1 **Spatiotemporal patterns in early life stage winter flounder (*Pseudopleuronectes***
2 ***americanus*) highlight phenology changes and habitat dependencies**
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13 Running Title: Winter flounder larvae
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15 Abstract
16 Decadal changes in the life history events of marine species are becoming increasingly important
17 to identify under a warming climate, yet many long-term monitoring programs do not collect
18 data at the spatiotemporal resolution needed to describe them. Such data are vital for
19 understanding the southern New England/Mid-Atlantic winter flounder (*Pseudopleuronectes*
20 *americanus*) stock, a species hypothesized to be adversely impacted by warming waters via
21 increased temporal overlap between its early life stages and predators. To provide insight into
22 winter flounder early life history dynamics and context for the stock's resiliency, we examined
23 ichthyoplankton data collected from two monitoring programs within Narragansett Bay, RI, USA
24 – one spatially comprehensive across the Bay proper (2001-2008, 2016-2017), and the other a
25 longer time series centered in one of the Bay's sub-estuaries (Mount Hope Bay, 1972-2017). By
26 leveraging these datasets together, we conducted a spatiotemporal synthesis of early life stage
27 winter flounder by evaluating changes in larval phenology, decadal coherence in larval spatial
28 patterns, and correspondence between larvae and their subsequent life stage. We identified
29 changes in larval phenology via earlier seasonal peaks in density through time. Results also
30 indicated stable larval spatial patterns during a period of larval decline, as well as spatial
31 coherence between larval and young-of-the-year stages. Using winter flounder as a model
32 species, our results highlight the importance of high resolution spatiotemporal ichthyoplankton
33 sampling to identify changes in phenology and site-fidelity for marine fishes.
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35 Key Words: winter flounder, larvae, Narragansett Bay, young-of-the-year, phenology, settlement
36 habitat
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1   1. Introduction

2   Long-term ecological datasets provide an opportunity to understand the timing of life

3   cycle events among species and assess how changes in phenology or variability over time may

4   impact ecosystem dynamics. Phenology changes have been documented in many processes

5   important to the function of ecosystems, including alterations in primary production patterns (Ji

6   et al. 2010), as well as shifts in marine species seasonal distributions (Perry et al. 2005, Mueter

7   and Litzow 2008), migration timing (Schindler 2019, Cherry et al. 2013, Langan et al. 2021),

8   molting season (Groner et al. 2018, Daniel et al. 2013), and spawning phenology (Poloczanska et

9   al. 2016). Climate-linked variations in spawning phenology have been documented in marine

10   (Asch, 2015, Fincham et al. 2013, Sims et al. 2004) and anadromous fishes (Bal et al. 2017,

11   Dempson et al. 2017, Kovach et al. 2013), sea birds (Mallory et al. 2010, Gaston et al. 2009,

12   Daunt et al. 2006), and marine mammals (Jemison and Kelly 2001, Rode et al. 2018). In marine

13   fishes, such changes can lead to early life history mismatches for prey availability (Asch et al.

14   2019, Llopiz et al. 2014) and the diminished presence of requisite physical and environmental

15   habitat requirements for successful development (Flitcroft et al. 2016, Krabbenhoft et al. 2014,

16   Falke et al. 2010).

17   Habitat dependencies for the early life history of marine species may be represented as a

18   continuously changing mosaic of multi-dimensional necessities (e.g., prey availability, predator

19   absence, physical oceanographic conditions); even small shifts in a species phenology may have

20   measurable impacts on survivorship and population productivity (Hovel et al. 2019). For many

21   species, specific habitat conditions are critical for the development of early life history stages

22   (Able and Fahay 2010, Collette and Klein-MacPhee 2002). If these conditions deteriorate with

23   environmental alterations or phenological shifts in predator-prey overlap, population bottlenecks

1 and declines may result. Therefore, spatial variability in species abundance often highlights

2 essential habitats and abiotic requirements needed to complete their life cycles. Such is

3 particularly true of species inhabiting temperate estuaries, which can experience relatively rapid

4 and extreme environmental changes over short time periods.

5 To properly study changes in the phenology and habitat requirements of marine species,

6 spatially resolved long-term datasets are required. Long-term monitoring of fish larvae provides

7 insight into changes in fish populations over time (Llopiz et al. 2014, McClatchie et al. 2014),

8 with applications including understanding interdecadal changes in larval fish assemblage

9 (Morson et al., 2019) and distribution (Walsh et al. 2015), estimating spawning stock biomass

10 (Richardson et al., 2010, 2020), inferring larval habitat requirements (McManus et al. 2018), and

11 discerning variability in recruitment (Payne et al., 2009). However, many of these long-term

12 ichthyoplankton programs do not collect data at spatial scales that allow for assessing fine-scale

13 spatial patterns and their ecological drivers (Brosset et al. 2020) or for developing spatial

14 management measures. Further, few long-term fisheries datasets implement the sampling

15 frequency necessary to detect phenology changes over time (Asch 2015, Staudinger et al. 2019),

16 despite the fact that marine species are particularly prone environmental conditions altering the

17 timing of their life cycle events (Edwards & Richardson 2004).

18 As a particularly vulnerable species sensitive to climate change within the Northeast U.S.

19 Continental Shelf ecosystem (Hare et al. 2016), winter flounder (*Pseudopleuronectes*

20 *americanus*) represent an ideal species to explore environmentally driven changes to phenology

21 and early life history habitat dependencies. A flatfish species once abundant throughout southern

22 New England, the winter flounder population has markedly declined since the 1980s (Bell et al.

23 2014, 2018). While fishing mortality has been attributed to initiating these declines, the southern

1   New England population has not recovered even with significant reductions in harvest and

2   remains at its lowest biomass levels on record (NEFSC 2020). Warming waters have been linked

3   to the decline in productivity of the stock (Bell et al. 2014), with prevailing hypotheses

4   suggesting that warming waters have increased temporal overlap between early life stage winter

5   flounder and predators, such as sand shrimp (*Crangon septemspinosa*) and mud anemones

6   (*Cerianthiopsis americana*) (Witting & Able 1995, Taylor & Collie 2003a, Keller & Klein-

7   MacPhee 2000). Others have postulated that predation impacting the species' productivity occurs

8   at the juvenile or adult stages by predators including summer flounder (*Paralichthys dentatus*),

9   striped bass (*Morone saxatilis*), and striped sea robin (*Prionotus evolans*) (Manderson et al.

10   2006, Frisk et al. 2018, Taylor et al. 2019). As such, environmental and ecosystem drivers appear

11   responsible for impeding population rebounds under low fishing mortality.

12   The southern New England/Mid-Atlantic (SNE/MA) winter flounder stock is considered

13   estuarine-dependent (Pereira et al. 1999) as it predominantly spawns within estuaries, including

14   their upper reaches (Collette & Klein-MacPhee 2002, Crawford & Carey 1985). Observations

15   have identified coastal and offshore spawning (DeCelles & Cadrin 2011, Fairchild 2017), yet

16   estuaries still seem to be most important for the SNE/MA stock (Siskey et al. 2020). Winter

17   flounder also exhibit a high degree of site fidelity, particularly during spawning (Collette &

18   Klein-MacPhee 2002; Buckley et al. 2008). The species' adhesive, benthic eggs, and negative

19   larval buoyancy favors local retention over distant larval transport (Pearcy 1962), with young-of-

20   the-year exhibiting strong site fidelity (Saucerman & Deegan 1991). This high degree of site

21   fidelity has also been used to support the notion that local subpopulations of winter flounder

22   likely exist within estuaries (Collette and Klein-MacPhee 2002, Buckley *et al.*, 2008; DeCelles

23   and Cadrin, 2011). With evidence that estuaries may be warming at rates faster than oceanic

1   environments (Scanes et al. 2020), estuarine-dependent species such as winter flounder may be

2   exceptionally vulnerable to phenology changes and the adverse effects of climate change.

3   Here, we use winter flounder as an example of a climate sensitive marine fish species to

4   assess early life history temporal patterns and spatial distribution that provide insight into

5   responses to a changing climate. To address these considerations, we collated multiple

6   ichthyoplankton sampling program datasets of varying spatial extent, time series length, and

7   periodicity of sampling from Narragansett Bay, Rhode Island, USA to examine winter flounder

8   early life history. To understand phenology changes in winter flounder larvae, we examined

9   temporal patterns in larval density in the context of the thermal environment. We then

10 characterized the spatial distribution of winter flounder larvae to identify areas of significant

11 spawning in Narragansett Bay and the stability of these spawning patterns across two decades.

12 This spatial assessment was then complemented with an analysis of the spatial coherence

13 between annual larval densities and those of young-of-the-year winter flounder from a juvenile

14 fish seine survey to ascertain whether larval flounder are predictive of subsequent settlement and

15 if this correspondence varies spatially. Through these analyses, we provide further insight into

16 the ecology and population dynamics for this well-studied and historically significant species

17 challenged by climate change as scientists and managers aim to rebuild the stock.

18 2. Materials and Methods

19 *2.1 Ichthyoplankton Sampling*

20   Winter flounder larval data were compiled from two ichthyoplankton surveys to

21 understand early life stage spatiotemporal patterns. Mount Hope Bay ichthyoplankton sampling

22 began in 1972 to understand possible adverse impacts to fishes from operation of the Brayton

23 Point power plant's cooling water system (BPE 2016). Annual sampling varied over time, but

during the larval winter flounder season, sampling always occurred once in February, then

weekly (1972 – 1992) or every 4 to 5 days (1993 – 2014) from March through at minimum mid-

May. The number of sampling locations also varied over the time series - 23 (1972 – 1979), 7

(1980 – 1985, 1993 – 2014) or 5 (1986 – 1992). Previous analysis of shifting from 23 to 7

sampling stations indicated that the spatial sampling variability was smaller than that of temporal

variability. As such, changes in the number of sampling stations over time are not believed to

influence inferences on changes in densities or phenology over time. For further details on the

stations sampled through time, see BPE (2016). Single oblique tows were made from bottom to

surface during the day using a paired 60-cm diameter bridleless bongo frame for 5 minutes, with

the goal of sampling at least 100 m^3 of water. The primary net mesh used changed from 505-µm

to 333-µm in 1995, but dual bongo tows using the two meshes from 1995-2017 were conducted

to allow for estimating annual larval extrusion and standardize to a 333-µm density estimate over

the time series (BPE 2016). Annual average larval densities prior to 1995 were standardized to

333-µm for a comparison to other surveys that used the same mesh (Supplement 1A). Hereafter

these data are referred to as the "Mount Hope Bay survey."

A more spatially holistic ichthyoplankton survey of Narragansett Bay was conducted by

the Rhode Island Department of Environmental Management (RIDEM) from 2001-2008, and

later renewed by RIDEM and the University of Rhode Island's Graduate School of

Oceanography (URI-GSO) in 2016 and 2017 (Figure 1). The 2001-2008 RIDEM survey

performed biweekly tows for six minutes at 15 stations within Narragansett Bay year-round. In

the winter period (January through April), bongo nets were equipped with 335 µm mesh, and

from May through December 500 µm mesh. The collected samples were identified to the species

level and reported as densities per 100 m^3 of water. The 2016-2017 RIDEM and URI-GSO

1   survey closely followed the methods of the earlier study, performing weekly 6-minute tows of

2   335 µm bongo nets at 15 stations within Narragansett Bay, but targeting only the spawning

3   period of winter flounder (February through April). Fourteen of the stations sampled during the

4   2016-2017 survey matched those sampled from 2001-2008, with one station relocated from the

5   mouth of Narragansett Bay to Mt. Hope Bay. As described in Bourne and Govoni (1988), both

6   surveys towed nets for 2 minutes each near the bottom, at mid-depth, and at the surface at

7   stations > 11 m depth, and 3 minutes each near the bottom and at the surface at stations ≤ 11 m

8   depth. Field data including date, location, depth, volume filtered by the nets, and surface/bottom

9   water temperature were recorded for each tow. Larval counts were converted to densities (#/100

10   m^3) using volume filtered estimates. In 2016 and 2017, larval lengths were measured for winter

11   flounder larvae to the nearest tenth millimeter. Hereafter, this 2001-2008 and 2016-2017 dataset

12   is referred to as the "Narragansett Bay survey." Additional details on Narragansett Bay survey

13   ichthyoplankton sampling are found in Langan *et al.* (2020). Analyses were constrained to

14   February through April data to allow for continuity between 2001-2008 and 2016-2017 data

15   (both temporally and plankton net mesh size used), and specifically focus on the winter flounder

16   spawning period.

17   *2.2 Temporal Analyses*

18   The Mount Hope Bay survey data were examined for long-term seasonal trends in winter

19   flounder larvae with linear regression. The weighted mean week of winter flounder larvae

20   occurrence (W_t) was calculated by multiplying a given week of year by its observed larval

21   density, with these values summed over weeks of a given year, and then divided by the sum of

22   the larval density of the entire sampling period:

23
$$W_t = \frac{\sum_1^n w_{n,t} \times d_{n,t}}{\sum_1^n d_{n,t}}$$
[1]

1 where $w_{n,t}$ is the week number in year t, and $d_{n,t}$ is the mean larval density for that week and year.

2 A seasonal cumulative density curve of larvae was calculated from the weekly larval density data

3 to determine the fifth and ninety-fifth percentiles of W_t. The beginning of the larval season was

4 considered the 5th percentile of the cumulative density curve and the end of the season was

5 considered the 95th percentile. The annual mean week of winter flounder larval occurrence was

6 then regressed against year to determine if the slope was significantly different from zero, and

7 thus whether the annual mean week has changed through time. The time series was examined

8 with the Durbin-Watson statistic to ensure a potential change in mean week through time was not

9 driven by autocorrelation. If the statistic was less than two ($D < 2$), an autocorrelation term was

10 included in the model and fit with generalized least squares to account for any potential

11 autocorrelation.

12 Mount Hope Bay annual average larval densities and the mean week of larvae occurrence

13 were also compared to various temperature metrics to determine if annual variability in larval

14 density or phenology corresponded to the thermal environment. Temperature data used for the

15 analysis were from the concurrent larval sampling conducted in Mount Hope Bay. Previous work

16 has suggested that the influence of temperature on winter flounder may vary with ecological

17 processes and the metrics used to represent those processes (Bell et al. 2014). To

18 comprehensively examine prospective impacts of temperature in winter flounder larvae, we

19 evaluated five thermal metrics for comparison with annual winter flounder larval mean density

20 and occurrence indices: mean annal temperature during the spawning period of approximately

21 February through April (T_{mean}), mean annual temperature when larvae were present ($T_{present}$),

22 annual mean temperature weighted by larval density (T_{weight}), the annual minimum temperature

23 observed during the spawning period (T_{min}), and the annual maximum temperature observed

1   during the spawning period (T_{max}). Winter flounder and thermal time series were compared using

2   linear regressions. Correlations with p-values < 0.05 after Bonferroni correction were deemed

3   significant (Table 1).

4   Generalized additive models (GAMs) were used to model the winter flounder larval

5   densities from the Mount Hope Bay survey to understand whether timing or thermal constraints

6   may be a greater determinant for larvae. GAMs use smooth, additive functions to construct non-

7   linear relationships between independent and dependent variables, resulting in curvature or

8   splines in the predictions (Hastie & Tibshirani 1986), and are often used to describe the

9   relationships between fish densities and covariates (Venables & Dichmont 2004). For the Mount

10   Hope Bay survey, concurrently measured temperature at three meters depth and week of the year

11   for the samples were used as explanatory variables for larval density, representing timing and

12   thermal niche drivers. While week of year and sea temperature can be collinear, our focus for

13   this analysis to understand the variables' influence on density rather than predict larval density

14   and risk overfitting concerns. Larval density was calculated as the sum of larval densities across

15   all stations within Mount Hope Bay in each sampling week and divided by the number of

16   stations sampled from Mount Hope Bay during the given period. Similarly, temperature

17   experienced by larvae was calculated as the mean temperature across all sampled stations on a

18   given date weighted by larval density on that date for the Mount Hope Bay dataset. Given the

19   high proportion of zeros in the data, the GAM was run with a Tweedie error distribution using R

20   package 'mgcv' (ver. 1.8-2.2). The Tweedie distribution is a compound distribution that is well

21   suited to data that have both large numbers of true zeros and positive continuous values.

22   *2.3 Spatial Analyses*

1   Mean larval densities from the Narragansett Bay survey dataset across stations and years

2   were natural log-transformed and evaluated with Analysis of Variance (ANOVA) and Tukey's

3   honestly significant difference test to discern if larval abundances differ through space and/or

4   time. Transforming the larval densities for these analyses caused the data to be approximately

5   normally distributed. To evaluate whether temporal observations in a localized portion of

6   Narragansett Bay were comparable to those using a more spatially comprehensive dataset,

7   annual larval densities from the Narragansett Bay survey were compared to the long-term Mount

8   Hope Bay time series standardized to 333-µm mesh.

9   Young-of-the-year (YoY) winter flounder abundance indices were compared to larval

10   densities to discern spatial synchrony across these two life stages and differences in survival

11   during the larval and settlement period. Since 1988, RIDEM has conducted a seine survey in

12   Narragansett Bay to assess juvenile fish assemblages. Each year, 18 fixed sites are sampled once

13   per month from June through October (one seine haul per site) using a 61×3.1 m seine (Figure 1,

14   Taylor et al., 2016). Sampling from approximately 0 to 1.5 m depth, seine hauls are typically

15   conducted during the day at high tide, with nets deployed by boat and retrieved from shore. All

16   taxa were counted and enumerated, with subsampling occurring for species in high abundance

17   (e.g. >3000 individuals); environmental data (e.g. temperature, dissolved oxygen) were

18   concurrently measured.

19   Annual larval densities and young-of-the-year abundances were compared by assigning

20   stations from each survey to broader geographic locations. Comparisons were conducted for the

21   following regions: Providence River Estuary, Upper Bay, the West Passage (upper and lower),

22   the East Passage (upper and lower), Greenwich Bay, and the Sakonnet River (Figure 1, Table 2).

23   Region designations were roughly adapted from Keller et al. (1999), and regional comparisons

1   were only conducted where Narragansett Bay larval survey data and RIDEM seine data co-

2   occurred. Seine data annual averages from June through August were used, as these months with

3   the greatest winter flounder presence (i.e. over >86% of winter flounder observed in the survey

4   during these months). Annual larval densities and young-of-the-year abundances were natural

5   log-transformed and compared for individual regions using linear regression. In addition, Bay-

6   wide correspondence between life stages using all regions' data was examined using a

7   generalized linear mixed model to account for fixed sites representing the larger population of

8   the Bay, with region modeled as a random effect. The mixed model was fit with a Gaussian error

9   distribution and implemented using R package 'glmmTMB', ver 1.2.12 (Brooks et al. 2017).

10   3. Results

11   *3.1 Temporal Analyses*

12   Annual larval densities from Mount Hope Bay were greatest and highly variable during

13   the 1980s through the 1990s, after which densities declined to low and stable numbers (Figure

14   2). Annual average densities from the Narragansett Bay dataset over the two decades also

15   showed a decline from 2004 to 2005, and a nearly eight-fold decline from the 2000s to 2010s.

16   Larval densities from Mount Hope Bay sampling standardized to the 333-µm mesh were

17   typically greater than those from the Narragansett Bay data, yet overlapping time series data

18   were not correlated (R^2=0.15, p-value=0.26).

19   The weighted mean week of larval occurrence was around mid-March, but in some years

20   was as late as mid-April and became earlier over time. Larvae were present in Mount Hope Bay

21   for four to eleven weeks with a mean of 7.4 weeks (standard deviation = 1.4). Larvae were first

22   detected (defined as the 5th percentile) around mid-February, though in some years they did not

23   appear until late March. Larvae tended to be absent from sampling by the end of April, but in

1   some instances extended into early May (95th percentile; Figure 3). No significant changes were

2   seen over time in the duration of larval occurrence over time. The weighted mean timing of

3   larvae in Mount Hope Bay fit with a temporal autocorrelation term exhibited a significant trend,

4   indicating a shift of larval presence earlier in the year over the time series (slope = -0.055 weeks

5   per year, p-value = 0.005; Figure 3). Through time, larvae became present in the Bay

6   increasingly earlier in the year and disappeared earlier. The Durbin-Watson statistic (1.55, p-

7   value = 0.048) indicated autocorrelation (ϕ = 0.27) necessitating the use of generalized least

8   squares regression.

9   Weak correlations were observed between annual larval densities and mean week of year

10   and temperature metrics from the Mount Hope Bay survey (Table 1). Annual larval density was

11   negatively correlated with the annual maximum temperature during the spawning period. The

12   mean week of year for larvae was negatively correlated with the annual mean and minimum

13   temperature during the spawning period, but positively correlated with the weighted mean

14   temperature (Table 1).

15   In the GAM using Mount Hope Bay survey data, temperature and week of the year

16   exhibited significant relationships with larval density and accounted for 51% of the deviance in

17   larval density. When using only temperature to predict larval density, 31% of the deviance was

18   explained, and using week of year explained 51% of the deviance. The model using both

19   covariates indicated that positive effects on larval density were observed at water temperature

20   below 10°C and from mid-March through early May (Figure 4). A preferred temperature range

21   was apparent, but the temperature range indicated little contrast in preference within this optimal

22   thermal window. The week of year preference indicated a more specified response (Figure 4),

1   represented as the strong contrast in week of year response from the GAM, suggesting that the

2   seasonal timing may be a stronger determinant of larval densities than the observed temperature.

3   *3.2 Spatial Analyses*

4   Larval densities varied through space and time within Narragansett Bay (Supplement 1B,

5   Figure 5). Annual station average larval densities ranged from 0.29 to 313.16 larvae per 100 m^3.

6   Larval densities tended to be greatest in northern portions of Narragansett Bay; however,

7   comparing average densities by station across years indicated only stations 9 and 13 were

8   statistically different from each other (One-way ANOVA: $F=2.56$, $p=0.002$, d.f=15). The strong

9   decline in larval densities evident in annually averaged data was also apparent between the two

10   decades across stations (Figure 5). While the total winter flounder larval density over

11   Narragansett Bay decreased from the 2000s to the 2010s, the stations of relative importance did

12   not. Across both decades, the general proportion of larvae at each station remained the same

13   (Figure 6). While Densities in the 2010s were lower than those of the 2000s (Figures 5 and 6).

14   Statistically, mean station densities in years 2001-2008 were significantly different than 2016,

15   years 2001-2004 and 2006-2008 were different from 2017, and 2016 and 2017 were different

16   from each other (One-way ANOVA: $F=18.9$, $p<0.001$, d.f=9).

17   The correspondence between winter flounder larval densities and young-of-the-year

18   abundance varied spatially within Narragansett Bay (Figure 7). The upper portions of

19   Narragansett Bay, such as the Providence River, Upper Bay, and northern East and West

20   Passages exhibited significant correlations between annual average larval densities and young-

21   of-year flounder (Table 2). Greenwich Bay and southern areas of the Bay (except the lower East

22   Passage) indicated little correspondence between the two life stages. Of the areas with significant

23   life-stage correlations, the Providence River and Upper Bay had higher rates of correspondence

1   (or young-of-the-year flounder per larval flounder) than lower regions (northern East and West

2   Passages). Varying from this pattern is the lower East Passage, with the highest rate of larval

3   correspondence to YoY of the Bay's regions (Table 2).

4   <u>4. Discussion</u>

5   *4.1 Changes in Spawning Phenology*

6   Over the course of the time series, earlier seasonal timing in peak winter flounder larval

7   densities was found within the Mount Hope Bay sub-estuary (Figure 3). This finding adds to the

8   growing literature on identifying changes in marine fish phenology of life cycle events (Asch

9   2015, Henderson et al. 2017, Staudinger et al. 2019, Thaxton et al. 2020). Phenological changes

10   in migration for marine fishes has also been observed locally for Narragansett Bay. Using data

11   from a weekly trawl survey, Langan et al. (2021) found that 12 species' residence periods

12   changed by as much 118 days, with those of warm-water species having expanded and those of

13   cold-water species contracted. While migration phenology was not detectable for winter flounder

14   (a known estuary-dependent species with limited migration patterns), changes in phenology may

15   manifest in other life history traits, such as spawning. Previous studies have suggested that

16   warming waters have negatively affected the winter flounder stock through increased predation

17   from a stronger temporal overlap between early life stage flounder and their predators (Taylor &

18   Collie 2003a, Keller & Klein-MacPhee 2011). The observed earlier timing of larvae may be a

19   product of spawning initiated earlier in the year, increased predation on larvae spawning later in

20   the season, or a combination of both. For this predation hypothesis to be true for marine species,

21   it requires the predators' phenology to track that of its prey (Thackeray et al. 2016, Bell et al.

22   2017). The earlier timing of larvae could be impacted by, or have ramifications on, life history

23   traits, such as larval growth. Larval length measurements from the Narragansett Bay survey

1   during a mild (2016) and cold (2017) year highlight interannual disparity in larval densities at

2   size through the season (Supplement 1C). Given larval growth can vary with temperature (Houde

3   2008), it is still to be determined how earlier spawning dynamics or larval presence could be due

4   to, or synergistically interact with, environmentally driven changes in egg incubation and larval

5   growth. Changes in larval dispersal pathways could also influence larval fish phenology, as

6   interannual spatiotemporal larval densities could be influenced by changes in larval transport

7   (DeCelles et al. 2015). However, the life history traits for larval winter flounder favor local

8   retention (Pereira et al. 1999) and are less favorable for distant larval transport. Further

9   hydrodynamic modeling would be needed to assess the degree of which larval transport

10   influences the observed larval phenology.

11   Winter flounder larvae have been observed over a range of water temperatures (Pereira *et*

12   *al*. 1999), with evidence of reduced survival at temperatures greater than 10°C (Able and Fahay

13   1998). The observed presence of larvae in these colder waters aligns well with previous reports

14   (Figure 4). The thermal window for winter flounder larvae in Mount Hope Bay was similar to

15   that from data over the larger Narragansett Bay system, which indicated a thermal preference of

16   4-10°C (Supplement 1D). There may also be additional factors beyond water temperature, such

17   as day length and moon phase, that are important for the time of spawning. The actual dates

18   when larvae were present were relatively constrained. Larvae were common by mid-March and

19   were effectively absent by early May. By week 20 (mid-May), it appears that larvae have settled

20   out of the water column or suffered mortality. With the stronger response in the week covariate

21   than temperature in the GAM (Figure 4) and deviance explained results when excluding each

22   variable, seasonal timing appears to be a better predictor of spawning rather than the thermal

23   conditions (Helm et al. 2013).

1 Larval densities from the long-term Mount Hope Bay monitoring highlighted a winter

2 flounder population decline through the 1990s, and the Narragansett Bay survey captured nearly

3 an 8-fold decline from the 2000s to the 2010s (Figures 2 and 4). Recent stock-wide assessment

4 for winter flounder indicates similar trajectories and a currently depleted state for the species,

5 with recent biomass estimates near their time series low (NEFSC 2020). Abundance trends for

6 older, spawning winter flounder in Narragansett Bay show similar reductions over the same

7 period (Langan et al. In Revision). Synchronous declines in abundance trends for winter flounder

8 have been observed across the stock's bounds (Manderson 2008, Bell et al. 2014).

9 Various sea temperature time series were found to correlate to those of winter flounder

10 larvae of Mount Hope Bay. Previous work has documented similar thermal ties to winter

11 flounder population dynamics; specifically, interannual changes in SNE/MA winter flounder

12 recruitment has been found to correspond to sea temperature, and temperature's inclusion in

13 stock assessment models has improved understanding stock-recruitment dynamics (Bell et al.

14 2014, 2018). However, correspondence between winter flounder and sea temperature varied

15 depending on the metrics of interest. Mean week of year of winter flounder larvae corresponded

16 better to annual changes in temperature than annual mean larval density (Table 1). Phenology of

17 life history events are sensitive to climate change, with such responses measured globally

18 (Walther et al. 2002). Several winter temperature metrics have been used to study its effect on

19 the SNE/MA winter flounder (Bell et al. 2014), with some more successful in discerning the

20 ecological role of temperature on winter flounder population dynamics than others. Our findings

21 further support this notion and that more traditional metrics, such as average abundance or

22 temperature, may not capture the interactions between organisms and their environment. Despite

23 the correspondence between temperature and winter flounder larvae, it is important to note that

1   the thermal environment is likely not the only factor influencing winter flounder larvae,

2   particularly given the weak correlations. For example, temperature may be serving as a proxy for

3   other ecological processes, such as predation (Keller and Klein-MacPhee 2000, Taylor and

4   Collie 2003b). Additionally, the decline in larval density tracks similarly to adult or spawning

5   stock trends, suggesting that reproductive capacity for the stock is also influencing observed

6   larval densities.

7   *4.2 Spatial Distribution of Early Life Stages*

8   Spatiotemporal patterns of winter flounder larval densities emerged for Narragansett Bay.

9   While annual larval densities were variable (Supplement 1B), northern areas of the Bay tended to

10   have greater annual larval densities than lower reaches of the Bay (Figures 5 and 6, Supplement

11   1D). Historical studies representing annual snapshots of spatial abundance for winter flounder

12   larvae in Narragansett Bay have provided varied findings. For example, winter flounder in 1973

13   followed a gradient of declining densities toward the Bay's mouth, whereas the same pattern was

14   not observed in 1990 (Keller et al. 1999). Pearcy (1962) noted seasonal progressions in larval

15   density spatially, with those in the Mystic River estuary greatest in the upper estuary earlier in

16   the spawning season, and larval development progression leading to greater abundances in the

17   lower estuary. It is hypothesized that more upstream areas of estuaries may provide

18   ichthyoplankton with regions of reduced predation and increase the likelihood of retention in

19   preferable inshore areas (Barletta-Bergan et al. 2002). The interannual variability in winter

20   flounder larval density found here highlights the challenges in identifying patterns from

21   individual years. For example, some years indicated a similar spatial gradient as found in 1973,

22   while other years resembled the more homogenous 1990 survey (Supplement 1B.) Statistical

23   tests did not identify many larval differences by station over the recent years; however,

1   examining the annual densities by site between the two decades highlighted the importance of

2   the upper Narragansett Bay in supporting higher larval densities (Figure 6), and that discerning

3   patterns in larval data with noise can be resolved via aggregation over longer time scales.

4   The strong correlations between larvae and young-of-the-year winter flounder in

5   Narragansett Bay highlights the importance of individual spawning sites supporting winter

6   flounder early life history (Table 2, Figure 7.) As noted in other systems, larval- juvenile

7   coherence offers insights for both spawning grounds and nursery areas (Pereira et al. 1999), with

8   these results suggesting spawning locations are important for winter flounder through their first

9   year of life. The importance of larval densities in predicting young-of-the-year abundances later

10   in the season was significant across regions of Narragansett Bay (Table 2), with upper reaches of

11   the Bay often having stronger correspondence between the life stages than southern areas (Figure

12   9), further highlighting the importance of areas further north in the estuary.

13   The high connectivity between larval and young-of-the-year stages for subregions

14   provides additional context for hypotheses on winter flounder subpopulations in Narragansett

15   Bay (Collette and Klein-MacPhee 2002). Tagging studies have suggested that three discrete

16   winter flounder spawning groups exist in Narragansett Bay: Mount Hope Bay, Sakonnet River,

17   and the East Passage/Upper Narragansett Bay (Saila 1962, Powell 1991). Genetic information on

18   Narragansett Bay larval and young-of-the-year winter flounder have indicated that those from the

19   same or nearby locations share genetic signatures (Buckley et al. 2008). These genetic results

20   have suggested 16 distinct subpopulations within the Bay, which is more discrete than tagging

21   studies. The geographic designations presented herein represent a spatial scale in between these

22   two studies yet allows for corroboration of both ideas put forth previously. All East Passage and

23   Upper Bay correlations between life stages were found to be statistically significant (Table 2),

1   which may represent the synchrony of this spawning contingent. However, the region-specific

2   correlations across life stages furthers the notion that distinct spawning groups may operate at a

3   smaller scale. We hypothesize that the correlation in life stages is aided by larval behavior and

4   physiology favoring local retention. An analysis examining larval lengths and estimated ages

5   from available measurements in 2016 and 2017 suggested individuals were between one and

6   three weeks old (Supplement 1E), smaller than the typical settlement size of 9-13 mm (Pearcy

7   1962). Typical larval hatch size coupled with larval behavior for spawning site fidelity may

8   suggest observed larvae were not only spawned within Narragansett Bay, but also spawned close

9   to where they were observed, and thus support metapopulation dynamics.

10   The differences in the life stage relationship across the Bay likely highlights the different

11   environmental conditions that have been known or suspected to influence early life history

12   patterns and survival. Traditional understandings of the species phenology and estuarine spatial

13   habitat gradients have corresponded to earlier post-larval, as well as rapid early juvenile growth

14   survivorship (Pearcy 1962, Manderson et al. 2006). The greater connectivity between the larval

15   and juvenile stages at northern reaches of Narragansett Bay likely reflect this gradient structure

16   driven by environmental habitat requirements. Meng and Powell (1999) documented how

17   juvenile fish abundance in Narragansett Bay has been greatest at northern and mid-Bay stations

18   than those in of lower Bay. Taylor et al. (2016) reported that early juvenile winter flounder

19   preferred oligohaline and mesohaline waters and avoided hypoxic waters and areas above 25°C.

20   Life history attributes of juvenile winter flounder (e.g. growth, condition, feeding habits) can

21   vary spatiotemporally within this system, and have been attributed to temperature, dissolved

22   oxygen, and water quality (Meng et al. 2001, Meng et al. 2008). The stronger coherence in larval

23   and juvenile life stages in the upper reaches of Narragansett Bay likely reflect the environmental

1   and physical oceanographic conditions that promote larval retention, earlier settlement, and suite

2   of environmental conditions that improve survivorship. These environmental habitat preferences

3   for early-life winter flounder can provide predation refuge; when conditions are sub-optimal,

4   such as at higher salinities, predators such as striped sea robin and summer flounder can enter

5   these nursery areas (Manderson et al. 2006).

6   The spatial heterogeneity in early life winter flounder abundances and connectivity

7   suggest that only certain locations within the Bay may promote growth and survival and be best

8   in describing Narragansett Bay winter flounder metapopulation dynamics. As previously

9   suggested (Yencho et al. 2015), these metapopulation dynamics should be considered in local

10   fisheries management plans. Further analyses on quantifying the factors influencing the

11   settlement rates to the early juvenile stage winter flounder may improve predictions of future

12   year-class strengths for the Narragansett Bay population (Able et al. 2011). Given that the

13   relationship between larval supply and the juvenile stage contributes to the rate and variability in

14   recruitment (Myers and Barrowman 1996), this analysis suggests additional spatial life-cycle

15   analyses across multiple stages are imperative to understand population bottlenecks for

16   Narragansett Bay winter flounder.

17   5. Conclusion

18   The coupling of ichthyoplankton and young-of-year fish monitoring at varying

19   spatiotemporal scales allowed us to provide new insights into a species life history and

20   population structure for a system that has experienced ecosystem changes. Using winter flounder

21   as a model species, we found evidence of an increasing shift toward earlier larval presence,

22   potentially due to changes in spawning phenology and/or predator-prey interactions. Analysis of

23   spatiotemporal larval densities indicated the importance of upper bay habitats. Importantly, this

1 research also found high connectivity between larval and young-of-year stages across Bay

2 habitats indicating strong subpopulation dependencies, and likely differences in habitat

3 suitability. The phenological changes and discrete habitat dependencies highlight critical areas of

4 concern for temperate estuary-dependent fish species. Identifying the population bottleneck in

5 declining species will require examination of many factors including physical and environmental

6 spawning triggers, predator-prey match/mismatch theory (Cushing 1990), and assessment of

7 critical habitats for early life history stages, which is only made possible with the appropriate

8 long-term monitoring at fine spatiotemporal scales. Our work highlights the value of such

9 datasets and supports improved monitoring internationally to address these questions endemic to

10 marine fishes.

11 The findings presented herein for winter flounder apply globally to species with

12 productivity that continues to decline with ecosystem changes. The prospects of rebuilding the

13 SNE/MA winter flounder stock to past high levels of abundance appear doubtful, as winter

14 flounder population models incorporating future climate conditions project that even fishing

15 moratoria may not suffice to rebuild winter flounder to previous stock levels (Bell et al. 2018).

16 Despite ominous stock-wide outlooks, fisheries managers should not be deterred from

17 developing informed strategies for species negatively impacted by climate. Identifying the

18 habitat dependencies of such environmentally sensitive species that display strong site fidelity

19 and metapopulations, as well as how these dependencies and life histories have changed through

20 time, is critical in constructing effective management tools that protect the species future

21 productivity. Such scientifically informed measures will be paramount in conserving these

22 species vulnerable to environmental change.

23 6. Acknowledgements

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1

Table 1. Correlation coefficient (^{r}) between the Mount Hope Bay survey winter flounder larvae
and temperature metrics. Winter flounder metrics included annual average density of larvae (D_t)
and average week of year of larval presence (W_t). Thermal metrics included mean annal
temperature during the spawning period (T_{mean}), mean annual temperature when larvae were
present ($T_{present}$), annual mean temperature weighted by larval density (T_{weight}), and both the
annual minimum and maximum temperatures observed during the spawning period (T_{min} and
T_{max}, respectively). Bold values represent correlations with p-values < 0.05 after Bonferroni
correction.

Thermal Metric	D_t	W_t
T_{mean}	-0.41	**-0.53**
$T_{present}$	0.21	0.24
T_{weight}	-0.02	**0.53**
T_{min}	-0.28	**-0.49**
T_{max}	**-0.46**	-0.42

1 Table 2. Regional correspondence between natural-log transformed winter flounder larval and
2 young-of-the-year indices (n=10 per region). Regions are defined by the larval (L) and seine
3 (YoY) survey stations used to represent the area. Linear regression slopes (mean ± standard
4 deviation, R^2 and p-values) from the correlation between regional annual larval and young-of-
5 the-year catch are presented, with significant relationships in bold. Slopes represent the rate of
6 settlement of young-of-the-year densities per larval abundance (YoY/L). The Bay-wide
7 correspondence used all sites' data (n=80), but was performed using a generalized linear mixed
8 model with site as a random effect.
9

Region	Larval (L) Survey	Seine (YoY) Survey	Slope (YoY/L)	R^2	p-value
Providence River	16, 15, 1	1	0.88 (±0.23)	**0.64**	**0.006**
Upper Bay	2	2, 17	1.01 (±0.22)	**0.72**	**0.002**
Greenwich Bay	3	3	0.12 (±0.26)	0.03	0.656
Northern West Passage	5	4, 5	0.65 (±0.16)	**0.66**	**0.004**
Northern East Passage	11, 12	8, 9	0.61 (±0.26)	**0.40**	**0.05**
Southern West Passage	6, 7	6, 7, 18	0.46 (±0.21)	0.42	0.06
Southern East Passage	9, 10	10, 16	1.14 (±0.18)	**0.83**	**0.0003**
Sakonnet River	13, 14	13, 14, 15	0.10 (±0.17)	0.04	0.595
Bay-wide			0.60 (±0.08)		

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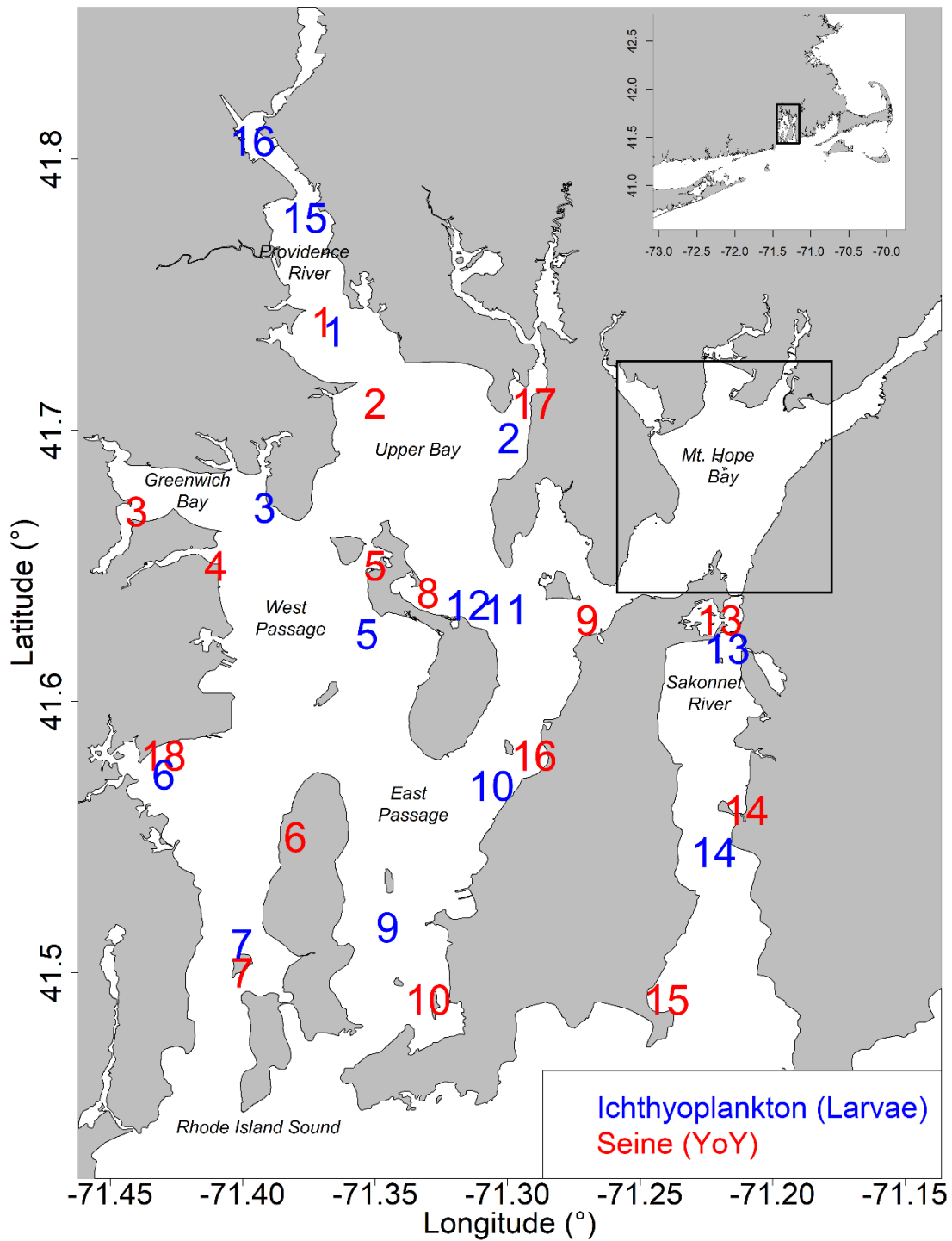
Figure 1. Narragansett Bay winter flounder survey stations: ichthyoplankton (larvae, blue) from the Narragansett Bay survey and seine (young-of-the-year [YoY], red). The Mount Hope Bay long-term ichthyoplankton sampling area is indicated by the box. Local regions of the system referenced in the text are identified. The locus map indicates the study area location within southern New England, USA.
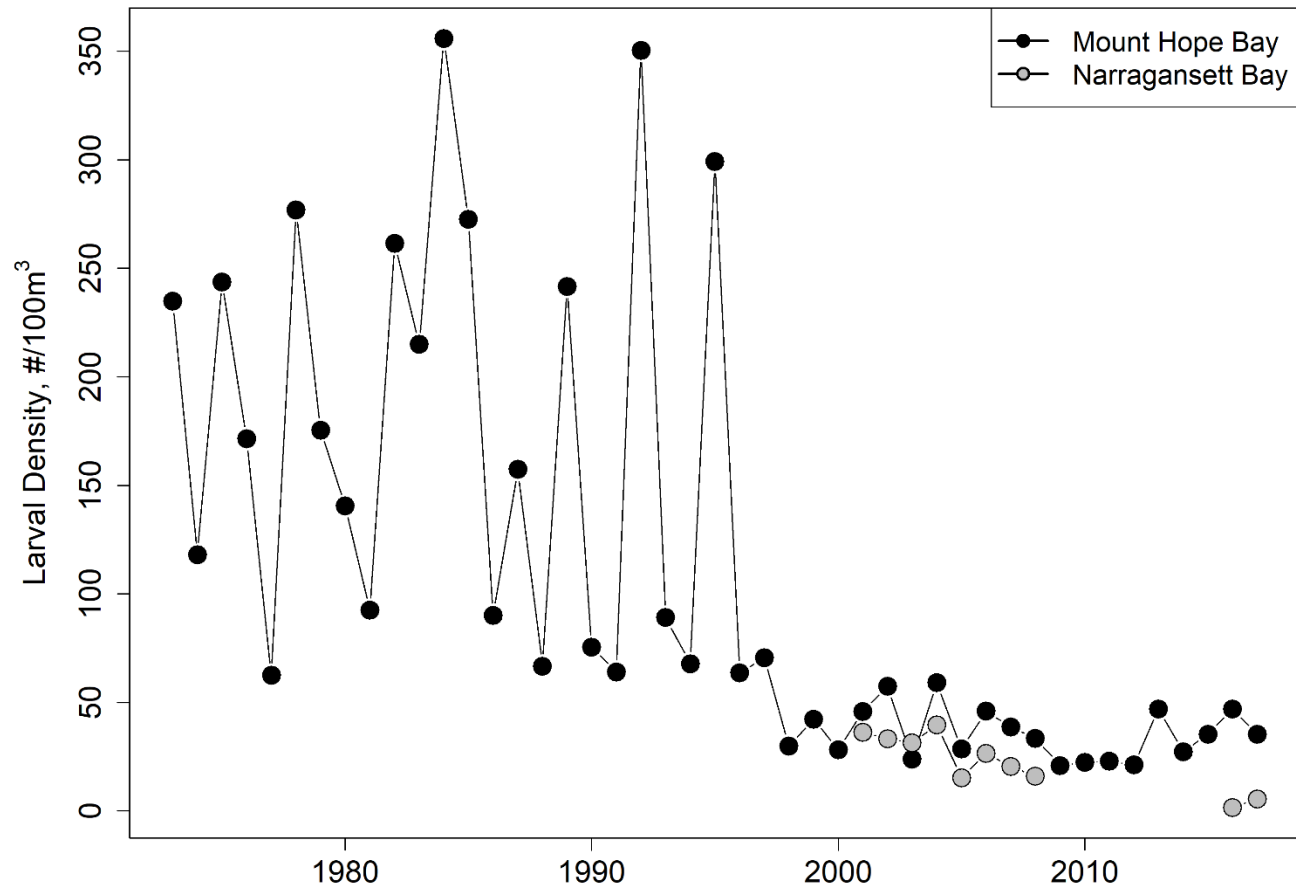
Figure 2. Annual average larval densities from Narragansett Bay (2001-2008, 2016-2017) and Mount Hope Bay (1973-2017) sampling. Mount Hope Bay samples from 1995-2017 were collected using 333-μm mesh gear; data in years prior were collected with 505-μm mesh but then calibrated to 333-μm equivalent densities based on dual mesh extrusion work (Supplement 1A) for comparison to the Narragansett Bay Survey. Annual average larval densities for the Narragansett Bay survey only included stations that were sampled all years.
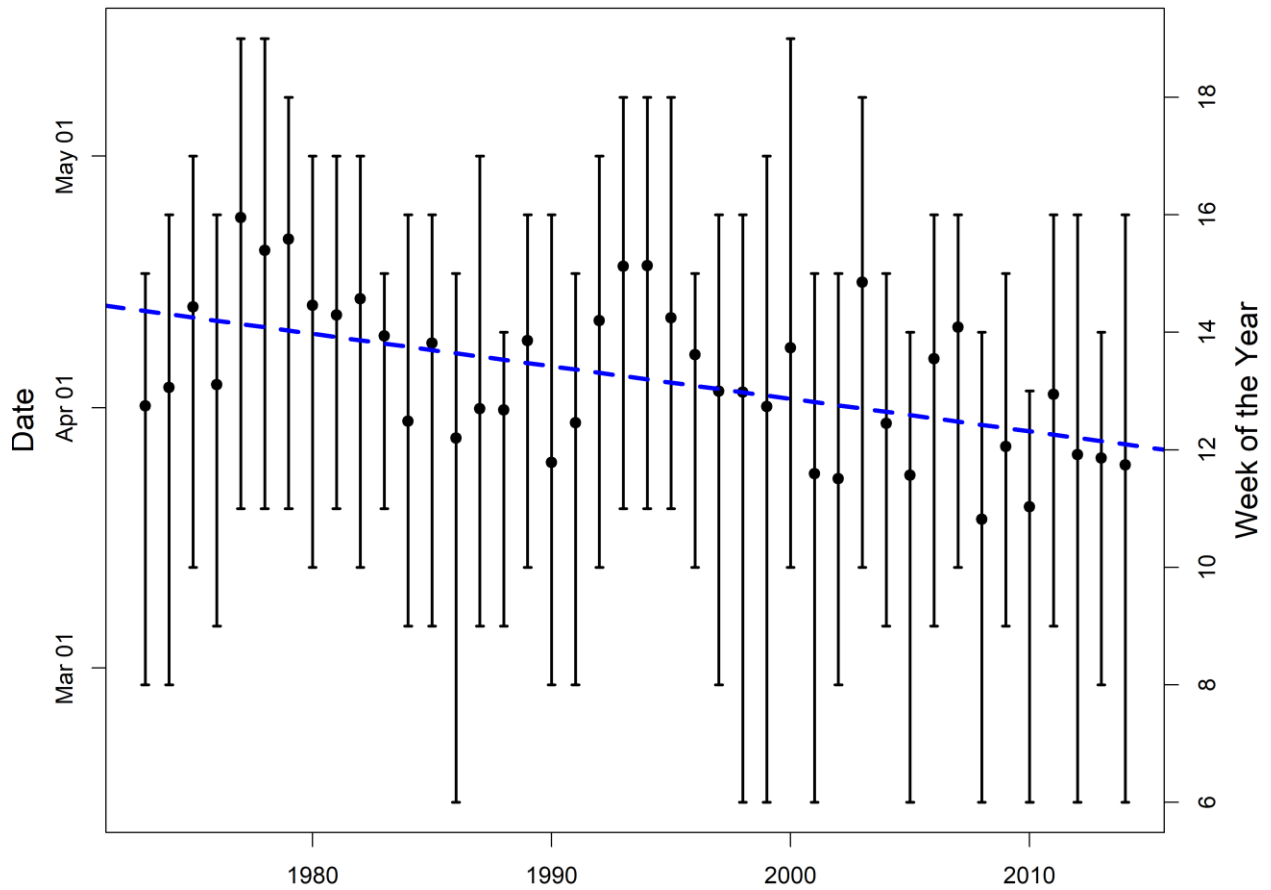
Figure 3. Mount Hope Bay survey-derived winter flounder larval phenology calculated as larval density-weighted mean date of occurrence for each year and the period which contains 90% of total abundance (5-95%ile). The trend in the larval density-weighted mean is also presented (blue dashed line; $W_t = -0.055 \times \text{year} + 123.6 + \phi$). Time periods are expressed as both week of year and date.
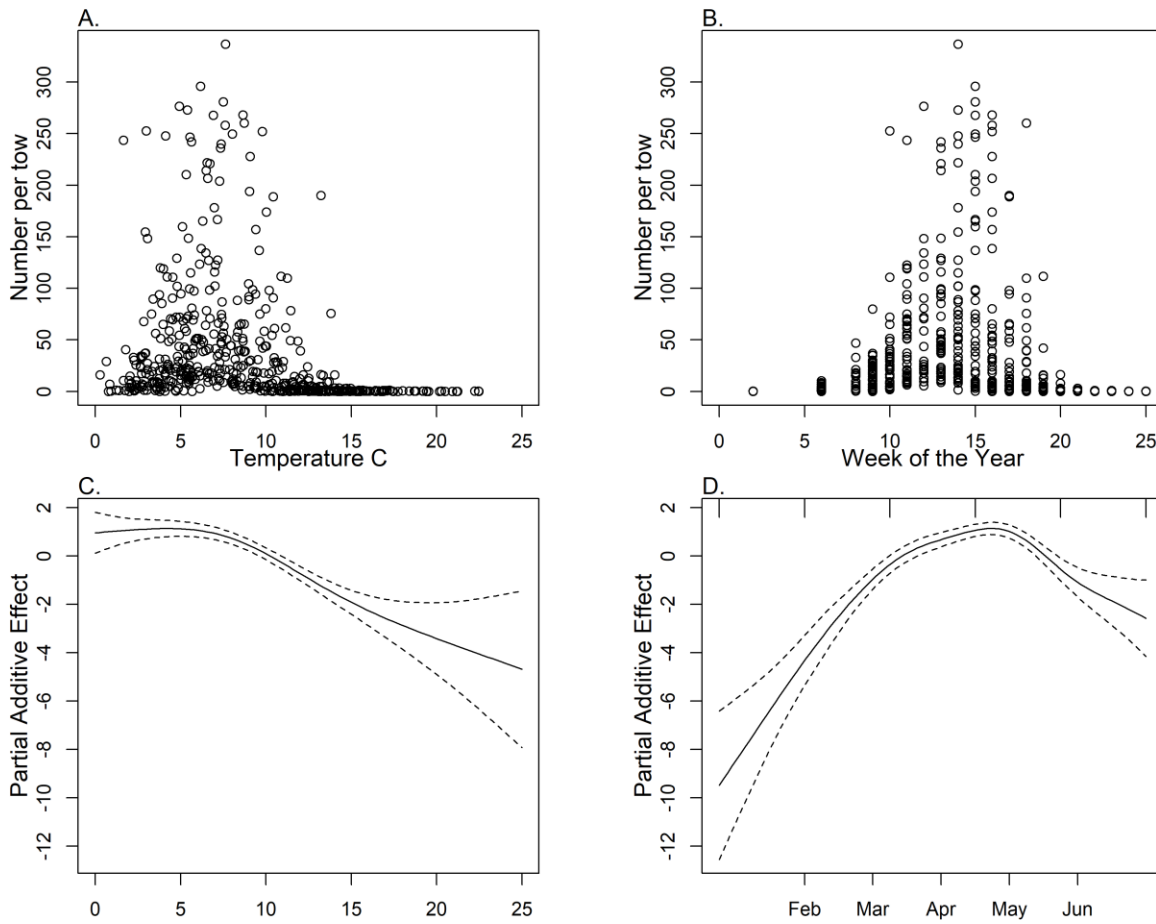
Figure 4. Observed Mount Hope Bay winter flounder larval densities (# per 100m³) by temperature and week of year (top row), and the estimated relationships between abundance and these covariates from the Tweedie GAM (bottom row). Left and right figure columns represent temperature and week of year, respectively.
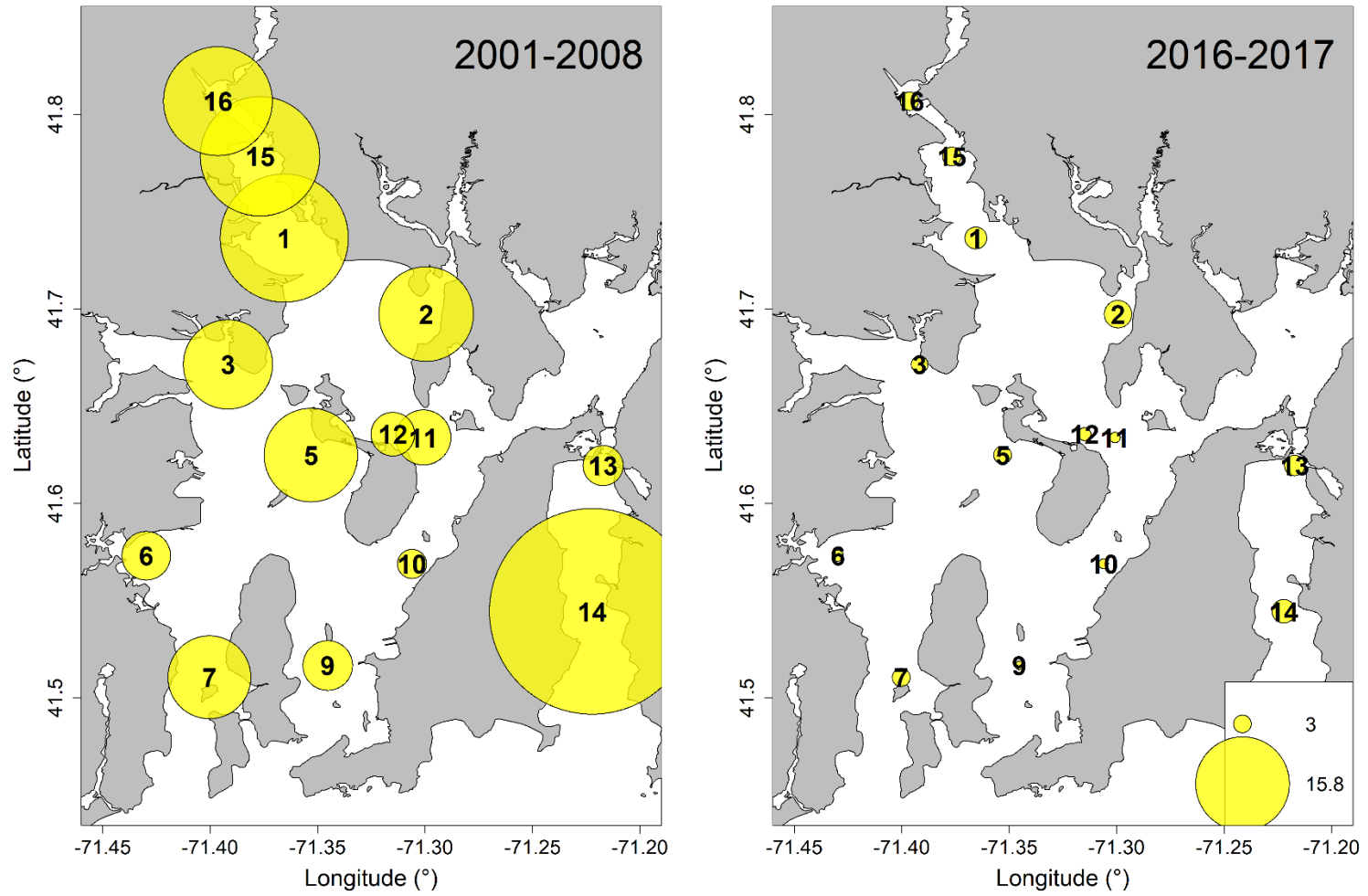
Figure 5. Narragansett Bay survey larval densities averaged by station for the two decades: 2000s (left) and 2010s (right). Size of points reflect differences in larval densities (no. larvae per 100m^3).
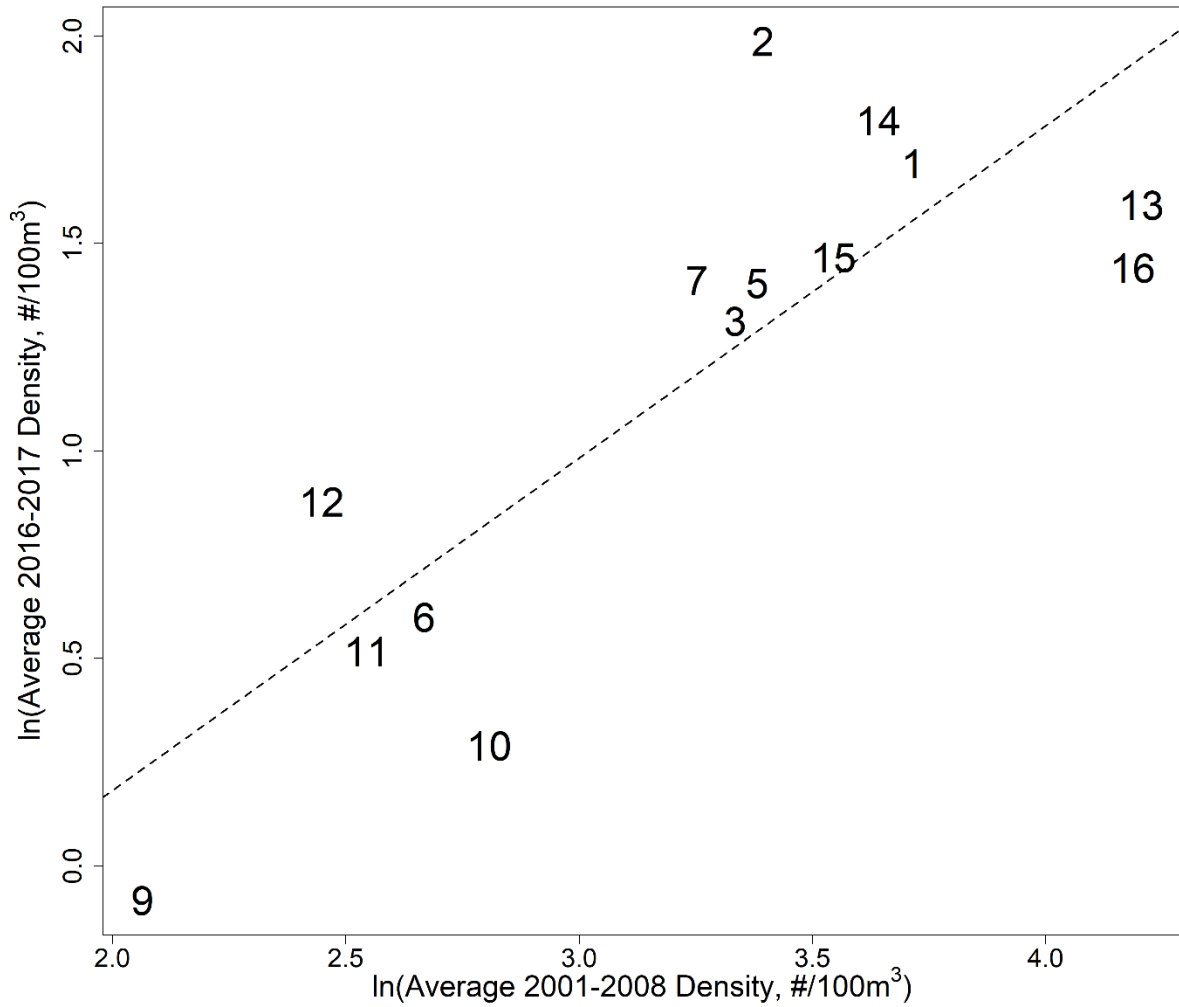
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Figure 6. Average natural log-transformed larval densities by station compared between the 2000s (2001-2008) and 2010s (2016-2017). Data points indicate the station number. The dashed line represents the linear relationship between the two periods (R^2=0.69, p-value<0.001).
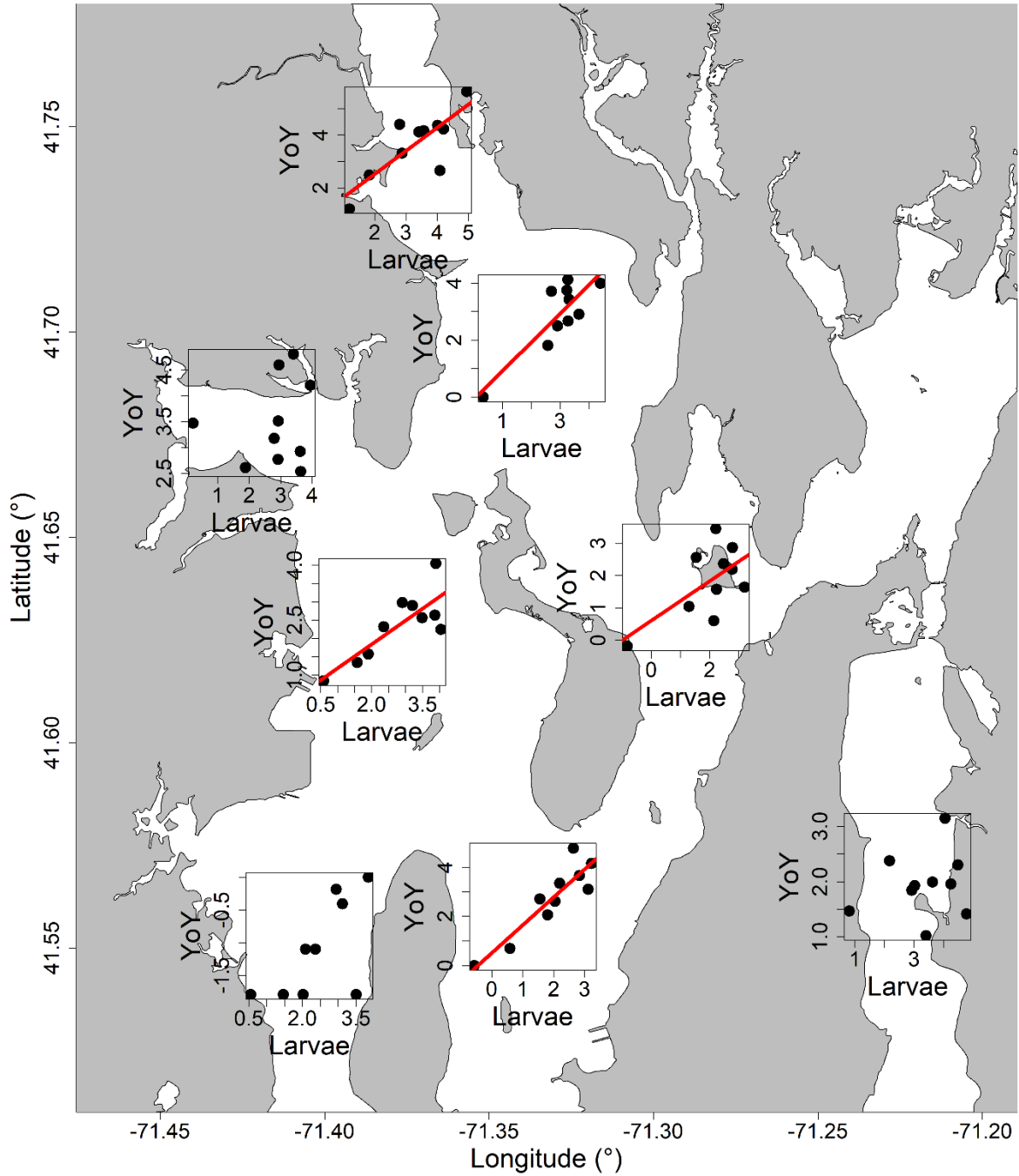
Figure 7. Spatial correspondence between winter flounder larval densities (Larvae, number per 100 m^3) and young-of-the-year abundances (YoY, number per tow) in Narragansett Bay. Data were natural log-transformed prior to correlations. Red lines within panels indicate the linear regressions where the correlations are significant. Regional groupings of stations by survey are presented in Table 2.