community structure across the North Carolina and Virginia trawls, we employed non-metric multidimensional scaling (NMDS). We calculated Bray-Curtis distances based on square-root-transformed relative abundances before applying functions in the 'vegan' package (Oksanen et al. 2022).

To assess the potential drivers of local pinfish abundance in Virginia, we fit a general linear mixed-effects model. We first $\log_{10}+0.1$-transformed the response (average pinfish abundance per 100 m tow) in the months from May to September, before pinfish historically emigrate from the system each year. We then regressed this against the following predictors: mean inshore water temperature for the preceding month, mean offshore SST for the preceding period from October to March, the total aerial extent (in hectares) of the meadow in South Bay as reported annually by the Virginia Institute of Marine Science (VIMS) SAV Mapping Program (https://www.vims.edu/research/units/programs/sav/access/), and the abundance of pinfish in the corresponding month and year in North Carolina (to capture variation in local abundance as the result of fluctuations in region-wide abundance). The VIMS mapping program was unable to fully map meadows in 2014 and 2016, so we interpolated values of seagrass extent for these years as the midpoint between the 2 adjacent years.

We specified a nested random effect of month within year, and further specified a continuous AR(1) correlation structure to account for temporal autocorrelation (i.e. the same populations repeatedly sampled across months within years). We implemented inverse variance weighting by abundance, to upweight months with stable pinfish abundance across trawls. We fit the model to a Gaussian distribution using the 'nlme' package (Pinheiro et al. 2023), and visually assessed the assumptions of normality of errors and constant variance. We confirmed that the 2 measurements of temperature were not excessively collinear using variance inflation factors calculated from the 'car' package (Fox & Weisberg 2019). We computed explained variance (R^2) using the 'piecewiseSEM' package (Lefcheck 2016). All analyses were conducted in R version 4.4.0 (R Core Team 2023). All data and code necessary to reproduce all analyses are hosted on figshare at: https://doi.org/10.6084/m9.figshare.26842261.

3. RESULTS

3.1. Trends in pinfish abundance

Pinfish were recorded in each region during the periods sampled, although their abundances declined sharply with increasing latitude. In North Carolina, 137 690 pinfish individuals were sampled since 2010; in Virginia, 17 450 individuals since 2012; and in Maryland, only 116 individuals were recorded in total since 1989. In Virginia where TLs were measured, pinfish generally entered the coastal bays as juveniles (<13 cm TL) and resided in place until they reached maturity in late summer (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m748p137_supp.pdf). All 3 regions experienced greater-than-average abundances of pinfish per 100 m tow in 2012, 2015,
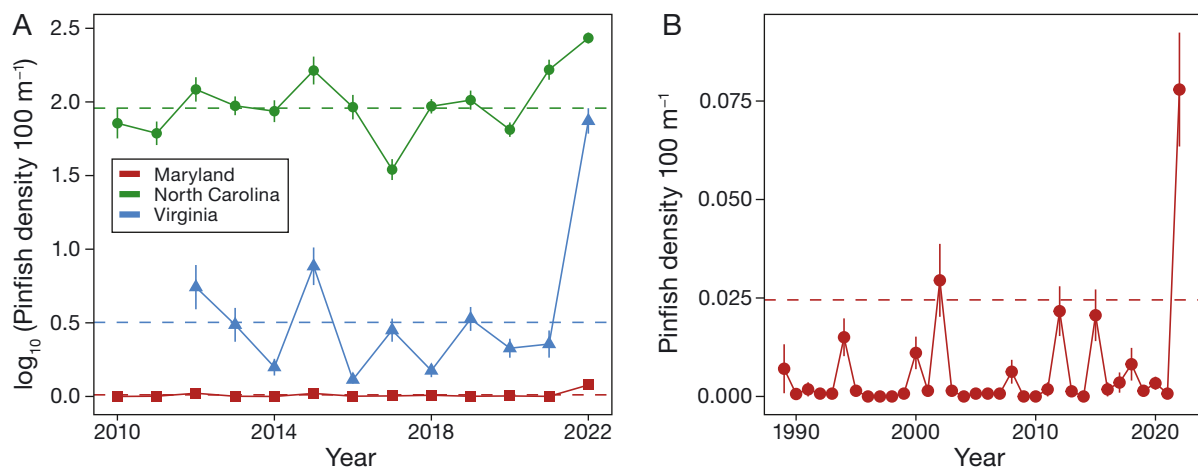

Fig. 2. (A) Local pinfish density per 100 m tow in each of the 3 regions sampled from 2010—2022. Dashed lines: long-term averages for each region across the total duration of sampling. Density has been $\log_{10}$-transformed to better separate the 3 regions. (B) Pinfish density showing untransformed Maryland data replotted on a separate axis to demonstrate peaks and show the full range of data from 1989—2022. Error bars are ± SE

and 2022 (Fig. 2), and additionally in 2002 in Maryland, whose records extend further back in time (Fig. 2B). That the trawl survey in Maryland did not always target vegetated bottom (in contrast to those in North Carolina and Virginia) may explain the overall lower abundances of pinfish reported there. Nevertheless, we feel it is important to show similar peaks in abundances across all 3 states in the years listed above, which may speak to multi-regional controls on pinfish abundance.

In North Carolina, pinfish were the dominant species in the fish community, comprising 68.4% of the total catch across all years and as much as 88% in 2015 (Fig. 3). While pinfish comprised, on average, only 14.4% of the total catch in Virginia, there were substantial differences among years: e.g. in 2014 and 2018, they accounted for <1% of the total catch, but rose to 44% in 2015 and as high as 66% in 2022 (Figs. 2A & 3). These sporadic but substantial intrusions indicate that, despite fish communities on either side of the ecotone remaining mostly different, the increase in pinfish dominance in certain years led those samples to move closer to North Carolina samples in multivariate space, as evidenced in the NMDS plot (Fig. S2 in the Supplement).

3.2. Passive drifter model

To understand the role of large-scale ocean transport in pinfish abundance in the Virginia coastal bays, we used a passive drifter model to examine potential for pinfish larval advection from off the coast of North Carolina to the nearshore Virginia and Maryland zone (<2 km offshore) at both surface (0 m) and subsurface (15 m) layers. The model showed that, in all years from 2011–2015, approximately 5–15% of drifters reached the coastal zone, and of these up to 40% remained in the coastal zone for 24 h, which we interpret as sufficient time for local processes to overtake the drifters and move them into the shallow-water bays (Fig. 4, Fig. S3 in the Supplement). Thus, the drifter model provides confirmation of possible transport pathways for offshore larvae to advect along the Gulf Stream, across the shelf break, and ultimately reach

coastal bays. Given that there has been historical presence of pinfish in the region since at least the 1980s (Fig. 2B), the transport result is not surprising but reveals the role played by large-scale circulation and provides some statistical bounds about the frequency of their occurrence. Nevertheless, the peaks in significant pinfish advection to the coastal zone did not appear to align well with known peaks in local abundance from the Virginia surveys. The simulations revealed the highest delivery of significant drifters at both depths in the 2014 season (Fig. 4), despite this year yielding among the lowest abundance and dominance of juvenile and adult pinfish in the inshore trawls (Figs. 2A & 3). This misalignment would indicate that factors beyond large-scale offshore circulation are controlling the observed pinfish density during peak years in the Virginia coastal bays, leading us to our next investigation of both inshore and offshore temperatures.
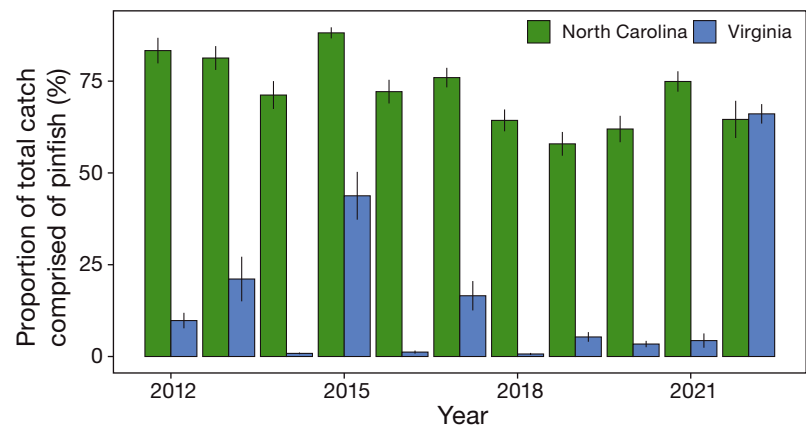

Fig. 3. Proportion of total catch (abundance) per tow comprised of pinfish in North Carolina and Virginia. Error bars are ± SE
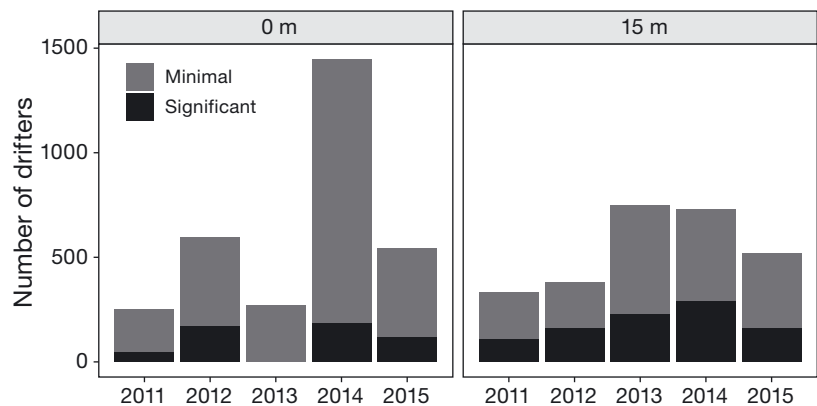

Fig. 4. Total number of modeled drifters that reach the coastal zone (<2 km offshore) at least once ('minimal') and those that were entrained in coastal waters for 1 full 24 h period ('significant') for both surface (0 m) and subsurface (15 m depth) waters
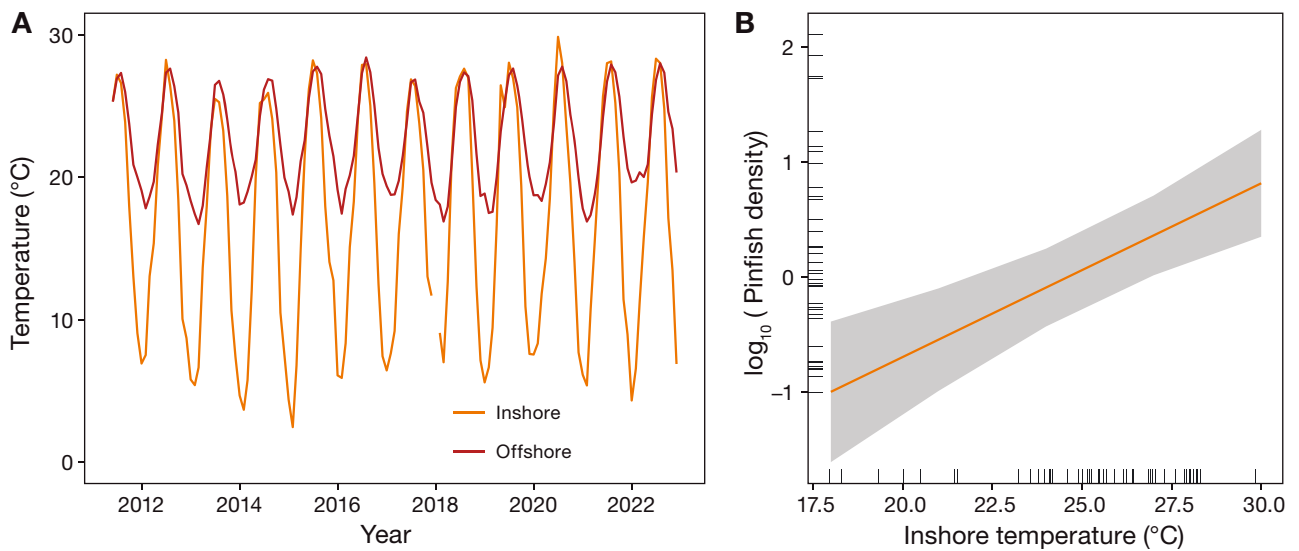
Fig. 5. (A) Inshore and offshore water temperatures as reported over the duration of the surveys in Virginia. (B) The partial effect of inshore water temperature on $\log_{10}$-transformed local pinfish density per 100 m tow. Red line: expected trend, given the other covariates in the model; shaded regions: 95% CIs. Rug plots of the distribution of raw data points are given along each axis

3.3. Linear regression

Over the study period, both inshore and offshore temperatures fluctuated predictably with season and across years (Fig. 5A), with periods of warmer- and cooler-than-average anomalies (Fig. S4 in the Supplement). To understand how these fluctuations might co-vary with local pinfish abundance in Virginia, we fit a generalized linear mixed-effects model including inshore and offshore water temperature, the annual aerial extent of the meadow, as well as mean monthly abundance of pinfish in North Carolina (to control for correlations in mid-Atlantic-wide recruitment). The model revealed a significant effect of inshore temperature ($\chi^2_1 = 18.63$, p < 0.001 from type II ANOVA) but not offshore SST ($\chi^2_1 = 1.30$, p = 0.25). With each 1°C increase in monthly water temperature, we expect ~1.32 additional pinfish per 100 m tow (Fig. 5B, Table 1). The abundance of pin-

fish in North Carolina also significantly correlated with local pinfish density in Virginia ($\chi^2_1 = 8.65$, p = 0.003), but had no significant relationship with annual seagrass extent ($\chi^2_1 = 2.07$, p = 0.15). We note that the inshore temperature effect is independent of, and indeed accounts for, the other covariates in the model.

Further, examining the standardized effect sizes — scaling the coefficient by the standard deviation of the response over that of each predictor, such that they are all now expressed in comparable units of standard deviations of the mean — revealed that the effect of inshore temperature is ~1.26× stronger than the influence of abundance in North Carolina (Table 1). This statistic reinforces the large influence of inshore temperatures in determining local pinfish abundance in Virginia versus coast-wide trends. For the entire model, the fixed effects alone explained $R^2 = 40.5\%$ of the variance in the response, suggesting more than a third of total variability in pinfish density in Virginia can be explained by inshore temperature and their abundance south of the ecotone (with lesser contributions by offshore temperature and meadows extent). An additional 59.5% of variance was explained by the random effects, indicating that the remainder of the variation in pinfish abundances can be attributed to the month and year in which the trawls were conducted.

Table 1. Output from a generalized linear mixed-effects model of $\log_{10}$-transformed local pinfish abundance in Virginia as a function of offshore sea surface temperature (SST), inshore temperature, corresponding abundance in North Carolina (NC), and annual extent of seagrass in South Bay, Virginia

Predictor	Estimate	Std. estimate	SE	df	t-value	p-value
Offshore SST	0.3637	0.2036	0.3194	8	1.1385	0.2878
Inshore temperature	0.1512	0.4720	0.0350	32	4.3164	0.0001
NC abundance	0.0033	0.3773	0.0011	32	2.9428	0.0060
Seagrass extent	−2.9301	−0.2525	2.0353	8	−1.4397	0.1879

4. DISCUSSION

Here, we present evidence that climate change in the form of increasing inshore water temperature has contributed to the periods of pinfish (*Lagodon rhomboides*) dominance in waters at the edge of its geographic range in the last decade. We show that pinfish comprise varying degrees of the fish community in Virginia from year to year, sometimes dominating and other times being virtually absent (Fig. 3), suggesting that current conditions do not yet enable consistent recruitment, survival, and/or growth of pinfish there. However, as temperatures continue to increase, we propose that pinfish will eventually come to consistently dominate the nearshore fish communities seasonally across the mid-Atlantic, as they already do south of the North Carolina ecotone.

There are several factors that may contribute to the interannual patterns in pinfish abundance and their variable dominance.

First, pinfish — like all ectotherms — have thermal optima that promote maximum recruitment and growth (Sunday et al. 2012). Many investigations have actually focused on establishing the lower thermal limits of pinfish, motivated by cold snaps leading to fish kills in places like Texas (Bennett & Judd 1992, Bennetti & Judd 1992, Reber & Bennett 2007). However, the thermal optimum for pinfish has yet to be established in formal lab experiments, as far as we can ascertain. Based on their observed range, FishBase suggests a thermal midpoint of 24.3°C (https://www.fishbase.se/summary/3576, cited there as pers. comm.), and other experiments have established increased metabolic demands (i.e. thermal stress) above 20°C through >30°C (Wohlschlag et al. 1968, Cameron 1969, Wohlschlag & Cech 1970, Hoss 1974). The average summertime water temperature recorded in South Bay was 24.8°C, very close to the optimum reported by FishBase. While summertime water temperatures within South Bay have increased by about +0.05°C yr^{-1} in the last decade based on our sonde data, this change is not significant based on a simple linear regression ($F_1 = 1.19$, p = 0.29). Nevertheless, should summertime water temperatures continue to remain around or in excess of 25°C, it should still provide excellent conditions for growth of pinfish in the Virginia coastal bays as long as other enabling conditions remain intact (e.g. seagrass habitat).

Second, pinfish — like many fishes along the western Atlantic — occupy the nearshore zone for only part of the year, moving offshore in the winter months to the warmer waters of the Gulf Stream. Thus, their abundances are, in part, constrained by conditions beyond those observed in the coastal bays. We see evidence for this assertion in the significant correlation between local pinfish abundance in Virginia and North Carolina in our linear model, suggesting that the 2 surveys are influenced by factors operating across both regions, with shared time by adults in the Gulf Stream being an obvious linkage. Larvae of many other species of shelf-spawners have been shown to span the boundary at Cape Hatteras, with implications for region-wide recruitment (Govoni & Spach 1999). Little is known about the factors that promote reproduction and larval survival offshore, although pinfish appear to occupy the upper strata of the water column (Darcy 1985) where they may benefit from periods of increased primary production. Chacin et al. (2016) also linked high inshore pinfish abundances to prolonged upwelling off the coast of Florida, which they suggest both increased food availability and enabled cross-shelf transport. Nevertheless, our own data from North Carolina, as well as other studies in Florida (Chacin et al. 2016, Faletti et al. 2019), demonstrate substantial interannual variability even within the historical range of pinfish, indicating that many additional factors are presumably at play. Ultimately, linking offshore conditions with recruitment, development, and delivery of larval pinfish will be key to understanding the two-thirds of unexplained variance in pinfish abundance in our study, and in that of Chacin et al. (2016).

Third, pinfish prefer to settle in structured habitats like seagrass, which provide food and shelter for maturing juveniles (Levin et al. 1997). Seagrass had been absent in the study area of South Bay, Virginia, from the early 1930s to the late 1990s, after which efforts to restore the meadow began in earnest (Orth et al. 2020). By the time the fish trawls were instituted in 2012, the meadows in South Bay proper were already extensive (~1067 ha), although they have continued to expand north and south of the area in which the trawls were conducted (approaching 1976 ha as of 2022). The large extent and relative stability of the core meadow in South Bay where the trawls were conducted likely explains why we did not recover a significant effect of seagrass area in our analysis. Pinfish may also respond to the quality of vegetation, including factors such as percent cover, shoot density, and patchiness (Hovel et al. 2002). Previous studies have shown that pinfish growth is lower in more densely vegetated patches (Spitzer et al. 2000, Harter & Heck 2006), presumably owing to the decreased ability to locate prey (Stoner 1980). The South Bay restoration experienced heat-related die-backs in 2012 and 2015, leading to pronounced reductions (and subsequent

recoveries) in local shoot density (but with minimal impacts to total extent) (Aoki et al. 2020, 2021), and future studies may wish to explore the role of these small-scale changes in affecting broader-scale pinfish densities within the restored meadow.

Loss of ~50% of the seagrass extent in Chincoteague Bay, Maryland, since 2000 (Lefcheck et al. 2017a) demonstrates why trawls there increasingly occurred over unvegetated bottom, and — in conjunction with an increasing distance from the historical ecotone — explains the overall lower abundances of pinfish there. Indeed, the North Carolina survey conducts trawls over a variety of substrates, and pinfish are an order of magnitude more abundant in seagrass than in mudflat and creek habitats: 168 ± 6.69 vs. 38.1 ± 7.51 individuals (mean ± 1 SE) over the 12 yr of the survey, a statistically significant difference based on a 2-sample t-test (t_{1538} = 1.29, p < 0.001). While these surveys do not characterize the substrate beyond 'seagrass habitat,' e.g. in the composition and cover/density of the meadows, it is clear that pinfish respond strongly to the mere presence of structured habitats. Thus, seagrasses represent a logical system in which to preliminarily assess the potential for a range expansion in this species, while future surveys may seek to clarify aspects of the seagrass habitat to which pinfish are responding most strongly.

Counter to our expectations, the results from our passive drifter model did not correlate with periods of high inshore pinfish abundance. Instead, that model predicted highest larval delivery in years of the lowest observed densities (Fig. 4). Without further validation of the HYCOM output driving the drifter model, it is not possible to say whether the interannual variability of drifter delivery is accurate; however, it is worthwhile to consider factors beyond model error that may result in a misalignment between passive tracking of large-scale transport and *in situ* trawl surveys. There are several potential explanations: foremost, that pinfish are massively abundant organisms along their range, and presumably release huge quantities of eggs into the Gulf Stream each year. The resulting larvae likely inundate all inshore areas influenced by the Gulf Stream, where they metamorphose only once they reach a suitable site (Darcy 1985). Thus, it may be that, given the overwhelming numbers of larvae delivered to the inshore areas, juvenile success is mostly a function of the recipient environment, not the originating one (Taylor et al. 2009). Nevertheless, the epicenter of pinfish spawning off the US east coast is unclear (Hildebrand & Cable 1938), and if it occurs farther south along the South Atlantic Bight, it is possible that the coastal

bays in Virginia and especially Maryland have been historically recruitment-limited. Any changes in the position and extent of offshore breeding zone with warming of the Gulf Stream may therefore increase the number of propagules reaching the mid-Atlantic coast and strengthen the observed correlation between abundances in North Carolina and Virginia. Identifying where and when pinfish spawn offshore, and the fate of the recruits, is a ripe avenue for future investigation.

However, the focus on transport processes ignores that larvae also respond to the physical environment offshore and require sufficient food resources to survive (Chacin et al. 2016). Springtime water temperature in the southern end of the Mid-Atlantic Bight (MAB) has been shown to increase at a rate of 0.63°C decade^{-1} for the period 1977 to 2016, the second fastest of any region in the MAB. Moreover, half of the temperature increase in the southern MAB can be attributed to a direct warming of the shelf water (salinity < 34 psu), while the other half can be attributed to the intrusion of warm and salty offshore water onto the shelf at depths (Wallace et al. 2018). These types of offshore water intrusions, often modulated by wind forcing, would provide a physical mechanism for transporting larval pinfish across the shelf-break front of the southern MAB. While our drifter model did incorporate surface and subsurface processes and temperature for a few years, additional data on thermal tolerance of both adults and larvae as well as diet information and resource availability with respect to conditions in the Gulf Stream would improve future efforts to model pinfish recruitment in this part of the world. At the same time, investigation of alternative transport mechanisms, extending HYCOM predictions to additional years, and application of more resolved regional models (e.g. ROMS DOPPIO) may yet reveal a role for offshore processes in determining the abundance and distribution of pinfish along the mid-western Atlantic.

Another potential mechanism for transporting pinfish larvae or juveniles into these warmer coastal bays is entrainment of these individuals in warm core rings (WCRs) that develop and break off from the Gulf Stream in late spring and migrate across the shelf break into the coastal inlets. WCRs have been shown to transport individuals of finfish species (e.g. *Pomatomus saltatrix*) from spawning grounds to nursery habitats (Warlen & Burke 1990). Given that larval pinfish are present in offshore gulf waters, development and movement of WCRs could bring larvae onto the continental shelf. Cross-shelf processes such as saline intrusions and Ekman transport could then bring them into the coastal inlets. Indeed, our preliminary

analysis of offshore temperatures from satellite images revealed what appeared to be WCRs present when pinfish abundances were expected to be in offshore gulf waters. These rings were present when pinfish were present in the coastal bays in higher-than-normal abundances, and not present when pinfish abundances were low or absent. We believe that, because these WCRs are transient and their interaction with the shelf break tends to be short-lived and unpredictable, most models are unable to capture the full spatial and temporal dynamics of their movements. Model predictions of tracers' paths around the vicinity of WCRs are usually highly uncertain and remain a challenge, but innovations in this space could provide significant insight into how and why pinfish arrive in mid-Atlantic coastal bays.

Given that pinfish are such strong interactors south of the ecotone, it is likely that their presence and increased abundance in coastal areas north of the ecotone will have implications for the ecology and ecosystem functioning of seagrass meadows there. Foremost is the fact that adult pinfish (>10 cm TL) will directly consume the plant itself (Stoner 1980), in contrast to almost all temperate fish and invertebrate grazers in the mid-western Atlantic (Heck et al. 2021). Heck et al. (2015) suggest that the abundance of adult-sized pinfish in the Gulf of Mexico is sufficiently low to prevent overgrazing of the seagrass (<1 m^2). However, pinfish exceeding the size at which they convert to omnivory have been observed in our Virginia surveys (Fig. S1), and constitute an increasing proportion of the fish community, particularly later in the summer. For example, pinfish that are >10 cm TL comprised 46.4% and 67.9% of the total catch during August and September in 2015 and 2022, respectively. In 2022, the year of highest pinfish abundance, there were on average 49.5 individuals per 100 m tow in late summer meeting this size threshold. While there is not much evidence that eelgrass *Zostera marina* comprises a large proportion of the pinfish's diet (Adams 1976a), it is also because this species has not been the dominant benthic substrate in its usual range. Whether and how pinfish may impact eelgrass in Virginia and beyond remains to be seen.

Complicating matters is that, while pinfish respond positively to warming in our analysis (Fig. 5B), eelgrass is particularly susceptible to rising temperatures and has experienced significant temperature-driven losses in the nearby Chesapeake Bay (Lefcheck et al. 2017b). Pinfish are also voracious predators of small crustaceans (Stoner 1980), which are highly abundant in the restored seagrass meadow (Lefcheck et al. 2017a). While pinfish have the potential to mas-

sively accelerate the movement of energy through the food web (Nelson et al. 2013), these invertebrates constitute an important feedback loop in seagrass meadows by removing the blades of fouling epiphytes (Orth & Van Montfrans 1984). Loss of these mesograzers may therefore have cascading effects that further compound temperature stress by increasing microalgal competition for light and nutrients.

Bates et al. (2014) propose a formal framework to describe how species are moving beyond their historic ranges. While pinfish have been present north of the ecotone at Cape Hatteras for many decades (Sobocinski et al. 2013) (our Fig. 2), they have been so at such low abundances as to be functionally absent. In this analysis, we show that increasing summertime nearshore temperatures are enhancing densities of pinfish in the mid-western Atlantic coastal bays in Virginia, in quantities that approach and even match their observed dominance south of the ecotone. Thus, we have satisfied both the arrival and population increase criteria of Bates et al. (2014), and we are left only to show that pinfish maintain a persistent inter-annual presence in Virginia for it to qualify as a true range expander. As there are few if any year-round fish residents in these coastal bays, persistence would be characterized as increasing in the frequency of years in which pinfish dominate the fish assemblage. Since pinfish have only dominated in 2 of the last 10 yr (Fig. 3), there is still scope for this phenomenon of tropicalization to play out fully in Virginia.

Continued surveys along the coast, including those in the Maryland coastal bays, are imperative for charting the further northward migration of pinfish or other subtropical range expanders, such as grouper and snapper. Extending the timing of surveys towards earlier and later months will also help to address another criterion put forth by Bates et al. (2014), namely, increased intra-annual occupancy. At the same time, multispecies surveys may shed light on contraction of cool-water species, such as silver perch *Bairdiella chrysoura*, which remains the other dominant species in the Virginia trawls. In the meantime, it will be equally important to study and anticipate the ecosystem consequences of more stable and abundant pinfish populations north of the historical ecotone to ensure the integrity of seagrass ecosystems there, and particularly of the restoration site in South Bay, Virginia.

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