



Gulf Stream intrusions associated with extreme seasonal fluctuations among larval fishes

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ABSTRACT: Change in phenology is one of the hallmarks of global climate change. In marine fishes, warming is expected to cause the advancement of a spring peak in larval occurrence or the delay of a fall peak. However, empirical evidence has not consistently upheld this broad prediction, implying that more nuanced hypotheses are needed. Our study investigates oceanic impacts on fish phenology by examining patterns in larval occurrence on the Northeast US continental shelf, one of the most rapidly warming regions of the global ocean. We use data from NOAA's Ecosystem Monitoring Program, which samples larval fish taxa across the shelf on a bimonthly basis. The sampling program began in 1999, thus documenting changes during a period of rapid warming. We calculated the central tendency of seasonal larval occurrence for 38 taxa and tested for temporal relationships with oceanic drivers thought to influence larval seasonality in other ecosystems. We did not find evidence for warming-related changes in larval phenology over the last 2 decades. Rather, we found high interannual variability in larval timing among many populations, especially those along the shelf break. Among examined factors, salinity maximum intrusions associated with Gulf Stream warm core rings showed the strongest explanatory power for variation in larval phenology. Additionally, the occurrence timing of highly variable larval populations overlapped with that of salinity maximum intrusions. Our results suggest that uniform phenological responses to warming are unlikely in this ecosystem, and that hydrodynamic processes connecting widely dispersed regions can strongly influence the phenology of fish.

KEY WORDS: Climate change · Salinity maximum intrusions · Larval fish · Northeast US continental shelf · Large marine ecosystem · Phenology

1. INTRODUCTION

For many organisms, life history events exhibit seasonality rather than occurring year-round. The seasonal timing (i.e. phenology) of reproduction can maximize survival and growth of offspring under dynamic environmental conditions (Cushing 1974, Donahue et al. 2015). Numerous environmental and

biological conditions, including temperature (Genner et al. 2010, Laurel et al. 2021), photoperiod (Pankhurst & Porter 2003, Varpe & Fiksen 2010), hydrodynamic forcing (Parrish et al. 1981, Anderson & Beer 2009, Asch 2015, Donahue et al. 2015, Thaxton et al. 2020), predator and prey abundance (Schweigert et al. 2013, Boldt et al. 2019), and population size and age structure (Ware & Tanasichuk 1989, Carscadden et al.

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1997, Jansen & Gislason 2011, Millner et al. 2011, Calhhan et al. 2015), have been shown to influence the reproductive phenology of fishes. In many ecosystems, climate change is causing spring-spawning fishes to reproduce earlier in the year and fall-spawning fishes to do so later (Pankhurst & Munday 2011, Poloczanska et al. 2013). For organisms that reproduce in summer, the period of reproductive activity is hypothesized to become prolonged, whereas winter spawners are projected to experience a shorter reproductive season (Asch & Erisman 2018, Asch 2019, Langan et al. 2021).

However, due to the multivariate nature of influences on fish reproductive phenology, not all species are likely to follow such straightforward trajectories (Asch et al. 2019). Phenologies of both prey and predators are changing simultaneously, but the drivers of and responses to seasonality changes can be species-specific. For these reasons, future asynchrony in the seasonal timing of trophic interactions, resulting in 'mismatches' between species, has been hypothesized (Cushing 1990, Asch et al. 2019, Ferreira et al. 2020). Such mismatches can affect growth and survival of early life history stages of fishes, resulting in potential declines in recruitment (Logerwell et al. 2003, Schweigert et al. 2013, Ferreira et al. 2020), which in turn can have economic ramifications for commercially and recreationally important species. In extreme cases, phenological mismatches can jeopardize the persistence of species and the fisheries that depend on them (Willis et al. 2008, Lindley et al. 2009, Anderson et al. 2013, Burkle et al. 2013).

Early work examining phenological mismatches between fishes and lower trophic levels assumed that fish reproductive phenology was nearly constant, with minimal interannual variability (Cushing 1974, Cushing 1990, Durant et al. 2007, Neuheimer & McKenzie 2014). More recently, a meta-analysis summarized multidecadal trends in larval fish reproductive phenology, showing spring occurrence advancing $11.2 \text{ d decade}^{-1}$ on average (Poloczanska et al. 2013). Some taxa are exhibiting much faster observed or modeled rates of change (Juanes et al. 2004, Langan et al. 2021, Gokturk et al. 2022). It should be noted that identification of timing change is sensitive to choice of phenology metric (Ji et al. 2010), with some metrics less robust to noisy data (e.g. seasonal duration, as in Langan et al. 2021) and others less capable of detecting small-scale changes (e.g. seasonal center of gravity, as in Gokturk et al. 2022). Less research has been done on interannual and decadal variability in fish phenology at an assemblage level, but the evidence suggests that short-term fluctuations can be

substantial, at times even exceeding the signal associated with climate change trends. For example, marine heat waves have precipitated changes in phenology as large as 2–3 mo among small pelagic fishes (Auth et al. 2018). Often, interannual variations in fish reproductive and migratory timing are associated with temperature changes caused by regional modes of climate variability, such as the El Niño–Southern Oscillation (Asch 2015), the North Atlantic Oscillation (Drinkwater et al. 2003, Sims et al. 2004), and the Atlantic Multidecadal Oscillation (Nye et al. 2014, Langan et al. 2021). However, at times, the effects of climate variability on fish phenology may be modulated by food web changes rather than a direct physiological response to temperature changes (Beare & McKenzie 1999, Beaugrand et al. 2003).

Interannual variations in fish phenology may be especially pronounced in ecosystems, such as the Northeast US (NEUS) continental shelf, that are subject to substantial climatic variability and change (Friedland & Hare 2007, Greene et al. 2013, Thomas et al. 2017, Gonçalves Neto et al. 2021). The NEUS continental shelf is among the fastest warming ocean regions globally, with temperatures rising at an average rate of $0.04^\circ\text{C yr}^{-1}$ and a steep recent increase in the frequency of marine heat waves (Mills et al. 2013, Chen et al. 2015, Pershing et al. 2015, Gawarkiewicz et al. 2019, Tanaka et al. 2020), although temperature changes are not spatially or temporally uniform (Kavanaugh et al. 2017, Chen et al. 2021, Mills et al. 2024). Another major recent physical change in this ecosystem is the observed stepwise increase in Gulf Stream warm core rings and their intrusion onto the NEUS continental shelf since 2000 (Gangopadhyay et al. 2019, Silver et al. 2023). Warm core rings are large (~100 km diameter) eddies that break off the Gulf Stream on its northern flank and propagate westward, transporting warm water towards the shelf (Saunders 1971, Bisagni 1983). These rings are a meaningful heat source in the region, with an additional 0.1 PW of heat added to the Slope Sea since 2000 attributed to the stepwise increase in the number of warm core rings generated (Silver et al. 2021). In addition to transporting warmer waters, warm core rings can impact salinity—specifically, Gulf Stream rings are strongly associated with intrusions of high-salinity water (at least 0.2 psu higher than ambient water masses) at midwater depths (10–30 m; Gawarkiewicz et al. 2022, Silver et al. 2023). The observed frequency of salinity maximum (S_{max}) intrusions in the NEUS has also increased in a stepwise fashion since 2000, with 72.3% of these intrusions associated with the local presence of a warm core ring (Silver et al. 2023).

We expect changing environmental conditions on the NEUS to have both direct and indirect consequences on larval fish phenology. Irregular transport of larvae by Gulf Stream warm core rings may contribute to variable abundance and distribution on the shelf (Flierl & Wroblewski 1985, Hare et al. 2002). Warm core rings also have the potential to affect nutrient distributions and primary productivity in the upper ocean (Nelson et al. 1989, Chen et al. 2021). Ocean warming in the NEUS is altering the timing of autumn phytoplankton blooms, although these changes vary by location (Friedland et al. 2023). Multidimensional changes to phytoplankton dynamics may impact the timing of larval fish occurrence through food availability (Bikhtashev et al. 2003, Asch et al. 2019). Temperature may more directly influence larval occurrence as a cue of reproductive initiation. While many fish species in the NEUS are known to spawn later as latitude increases or decreases, tracking a preferred spawning temperature (Berrien & Sibunka 1999, Neuheimer & MacKenzie 2014), how this translates to the interannual-to-decadal time scales of ocean warming is not well understood. Uncertainty therefore remains as to whether the hypothesized impacts of changing temperatures on larval fish phenology (Pankhurst & Munday 2011, Anderson et al. 2013, Staudinger et al. 2019) hold true on the NEUS continental shelf. The one assemblage-wide study of larval occurrence on the NEUS showed some alignment with predictions (Walsh et al. 2015), but we do not know if or how these trends have continued in the rapidly warming years since 2008, nor do we understand how any directional changes in phenology among larval fish compare to underlying interannual variability.

Thus, the present study aims to develop a robust understanding of recent fluctuations in larval fish phenology across the entire NEUS shelf. Using data from frequent shelf-wide surveys since 1999, we assessed whether assemblage-wide changes in phenology align with general predictions for a rapidly warming system. We hypothesized that given observed differences in warming trends by depth (Kavanaugh et al. 2017), adult habitat (i.e. benthic vs. pelagic) would explain differences in phenological trends between species. Bottom-dwelling adult fishes are thought to be less sensitive to shifting temperatures than their pelagic counterparts (Montero-Serra et al. 2015, Petrik et al. 2020, Roberts et al. 2020). In addition, warming on the NEUS shelf has been vertically heterogeneous, and thus benthic and pelagic species have experienced different exposure to temperature change in recent years (Kleisner et al. 2016,

Kavanaugh et al. 2017). To enhance our understanding of phenological change, we also evaluated phenological variability and how it changes taxonomically, seasonally, and spatially across this broad region. Finally, we determined which environmental variables and species traits were most likely responsible for observed patterns. We specifically tested for the impacts of Gulf Stream ring-associated intrusions on larval phenology, which have not been previously examined. Understanding phenological changes on the NEUS continental shelf is key to forming a complete picture of warming impacts on its economically valuable fisheries (Le Bris et al. 2018). Observations in this rapidly warming region may also portend future climate change effects in other parts of the global ocean that have not yet experienced temperature changes of the same magnitude as the NEUS.

2. METHODS

To examine trends in larval fish phenology, we used data from the Northeast Fisheries Science Center's Ecosystem Monitoring (EcoMon) program—the most temporally and spatially extensive plankton survey of the NEUS. EcoMon surveys occur every other month and randomly sample 47 geographic strata. Strata are grouped into the following regions: Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB), and Gulf of Maine (GOM). Strata are also classified into oceanic provinces: coastal, inner shelf, middle shelf, shelf break, bank, and basin (Fig. 1). In this study, the term 'region' refers to the latitudinally segregated biogeographic zones, while 'province' refers to habitats found across distinct segments of the continental shelf.

The EcoMon survey collects ichthyoplankton using a 61 cm diameter bongo frame with a 333 μm mesh, towed obliquely at approximately 1.5 knots. Tow duration is at least 5 min, and tow depth is within 5 m from the bottom, or a maximum depth of 200 m for deeper waters. Double oblique tows occur during both day and night. Mechanical flowmeters mounted on the net allow for the calculation of total volume of water filtered (NOAA Fisheries Northeast Fisheries Science Center 2019). Starting in 1999, ichthyoplankton have been identified to the lowest taxonomic level possible by the Sea Fisheries Institute Sorting and Identification Center in Poland, with data reported in units of individuals per 10 m^2 for each tow (Ejsymont & Sherman 2000, Richardson et al. 2010). Our analyses run from 1999 through 2019, the last year before COVID-19 pandemic disruptions in sampling.

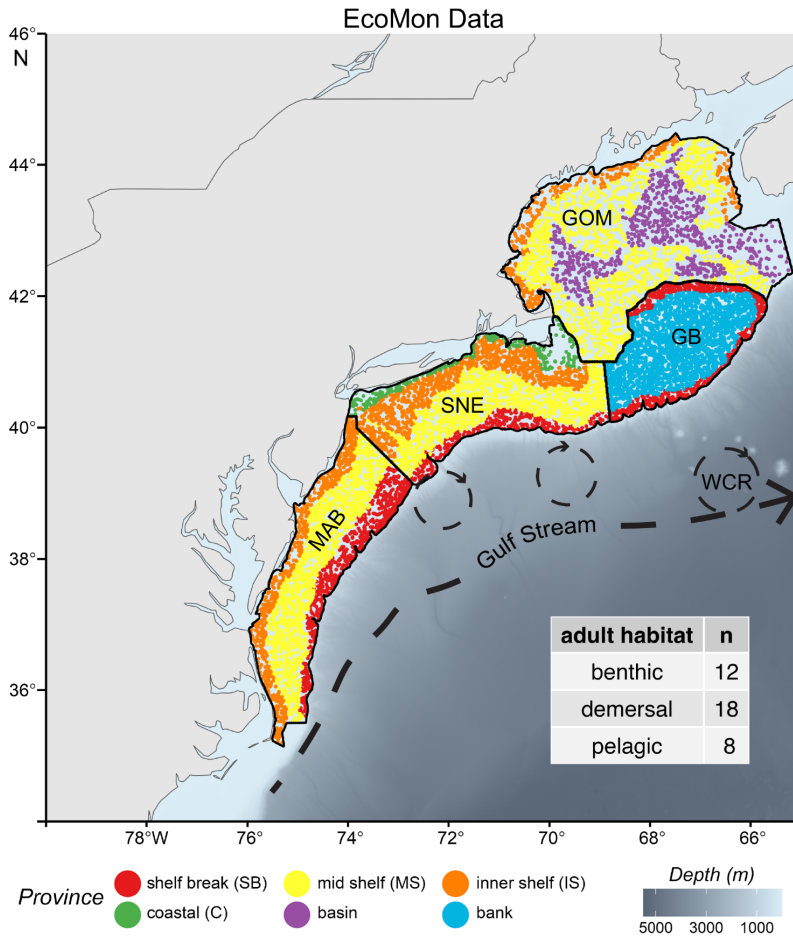


Fig. 1. Spatial distribution of EcoMon sampling effort. Points: plankton tows; colors: oceanic provinces; black lines: represent regions (GOM: Gulf of Maine; GB: Georges Bank; SNE: Southern New England; MAB: Mid-Atlantic Bight). Black dashed lines: trajectories of the Gulf Stream and its warm core rings (WCR). The table indicates the number of species (n) per adult habitat type—category utilized for this analysis

We grouped the ichthyoplankton data by province within each region and analyzed unique species–region–province combinations. For example, we consider goosefish *Lophius americanus* larvae found in the SNE inner shelf separately from goosefish larvae found in the SNE middle shelf and in the MAB inner shelf (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m739p157_supp.pdf). Some organisms can only be identified to the genus level (see Table 1). We grouped these data into unique genus–region–province combinations. Hereafter, we refer to species–(or genus)–region–province combinations as larval fish ‘populations’ as in Sabatés (1990). We excluded rare populations from the analysis by removing any populations that contained less than 5% of that year’s taxa-specific abundance. Due to region and province subsetting, tem-

poral coverage was incomplete. To take advantage of the whole data set while accounting for these gaps, we binned the data into 5 subsets of 4 years each (year bins: 1999–2002, 2003–2006, 2007–2010, 2011–2014, and 2015–2019) such that each subset contained data for each region and province combination (Fig. S2). This was the fewest possible years per bin for which all combinations of region, province, and bimonthly sampling period were represented. Sensitivity testing showed that our choice of binning window did not significantly impact results (Table S1).

We calculated the central tendency (CT) of larval abundance (Eq. 1) for each population within each year bin. Sometimes referred to as the seasonal center of gravity, CT has been used to track changes in the reproductive and migratory phenology of multiple fish stocks in the North Atlantic and North Pacific (Edwards & Richardson 2004, Jansen & Gislason 2011, Asch 2015, Thorson et al. 2020). CT is a weighted average where the larval abundances are the weights and the bimonthly sampling period (a month proxy) is the value. Month proxy values are 1 for January–February, 2 for March–April, 3 for May–June, 4 for July–August, 5 for September–October, and 6 for November–December. We calculated

total abundance per cruise for each species by multiplying stratum area by average areal density per stratum and then summing:

$$CT_{\text{species}} = \frac{\sum_{i=1}^6 (\text{abundance}_i \times \text{month proxy}_i)}{\sum_{i=1}^6 \text{abundance}_i} \times 2 \quad (1)$$

In Eq. (1), we multiply by 2 so the resultant CT is on the familiar 0–12 scale for months of the year, with 0 representing January 1st and 12 representing December 31st. There are many metrics for identifying phenological change (Rolinski et al. 2007, Ji et al. 2010, Mackas et al. 2012, Brody et al. 2013). Ji et al. (2010) compared several of these methods and found that CT was a better indicator when sampling was temporally sparse (monthly to bi-monthly) and provided a relatively conservative estimate of change.

The CT metric as we have defined it here is challenging to calculate for larval populations that occur during winter. Species whose larvae occur in both December (month proxy 6) and January (month proxy 1) might appear to occur in May–June (month proxy 3) when we average their month proxies. Winter-occurring larvae, as identified empirically from the EcoMon data, represented 35% of populations (Table S2). For simplicity, we decided to exclude these winter populations from our analyses.

To create confidence intervals (CIs) around CT to inform our understanding of CT variability, we performed a bootstrapping routine. First, one year bin was selected. Then we determined how many tows (n_{tow}) occurred in that year bin. Next, we randomly sampled the tows with replacement, n_{tow} times. Using resampled data, we calculated the abundance per stratum and determined the CT for each species based on Eq. (1). We repeated this process 1000 times, recording the CT each run for each species and year bin. We used the results of this bootstrapping to calculate the mean_{CT} (for each of the 5 yr bins and an overall mean) and the range in CT (the width of the 95% CI, based on bootstrapping range_{CT}) for each population. Our resulting data set of mean_{CT} and range_{CT} consisted of 38 species with 143 unique populations (Fig. 1, Table 1).

To test our hypothesis that a warming NEUS could cause linear shifts in larval occurrence, such as earlier larval occurrence in spring spawners or later larval occurrence in fall spawners, we ran a linear regression on mean_{CT} and year bin for each of the 143 populations, treating each population as a separate data set.

Next, we examined several environmental variables to see which would best explain phenological variability. Sea surface temperature, bottom temperature, sea surface salinity, and bottom salinity from CTD sensors were included in the EcoMon data set (NOAA Fisheries Northeast Fisheries Science Center 2019). We determined the mean, standard error, range (width of the 95% CI), CT, and CT's standard error for each of these environmental variables. We also examined S_{max} intrusions (Gawarkiewicz et al. 2022), which is indicative of Gulf Stream ring influence (Silver et al. 2023). We used the presence or absence of an S_{max} intrusion in an EcoMon CTD cast from the data set created by Gawarkiewicz et al. (2022). We also calculated the mean, CT, and standard error of frequency of the S_{max} for each region–province combination. In addition to these environmental variables, we included province, region, and adult habitat as categorical, independent variables in our analyses.

Adult habitat was set as either pelagic, demersal, or benthic by searching the literature and FishBase for the section of the water column most commonly used by adult fish of each species (Froese & Pauly 2000, McHenry et al. 2019). We also included adult habitat classifications from Walsh et al. (2015) as a separate variable, as these did not always align with our literature search results. Table S3 lists all 31 explanatory variables.

We examined variability in CT in all further analyses. We performed a series of mixed effect generalized linear models ('glmmTMB' package in R, version 3.6.2) with range_{CT} of larval abundance as the response variable, species (or genus) as a random effect, and looped through each of our 31 explanatory variables, calculating the Akaike information criterion (AIC) as a metric to assess model performance. AIC adjusts for degrees of freedom, which is required when having continuous and categorical explanatory variables (Burnham & Anderson 2002). Since we examined AIC for each explanatory variable independently, we did not consider multicollinearity. Also, we did not assess multiple comparison issues, as no significance testing was performed. Our response variable was non-negative and continuous, so we tested model fitting using either a Tweedie distribution or a Gaussian distribution. We determined that the Tweedie distribution fit the data best (see Text S1, Supplementary Methods, for more details on mixed effects modeling).

To understand whether certain times of the year and/or regions were characterized by large phenological variability, we ran mixed effect models to examine the effect of mean_{CT} on range_{CT} while accounting for the random effect of species. We tested the significance of the fixed effect (mean_{CT}) using a likelihood ratio test by running an ANOVA comparing the model with only the intercept and random effect of species to the same model with mean_{CT} added. Significance was calculated using a χ^2 distribution. We then visualized the marginal effect of mean_{CT} .

Next, to test spatial differences in environmental conditions across the large NEUS region, we conducted a series of principal component analyses (PCAs) on the environmental variables grouped by region, province, and year bin. Since there was no S_{max} intrusion data in the GOM, we ran separate PCAs with and without this region. Variables were scaled by their mean and standard deviation prior to the PCA. The PCA was computed by a singular value decomposition of the scaled data matrix ('stats' package in R, version 3.6.2). We report the first 2 principal

Table 1. Details of all taxa included in analyses. Taxon abbreviations are from the EcoMon data set. Adult habitat is based on a literature review (Froese & Pauly 2000, McHenry et al. 2019). See Fig. 1 for region abbreviations

Taxon	Common name	Abbreviation	Adult habitat	Region(s)
<i>Ammodytes</i> spp.	Sand lance	ammspp	Benthic	GB, SNE
<i>Auxis</i> spp.	Tunas	auxspp	Pelagic	MAB, SNE
<i>Benthoosema</i> spp.	Lanternfishes	benspp	Pelagic	GB, GOM, MAB, SNE
<i>Bothus</i> spp.	Lefteye flounders	botspp	Benthic	GB, SNE
<i>Centropristis striata</i>	Black sea bass	centstr	Demersal	MAB, SNE
<i>Ceratospopelus maderensis</i>	Madeira lanternfish	cermad	Pelagic	GB, SNE
<i>Citharichthys arctifrons</i>	Gulf stream flounder	citarc	Benthic	MAB, SNE
<i>Cyclothone</i> spp.	Bristlemouths	cycspp	Pelagic	GB, SNE
<i>Cynoscion regalis</i>	Weakfish	cynreg	Demersal	MAB
<i>Diaphus</i> spp.	Lanternfishes	diaspp	Pelagic	GB, SNE, MAB
<i>Enchelyopus cimbrius</i>	Fourbeard rockling	enccim	Demersal	GOM, SNE
<i>Etropus</i> spp.	Large-tooth flounders	etrsp	Benthic	MAB, SNE
<i>Glyptocephalus cynoglossus</i>	Witch flounder	glycyn	Benthic	GB, GOM, MAB, SNE
<i>Hippoglossina oblonga</i>	Fourspot flounder	hipobl	Benthic	GB, SNE, MAB
<i>Hippoglossoides platessoides</i>	American plaice	hippla	Benthic	GB, GOM, SNE
<i>Limanda ferruginea</i>	Yellowtail flounder	limfer	Benthic	GB, SNE
<i>Lophius americanus</i>	Goosefish	lopame	Benthic	GB, GOM, MAB, SNE
<i>Melanogrammus aeglefinus</i>	Haddock	melaeg	Demersal	GB, GOM, SNE
<i>Menticirrhus</i> spp.	Kingfish	menspp	Demersal	MAB
<i>Merluccius albidus</i>	Offshore hake	meralb	Demersal	GB, SNE, MAB
<i>Merluccius bilinearis</i>	Silver hake	merbil	Demersal	GB, GOM
<i>Myoxocephalus aeneus</i>	Little sculpin/grubby	myoae	Demersal	GB, GOM, SNE
<i>Myoxocephalus octodecemspinosus</i>	Longhorn sculpin	myooc	Demersal	GB, GOM, SNE
<i>Peprilus</i> spp.	Butterfish	pepspp	Pelagic	SNE
<i>Pholis gunnellus</i>	Rock gunnel	phogun	Demersal	GB, GOM, SNE
<i>Pollachius virens</i>	Pollock	polvir	Demersal	SNE
<i>Pomatomus saltatrix</i>	Bluefish	pomsal	Pelagic	MAB
<i>Prionotus</i> spp.	Sea robins	prispp	Demersal	GB, SNE, MAB
<i>Pseudopleuronectes americanus</i>	Winter flounder	pseame	Benthic	GB, SNE
<i>Scophthalmus aquosus</i>	Windowpane flounder	scoaqu	Benthic	GB, SNE
<i>Scomber scombrus</i>	Atlantic mackerel	scosco	Pelagic	GOM, SNE
<i>Sebastes</i> spp.	Rockfishes/redfishes	sebspp	Demersal	GB, GOM
<i>Syacium</i> spp.	Large-tooth flounders	syaspp	Benthic	GB, SNE, MAB
<i>Symphurus</i> spp.	Lefteye flatfishes/tonguefishes	sypspp	Demersal	MAB
<i>Tautoglabrus adspersus</i>	Cunner	tauads	Demersal	GB, GOM, SNE
<i>Tautoga onitis</i>	Tautog	tauoni	Demersal	GOM, SNE, MAB
<i>Ulvaria subbifurcata</i>	Radiated shanny	ulvsub	Demersal	GOM, SNE
<i>Urophycis</i> spp.	Hakes	urospp	Demersal	GOM, SNE

components, as well as the top 2 loadings (absolute value of eigenvectors) from each principal component (4 loadings total).

Finally, we ran 2 comparison tests to assess how phenology varies across space. We explored how the range of larval CT differs across provinces using a Fisher's exact test to account for small expected values in the basin province, separating variability into quartiles (lowest, low, high, and highest). We utilized a Kruskal-Wallis test to compare differences in mean CT across provinces, given that our data failed to pass the assumption of normality required for a parametric ANOVA (Shapiro-Wilks normality tests with $p < 0.05$ for the following provinces — Basin: W

(Shapiro-Wilks) = 0.751, $p = 0.003$; inner shelf: $W = 0.926$, $p = 0.012$; shelf break: $W = 0.818$, $p = 0.001$).

3. RESULTS

Despite steady warming in the NEUS over the last decades, we did not observe expected linear trends in larval phenology. The 143 populations examined, which excluded larvae that occur in winter, showed a range in their mean_{CT} (minimum: 2.521 [approximately 17 March]; maximum: 10.682 [approximately 21 November]; median: 7.428 [approximately 14 August]; standard deviation: 2.020 months; Fig. 2A). Out

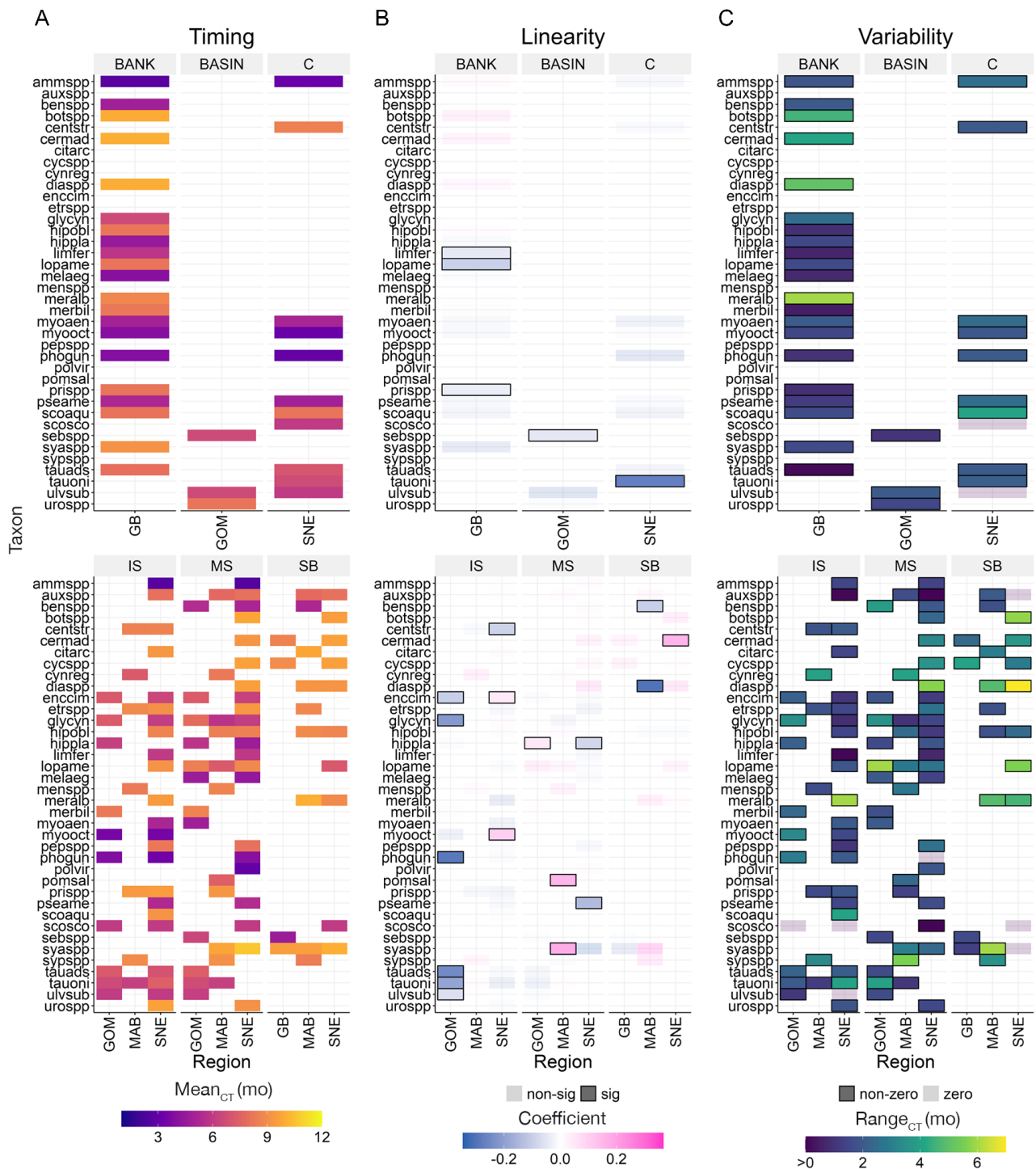


Fig. 2. (A) Mean central tendency (mean_{CT}) of larval abundance for each taxon, separated by region and province. Cool colors represent earlier CT of abundance; yellow represents later CT. (B) Linearity of trends in CT calculated as a linear coefficient regressing mean_{CT} as a function of year bin (units: months per year bin). Cool colors represent negative regression coefficients; warm colors represent positive coefficients. Darker colors with black borders signify $p < 0.05$. (C) Range in the CT (range_{CT}) of larval abundance calculated as width of the 95% CIs based on bootstrapped data. Darker colors with black borders signify range_{CT} > 0; cool colors represent a narrow range; yellow represents a range of roughly 6 mo; grey signifies range_{CT} = 0. Blanks represent that a particular species, province, or region combination was not included in analyses due to its rare or non-existent occurrence in the EcoMon data set or due to its occurrence in winter months (A,B,C). Full species names given in Table 1; region and province abbreviations as in Fig. 1

of these 143 populations, only 22 (15%) showed a significant trend over time based on linear regression (Fig. 2B & Fig. S1). Of these populations, 6 showed a positive trend in CT (occurrence delayed over time), while 16 were negative (occurrence advancing over time). The advancing group did not have a statistically different mean_{CT} than the delayed group (Fig. S3). In other words, we did not find evidence supporting the idea that the phenology of spring larvae is trending earlier, nor that fall larvae are trending later in the NEUS continental shelf (Fig. 2A,B). Although the statistical power of testing a linear model with 5 data points (one per year bin) is low, visual examination of the data also failed to provide evidence for consistent linear trends (Fig. S2).

Instead of consistent linear trends, we noticed extremely wide ranges in the CT of several populations. Our metric of range_{CT}, the width of the 95% CI of CT, is based on bootstrapped data. Some populations, such as Atlantic mackerel *Scomber scombrus* in the GOM inner shelf, exhibited no variability in CT, meaning this population's phenology was consistent across the analyzed period. However, other populations showed strong fluctuations. For example, off-

shore hake *Merluccius albidus* in the inner shelf province of SNE showed a 6 mo range in its CT. In other words, the 95% CI of the mean time when we expect to see offshore hake larvae on the SNE inner shelf ranged from June to December. Most populations (134 out of 143, or 94%) showed some range in CT, with a median of 1.9 mo (Fig. 2C).

Mixed effects models and correlation analyses helped explain drivers of variability in CT across the 143 larval populations of 38 species. Among the 31 explanatory variables tested in our mixed effects modeling, the best-performing models (those with the lowest AIC values) all related to S_{max} intrusions (Fig. 3A). Specifically, we found positive relationships between the range of larval CT and the variability, timing, and number of S_{max} intrusions. None of the other variables—including those related to timing, variability, and magnitude of temperature and salinity as well as factors describing both adult and larval fish habitat—could explain larval CT variability as well, as evidenced by the fact that AIC values jump from under 200 for S_{max} variables to greater than 230 for all other variables (Fig. 3A).

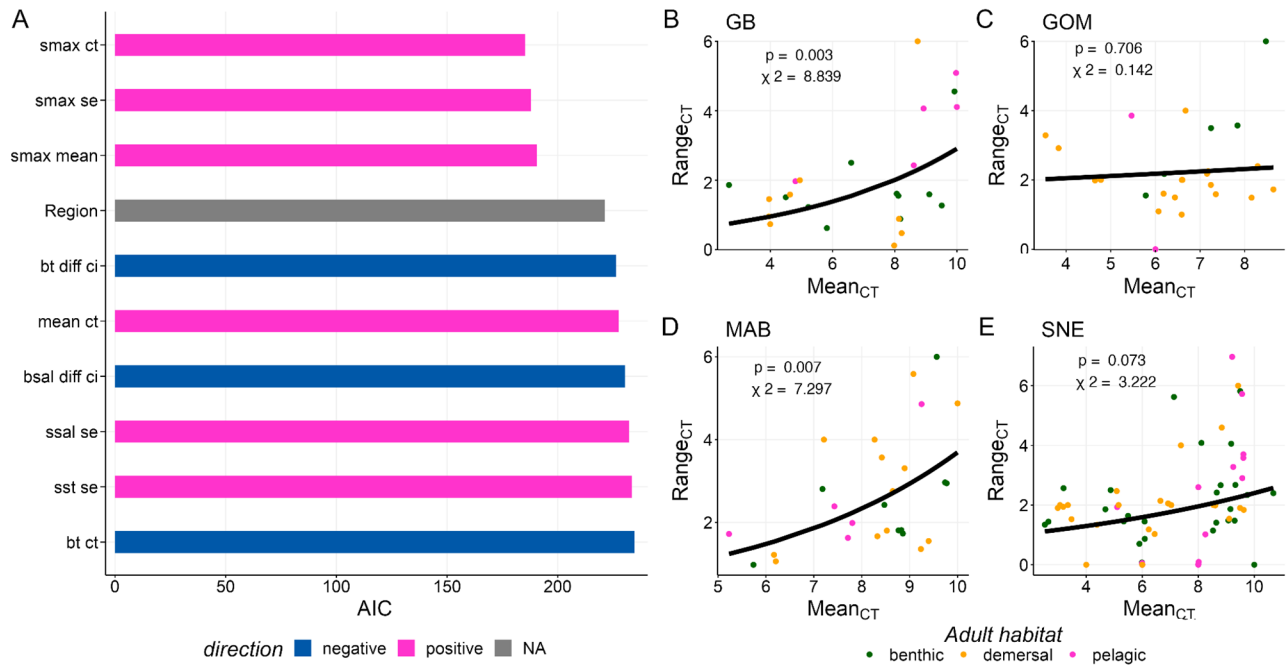


Fig. 3. (A) Akaike's information criteria from generalized linear mixed effect models with central tendency range (range_{CT}) of larval abundance as the response variable, species (or genus) as a random effect, and a Tweedie distribution for modeling the responses. Colors represent positive (pink) or negative (blue) relationships between predictor and response variable coefficients; top 10 variables are shown. (B–E) Regionally separated marginal effect of mean_{CT} on range_{CT}. p-values represent probability of chi-squared test statistic from ANOVA (GB: $\chi^2_1 = 8.8$, $p = 0.0029$; GOM: $\chi^2_1 = 0.14$, $p = 0.7063$; MAB: $\chi^2_1 = 7.29$, $p = 0.0069$; SNE: $\chi^2_1 = 3.22$, $p = 0.0727$), colors represent species' adult habitat, individual points represent populations. See Fig. 1 for region abbreviations; bt: bottom temperature; bsal: bottom salinity; ct: central tendency; diff ci: confidence interval width; smax: salinity maximum intrusions; sst: sea surface temperature; se: standard error; ssal: surface salinity

Another association of note is a positive relationship between seasonality (i.e. a population's mean_{CT} and range_{CT}). Populations with a later CT tended to have wider ranges (Fig. 3B–E). Spatially, we found strong relationships between mean_{CT} and range_{CT} in the MAB and GB (GB: $\chi^2_1 = 8.839$, $p = 0.003$; Fig. 3B; MAB: $\chi^2_1 = 7.297$, $p = 0.007$; Fig. 3D), a weaker relationship in SNE ($\chi^2_1 = 3.222$, $p = 0.073$; Fig. 3E), and no relationship in the GOM ($\chi^2_1 = 0.142$, $p = 0.706$; Fig. 3C). We interpreted this to mean that the underlying driver of the relationship between mean_{CT} and range_{CT} is likely relevant to all regions except the GOM.

PCA further elucidated spatial differences in environmental conditions across the large NEUS region. PCA biplots indicate that clustering is more evident

when grouping data by province than by region. Looking across provinces, we see that the environment in the shelf break differs the most from the other provinces (Fig. 4). The shelf break differs from the other regions in both timing and magnitude of a variety of environmental factors. Most notably, the shelf break has a low CT of bottom temperature (i.e. a tendency towards an early peak in bottom temperature compared to other provinces), a high number of S_{max} intrusions, and high surface salinity (Fig. 4).

To better understand how this spatial heterogeneity might relate to phenology, we explored how both the mean and range of larval CT changed across provinces. Range in larval CT appears to be spatially heterogeneous, with a Fisher's exact test showing

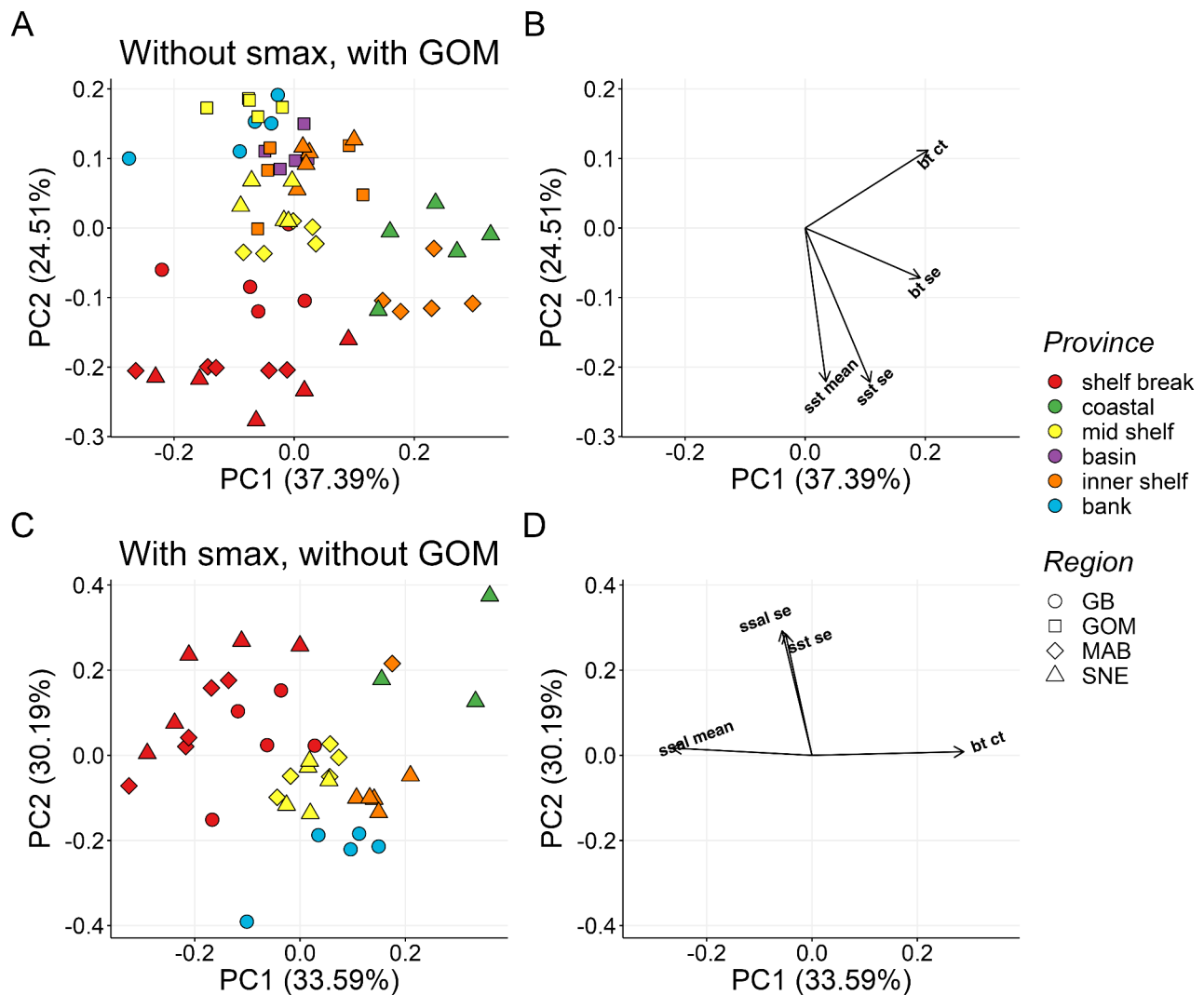


Fig. 4. Principal component analysis for (A,B) all regions and (C,D) removing GOM to incorporate salinity maximum intrusion (smax) information. Top 2 loadings per principal component (PC1 and PC2) are visualized in (B) and (D). Colors represent provinces and shapes represent regions. See Fig. 1 for region abbreviations; bt: bottom temperature; ct: central tendency; sst: sea surface temperature; se: standard error; ssal: surface salinity

that populations with the widest ranges are over-represented on the shelf break ($p = 0.036$; Fig. 5A). Kruskal-Wallis ANOVA testing revealed significant differences in $mean_{CT}$ between provinces ($H = 18.9$, $df = 5$, $p = 0.002$), and post hoc tests showed that the $mean_{CT}$ on the shelf break is significantly later than the $mean_{CT}$ observed in the other provinces (Fig. 5B, see Table S3 for full test statistics). Note that it was difficult to detect differences between the basin and other provinces because the number of examined popula-

tions in the basin was low ($n = 3$). Regional differences are shown in Table S5 & Fig. S4.

Finally, we examined how the timing of S_{max} intrusions might relate to observed timing and variability in larval phenology (Fig. 6). Looking across all populations, we see that the low-variability populations ($range_{CT} < 3$ mo) are equally distributed in their timing (no bias in $mean_{CT}$). However, the high-variability populations ($range_{CT} > 3$ mo) show a strong skew towards later timing (greater $mean_{CT}$; Fig. 6B). The

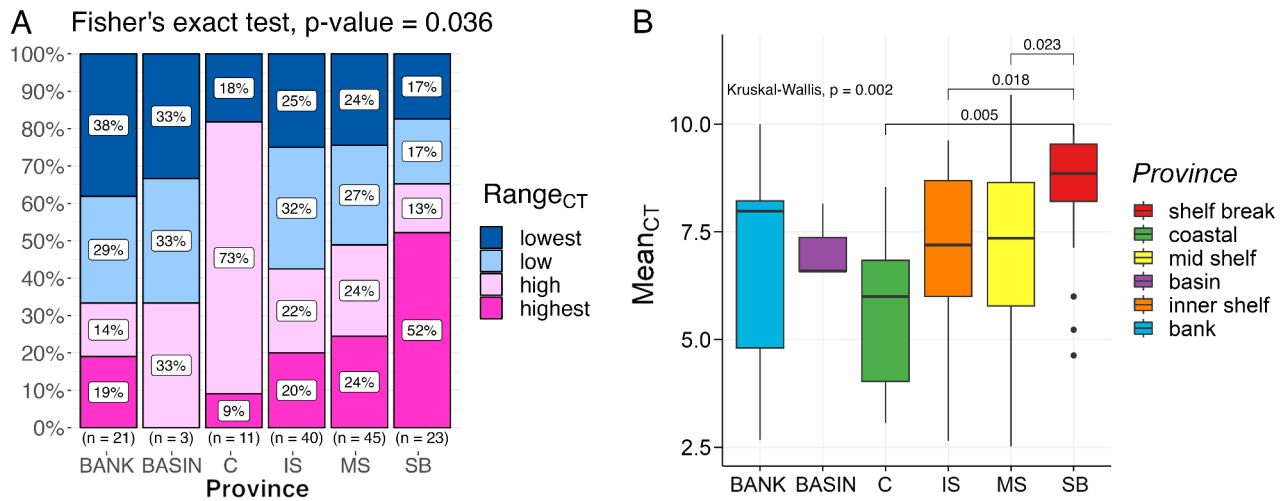


Fig. 5. (A) Fisher's exact test for differences in central tendency range ($range_{CT}$) among provinces. Colors represent quartiles of $range_{CT}$ (lowest, low, high, highest), and proportion of each $range_{CT}$ quartile within each province is noted in white. (B) Kruskal-Wallis differences in $mean_{CT}$ among provinces. Horizontal line: median; boxes: interquartile range; whiskers: 1st and 3rd quartiles $\pm 1.5 \times IQR$; dots: outliers, respectively. Overall Kruskal-Wallis p-value and post hoc Games-Howell p-values noted above each significant comparison, with extended test results presented in Table S4

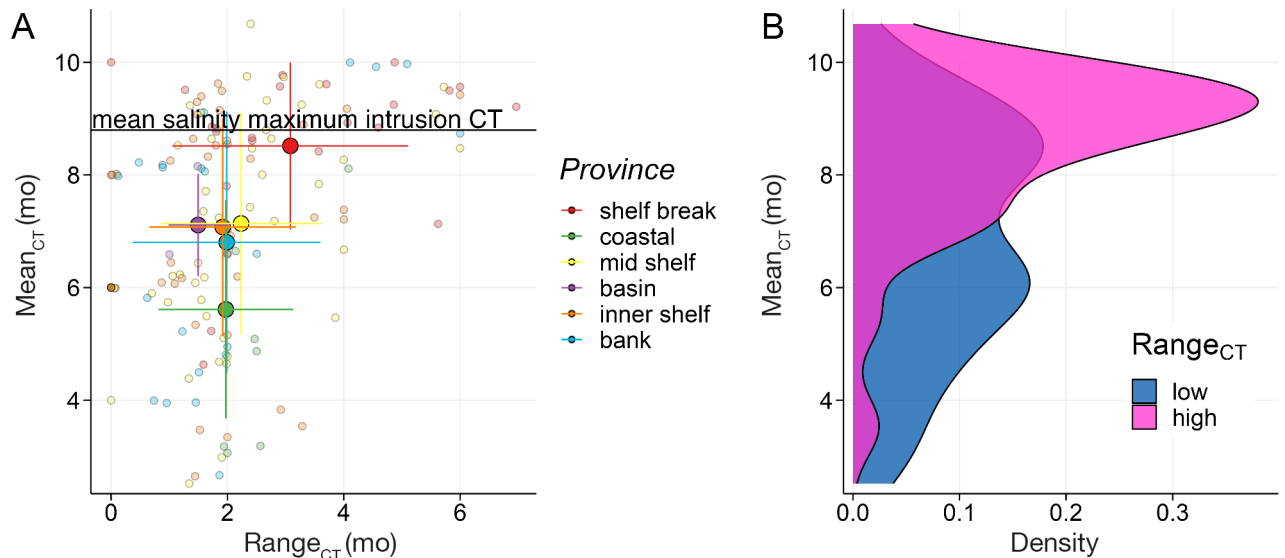


Fig. 6. (A) Central tendency (CT) mean ($mean_{CT}$) versus variability in CT ($range_{CT}$) colored by province. The province average \pm SD is shown in the foreground by larger symbols, with population-level values shown in the background with smaller markers. $mean_{CT}$ of salinity maximum intrusions is noted as a horizontal line. (B) Density of $mean_{CT}$ values associated with narrow $range_{CT}$ (blue, < 3 mo) and wide $range_{CT}$ (pink, > 3 mo)

mean_{CT} of the high-variability populations is 8.4 (approximately 12 August), which is similar to the mean timing of S_{\max} intrusions, which is 8.7 (roughly 21 August).

4. DISCUSSION

Our analyses of phenology across 21 yr of data on 143 populations of 38 species of larval fish in the rapidly warming NEUS failed to show cohesive temporal trends related to temperature but instead revealed strong interannual fluctuations in seasonality in many populations. The cause of this extreme interannual variability is not fully understood, but our analyses suggest that it is related to S_{\max} intrusions tied to the presence of Gulf Stream warm core rings. Across provinces, populations at the shelf break had the latest larval occurrences and were the most variable between years. The shelf break is where the fresher shelf waters meet the saltier Slope Sea (Bigelow & Sears 1935, Greene et al. 2013). Among examined oceanic and ecological factors, S_{\max} intrusions showed the strongest power to explain variations in larval fish phenology. Finally, the timing of populations with high range_{CT} values overlapped strongly with the timing of S_{\max} intrusions, which are midwater depth (10–30 m), high-salinity patches of seawater associated with Gulf Stream warm core rings (Gawarkiewicz et al. 2022, Silver et al. 2023). This suggests that hydrodynamic processes connecting widely dispersed regions can have key influences on the timing of larval fish occurrence. Populations with wide-ranging CT values tended to occur later in all regions except in the GOM. The GOM is the only region without a shelf break province, and relatedly the only region lacking data on S_{\max} intrusions.

Our analyses of CT suggest that even under steady warming, we should not anticipate assemblage-wide, coherent changes in larval phenology, at least not at the temporal resolution possible with bi-monthly sampling. This finding builds on results from Walsh et al. (2015), in which larval data from EcoMon and MARMAP, a similar previously conducted sampling program, were compared between 1999–2008 and 1977–1987. Walsh et al. (2015) reported phenological changes between these 2 decadal periods in roughly half of the species tested, and even fewer (~35%) showed a shift in the seasonality of their peak abundance between the 2 time points. However, Walsh et al. (2015) found that winter and spring larvae shifted earlier, while summer and fall taxa trended later. By contrast, our analyses did not reveal any connection

between seasonality and temporal trends (Fig. S3). Our approach to understanding larval fish phenology on the NEUS differs from that of Walsh et al. (2015) in a few important respects. We focused on phenological variability, which has not previously been reported for NEUS larval fish assemblages. In addition, our spatial analyses differentiated between cross-shelf provinces as well as latitudinal regions. Only the latter were included in previous work on EcoMon data. As a result, we uncovered spatial effects that had previously been undetected. In particular, we found evidence for an impact of warm core ring-associated S_{\max} intrusions on phenological variability.

Our finding of a link between S_{\max} intrusions associated with Gulf Stream warm core rings and larval fish phenology adds new insight to a topic that has been studied for decades. A proposed connection between warm core rings and fish larvae dates back to the 1960s (Colton & Temple 1961). Warm core rings can entrain and transport larvae from southerly latitudes onto the NEUS shelf (Hare et al. 2002) and can also move larvae of NEUS-resident fish off the shelf (Flierl & Wroblewski 1985, Myers & Drinkwater 1989). However, the vast majority of prior research has focused on the impact of warm core rings on larval abundance and fisheries recruitment rather than on phenology, despite evidence that the timing of temperature changes at the shelf break can determine the recruitment timing of some species, such as bluefish *Pomatomus saltatrix*; Hare & Cowen 1996). Furthermore, most work on the relationship between warm core rings and larval fish pre-dates contemporary warming and the observed stepwise increase in annual warm core ring abundance in 2000 (Gangopadhyay et al. 2019), even though such changes are presumed to impact larval transport and recruitment (Silver et al. 2023). Our results suggest that phenology, in addition to abundance and spatial distribution, must be carefully considered if we are to fully understand the implications of recent changes in Gulf Stream and shelf break exchange processes (Andres 2016, Gawarkiewicz et al. 2018, Gangopadhyay et al. 2019) for NEUS fish populations.

In addition to testing the impacts of physical conditions on larval fish phenology in the NEUS, we also tested an explanatory variable based on which section of the water column adults of each species occupy. Although fish experience different environmental conditions and cues in pelagic, demersal, or benthic waters, our hypothesis that adult habitat would significantly affect larval mean_{CT} and range_{CT} was not supported. By contrast, a study on larval fish occurrence in the California Current ecosystem

showed opposite trends in pelagic and demersal species, with pelagic species more likely to exhibit earlier peaks in larval abundance over the years and demersal species showing delays (Asch 2015). The difference between these past results and the present study highlights the importance of examining each ecosystem independently. The changes observed in the California Current system appear to be linked to earlier surface warming in conjunction with delays in the upwelling-related spring transition that is particular to this region (Snyder et al. 2003, Asch 2015), which may help explain why a similar pattern was not observed in the NEUS, which lacks the consistent coastal upwelling characteristic of the US west coast.

It is nonetheless surprising that no significant differences in mean_{CT} or range_{CT} were detected among pelagic and bottom-dwelling taxa, given that stratification leads to differences in surface and bottom temperatures (Mann & Lazier 2005). In the NEUS, these groups are also experiencing differential rates of climate change (Kavanaugh et al. 2017). Benthic and demersal fishes tend to show less sensitivity than pelagic fishes to changing temperatures (Montero-Serra et al. 2015, Petrik et al. 2020, Roberts et al. 2020), and given that temperature is often a strong cue for reproduction (Pankhurst & Munday 2011), demersal and benthic species may also be expected to show less variability in reproductive phenology. However, our finding that temperature did not play a significant role in larval fish phenology suggests that differential temperature sensitivities of adults across species do not necessarily translate into differences in the timing of larval occurrence, at least at the levels of temperature variability experienced in this region. Similarly, a previous study of phenology changes in adult fish in the NEUS did not detect phenological changes despite surface water warming earlier over time and fall temperatures cooling later (Henderson et al. 2017).

One surprising result uncovered by this research was the very large degree of interannual variability in CT in this ecosystem. For example, CT varied by ~5 mo between year bins for offshore hake *Merluccius albidus* found on the bank in GB and the inner shelf in SNE (Fig. S2). Although this example is somewhat extreme, a high rate of variability does not represent an unusual outlier among our data set, as similarly large fluctuations in seasonality were found among some populations of left-eye flounder *Bothus* spp., large-tooth flounder *Syacium* spp., and goosefish *Lophius americanus* (Fig. 2B). This large extent of interannual variability exceeds the rates of change in phenology typically attributed to global warming

among marine fishes in most parts of the world. To illustrate this point, the variability in phenology for *M. albidus* between 2 consecutive 5 yr time blocks corresponds to a change at a rate of roughly 30 d yr^{-1} . By contrast, Poloczanska et al. (2013) found that the mean rate of phenological change among larval fishes that was attributable to climate change was $11.2 \text{ d decade}^{-1}$, or 1.12 d yr^{-1} . A literature review by Gokturk et al. (2022) indicated that climatically induced changes in phenology of $>15 \text{ d decade}^{-1}$ occurred among many marine organisms but were relatively rare. As a result, the high interannual variability in larval fish phenology in the NEUS may be obscuring our ability to detect any underlying linear trends related to climate change.

Another factor that may have contributed to this extreme variability is differences in stock structure. Many species included in this analysis, such as haddock *Melanogrammus aeglefinus*, yellowtail flounder *Limanda ferruginea*, and winter flounder *Pseudopleuronectes americanus*, have multiple stocks that occur throughout the NEUS (New England Fishery Management Council 1985). Different fish stocks are known to have distinct reproductive phenology (Neuheimer & MacKenzie 2014). If larvae from stocks with different reproductive timing are mixed together by advection or other hydrodynamic processes, then this could potentially result in increased interannual variation in observed phenology, especially if the population sizes of each stock are fluctuating out-of-sync. While exploring this hypothesis is beyond the scope of our current study, this represents an interesting avenue for future work, especially in cases where there are genetic differences between stocks that could be used to identify the populations of origin of larval fishes.

In this study, we did not consider changes in population size as a factor influencing phenology. Larger population sizes increase season duration of phenological events, given that a larger population will be characterized by more variability among individuals that can result in a greater likelihood of precocious individuals that are early migrators or stragglers that are later migrators (Primack et al. 2023). In addition, increases in population size are often associated with changes in age structure among fishes, such that larger populations are often characterized by a greater diversity of ages and a higher proportion of older fishes (Hsieh et al. 2006). As larger and older fish often exhibit different migration routes than smaller individuals (Zwolinski & Demer 2012, Callihan et al. 2015), this can impact their migration timing to spawning grounds, which then influences larval

fish phenology. The direction of this effect varies between species, with larger individuals of some species arriving at spawning sites earlier due to quicker migration speeds and larger individuals of other species arriving later due to longer distance migrations (Ware & Tanasichuk 1989, Carscadden et al. 1997, Wieland et al. 2000, Jansen & Gislason, 2011, Millner et al. 2011, Callihan et al. 2015). While potentially important, we did not analyze the effects of population size on phenology in this study because stock assessments estimating population size have not been conducted for all our study species. Nonetheless, this topic represents another productive area for future research.

An additional caveat to our results is that we assumed CT and its interannual variability can be adequately characterized by the EcoMon fisheries-independent survey, which conducts research cruises typically 6 times per year. Mismatches between survey timing and fish migration or reproduction dynamics can impact the ability of fisheries-independent surveys to characterize phenology (Olmos et al. 2023). Nonetheless, previous work on ichthyoplankton (Walsh et al. 2015, Rogers & Dougherty 2019) and zooplankton (Mackas et al. 2007) has successfully characterized phenology change and variability using data sets with sparse seasonal sampling. Also, to mitigate against this issue, we choose to conduct all analyses using CT, which is a conservative phenological metric that can be estimated from data sets with less frequent sampling (Ji et al. 2010). Still, this metric cannot detect multi-modal, seasonal peaks in larval fish abundance. If any species exhibited multiple peaks in larval abundance per year, our use of CT may have contributed to the high level of interannual variability in phenology that we observed.

Nevertheless, our analyses strongly suggest that Gulf Stream dynamics are a dominant source of phenological variability in the NEUS continental shelf—more so than other environmental variables, including temperature. This is particularly noteworthy given the increasing trend in S_{\max} intrusions in recent years (Silver et al. 2023). Our results do not reveal the exact mechanisms for how Gulf Stream warm core rings influence larval variability, instead leaving open a suite of intriguing hypotheses worthy of further study. S_{\max} intrusions and associated warm core rings may directly affect spawning timing or larval development duration, as temperature increase is known to cue spawning and accelerate development in many species (Pankhurst & Munday 2011). They may less directly affect phenology through their influence on food availability or predator–prey dynam-

ics. Any combination of these factors may impact larval survival. Physically, Gulf Stream rings may alter larval advection and/or retention across the region. Further elucidation of the relationship between Gulf Stream dynamics, eddies, and larval phenology, as described here, will aid in preparing for climate change impacts on resident fish species, including those of high commercial import.

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