Title: Drivers of Winter Flounder subpopulation catch rates in a fisheries-independent fixed gear survey

Running Head: Winter Flounder survey catch rates

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Abstract

Objective: This study seeks to better understand the behavior and abundance of Winter Flounder in subpopulations from three coastal ponds by evaluating catch rates in a fixed gear survey, and accounting for catchability considerations to calculate an abundance index.

Methods: We modeled Winter Flounder catch rates as a function of environmental and sampling factors for a fyke net survey conducted in three Rhode Island salt ponds over 25 years. The survey deployed fyke nets throughout the winter spawning season in Point Judith Pond, Potter Pond, and Ninigret Pond beginning in the winter of 1998–1999. Sampling variables (e.g., location, soak period) and environmental variables (e.g., water temperature, precipitation) were either collected during the survey or compiled from external sources. Random forest models were used to predict relationships between candidate predictors and the occurrence and abundance of Winter Flounder in the catch.

Result: Seasonality (day of year) was strongly predictive of Winter Flounder capture, while most environmental variables were not, suggesting consistently timed migration and spawning movements that do not respond to environmental cues. Water temperature predicted abundance but not occurrence, consistent with previous observations of behavioral adaptations but not taxis during cold periods.

Conclusion: The decoupling of environmental parameters from Winter Flounder catch rates suggests that behavioral rigidity in breeding adults may contribute to this species' lack of recovery. Improved abundance predictions suggest a continued decline for Rhode Island Winter Flounder..

Lay Summary

Modeling catch rates for a spawning stock survey of three Winter Flounder subpopulations provides improved abundance estimates and shows behavioral rigidity across environmental conditions.

1. Introduction

The Southern New England/Mid-Atlantic (SNE/MA) Winter Flounder *Pseudopleuronectes americanus* population experienced a severe decline through the 1990's, and current estimates place stock biomass at less than 15% of its observed peak in 1982 (NEFSC 2022). Despite significant reductions in fishing effort, Winter Flounder show no signs of recovery (NEFSC 2022). Persistently low biomass in the absence of fishing pressure demonstrate the failure of traditional management efforts to achieve biomass recovery (Frisk et al. 2018). The reasons for this lack of recovery are unclear, but various lines of evidence suggest some combination of warming of estuarine spawning habitat, changes in phase synchrony, increased competition from range-expanding conspecifics, and increased predation on early life stages by avian, pinniped, and other predators (Keller and Klein-MacPhee 2000; Taylor and Danila 2005; Manderson 2008; Bell et al. 2014; Frisk et al. 2018; Langan et al. 2022; Balouskus et al. 2024). If recovery is possible for this species, it will likely be achieved through management and restoration efforts that address multiple pressures in addition to fishing (McManus et al. 2021a; Langan et al. 2023). Such efforts will benefit from improved estimates of Winter Flounder abundance at finer spatial scales and life stages, as well as an improved understanding of this species' behavioral responses to environmental change.

Catchability studies can help refine survey abundance estimates and provide insight into fish behavior (Arreguín-Sánchez 1996). Catchability theory holds that catch rates are a function of total abundance and availability to fishing gear, such that the abundance of fish in a catch sample is proportional to the total abundance in the sampled area (Arreguín-Sánchez 1996). For example, seasonal patterns in foraging activity are correlated with trap catchability in the Ballan Wrasse *Labrus bergylta* (Villegas-Ríos et al. 2014); gear and sediment type impact catchability of the Northern Quahog *Mercenaria mercenaria* (McManus et al. 2020); and current strength and salinity strongly affect catchability of Atlantic Cod *Gadus morhua* in trapnets and gillnets (Rose and Leggett 1989). Because the catchability relationship can vary across seasons, gears, and environmental conditions, accounting for these factors improves abundance estimates derived from catch sampling (Hoyle et al. 2024). Furthermore, identifying and characterizing these relationships can suggest hypotheses concerning fish behaviors that affect interactions with fishing gears.

In Rhode Island, Winter Flounder migrate to shallow coastal waters and estuaries in late fall and early winter to spawn (Klein-MacPhee 2002; Ziegler et al. 2019; Siskey et al. 2020). Individuals exhibit high site fidelity, returning to the same inshore locations each year, and remaining resident in the ponds throughout the winter (Saila 1961; Grove 1982). This highly defined population structure, while unusual for Winter Flounder (DeCelles and Cadrin 2007; Wirgin et al. 2014; Dolan et al. 2024), is plausible in the Rhode Island coastal ponds. As many as 16 genetically distinct subpopulations have been identified in Rhode Island state waters (Buckley et al. 2008). Moreover, between 1999 and 2023, a mark-recapture study of adult Winter Flounder tagged in Point Judith Pond never recovered a tagged individual in any other coastal pond (Balouskus et al. 2024). Consistent with this reproductive strategy, Winter Flounder do not appear to be shifting their range northward to track warming water temperatures, and it is possible that this behavioral rigidity has contributed to their persistent lack of recovery (Bell et al. 2015, 2018)

In this study, we draw on catchability theory to analyze catch rates of three Winter Flounder subpopulations in their estuarine breeding locations. Specifically, we model occurrence and abundance of Winter Flounder from a 25-year survey monitoring their seasonal spawning aggregations using random forest models (RFMs). In doing so, we aim to (1) understand environment-behavior-gear interactions for this depleted species and (2) report a corrected abundance index for the surveyed areas. Given the breeding ecology of Rhode Island Winter Flounder, we assume no intra-annual changes in abundance within each pond/subpopulation. Building on this assumption, we quantified the occurrence and abundance of Winter Flounder in the catch attributable to nineteen spatial, environmental, and sampling variables, interpreting the interannual effect as a true indicator of abundance and all other effects as influencing only catchability.

2. Methods

2.1 Study Location

The south shore of Rhode Island contains numerous coastal lagoons and embayments. The coastal lagoons, or "salt ponds," are shallow bodies of brackish water located behind barrier beaches and often connected to the ocean via breachways. The salt ponds provide critical habitat for commercial and recreational finfish and shellfish (Conover 1961; Meng et al. 2000; Ayvazian et al. 2020). Three salt ponds are included in this study: Point Judith Pond, Potter Pond, and Ninigret Pond (Figure 1). All three ponds have historically been fished both commercially and recreationally for winter flounder (Crawford 1990).

Point Judith Pond is the easternmost of the surveyed salt ponds. Point Judith Pond has a surface area of approximately 6.58 km^2, a mean depth of 1.8 m, and is connected to Block Island Sound by an artificial breachway (Lee 1980). The Saugatucket River flows into the north end of Point Judith Pond, providing the greatest freshwater flow of any of the surveyed ponds. Salinity within the pond ranges from approximately 20 PSU in the northern reaches to full oceanic salinity at the breachway. Due to the developed watershed, shallow depths, and relatively low flushing rates, Point Judith Pond can experience eutrophication and increased growth of macroalgae (Lee and Olsen 1985; Meng et al. 2000). The pond is home to the largest fishing port in Rhode Island, the Block Island ferry terminal, and numerous marinas.

Potter Pond is situated immediately west of Point Judith Pond and joined to Point Judith by a permanent tidal channel. The surface area of Potter Pond is approximately 1.38 km^2. The primary source of freshwater into Potter Pond is from Fresh Pond, which empties into Potter's northern reaches. This northern section of Potter Pond is also characterized by a glacial kettle hole that reaches over 40 feet in depth, a unique feature among the Rhode Island coastal ponds. Potter Pond has no direct outlet to the ocean.

Ninigret Pond is the largest salt pond in Rhode Island with a surface area of approximately 6.74 km^2 and has a permanent, maintained breachway to the ocean. The mean depth throughout Ninigret Pond is approximately 0.4 m, and it is connected to Green Hill Pond to the east by a tidal channel (Lee 1980). The watershed of Ninigret Pond includes residential housing, marinas, and the United States Fish and Wildlife Service Ninigret Wildlife Refuge.

2.2 Winter Flounder Survey

The Rhode Island Division of Marine Fisheries (RI DMF) has conducted an adult spawning stock Winter Flounder monitoring survey since 1999 using fyke nets. The survey was initiated to better understand the stock's local subpopulation dynamics in response to declining commercial landings and fishery independent relative abundance indices from the late 1980's through the mid-1990's. The survey design was developed in collaboration with commercial fishermen who historically fished for Winter Flounder in Rhode Island coastal ponds. Both the sampling effort (e.g., number of hauls per month and year) and spatiotemporal range (survey season, station locations) of the survey have varied over time due to staffing resources and funding availability (Figure S1; Tables S1–3). Despite these logistical limitations, however, this 25-year dataset provides a unique insight into several Rhode Island spawning stock biomass subpopulations, which can provide insight into wider, stock-level changes (Balouskus et al. 2024).

Fyke nets were set perpendicular to the shore during mean low tide. The nets were constructed of a vertical section of net wall referred to as a leader that directs fish toward the body of the net where the catch is funneled through a series of parlors, eventually being retained in the terminal parlor (i.e., cod end) (Hubert et al. 2012). The wings of the net provide further direction of animals intercepted into the parlors (Hubert et al. 2012). The landward end of the leader was positioned at approximately the mean low water elevation. The cod end of the net was positioned at between 5 and 8 feet of water depth depending on station location. The dimensions of fyke nets used in this survey were: 30.5 m long x 1.5 m tall leader, with 7.6 m wings, a 4.9 m spreader bar, and 6.35 cm mesh throughout. Fyke nets were deployed for three- to seven-night sets depending on weather and field logistics, including ice cover in the ponds.

Fixed sampling stations within Point Judith Pond and Potter Pond have been surveyed at varying levels of effort since 1999 (Figures 1, S1; Tables S1–3). Ninigret Pond was added to the survey in 2012. Within each respective pond, between one and three fyke nets were set concurrently at any given time within the pond and then rotated haphazardly among fixed stations over the course of the winter. Sampling was conducted from December through May, when mature Winter Flounder are most abundant in the ponds (Saila 1961). Captured Winter Flounder were counted and measured (total length, cm). Each fish > 30 cm total length was tagged with a Peterson disc tag as part of a mark-recapture study. Beginning in the winter of 2023–2024 all fish were fin clipped. All fish are released alive and discard mortality rate is assumed to be 0% based on the condition of fish returned to the water (Morgan and Walsh

1993). Any fish that experienced survey induced mortality (e.g., external predation within the net) were noted as deceased. Water quality parameters including temperature, salinity, and dissolved oxygen were measured at each station at the time of setting and hauling the nets with a YSI water quality probe. Beginning in 2019, *in situ* loggers (Star-Oddi DST CTD) collected water temperature, salinity, and depth observations at 15-minute intervals over each net set.

2.3 Data Processing

Analyses were conducted for two time periods based on the availability of covariate data. We prepared one dataset for the years 1998–2024 (“all years dataset”) and a second dataset that included additional water quality data available from the *in situ* loggers beginning in 2019 (2019–2024; “five-year dataset”). All data processing and analyses were carried out in R (v4.3.3) and RStudio (Posit Team 2024; R Core Team 2024). We selected candidate predictors based on literature showing that time of day, illumination, water temperature, and gear configuration can influence flatfish behavior and catchability (Ryer and Barnett 2006; Fraser et al. 2007; Richardson et al. 2014). We also drew on behavioral findings that support relationships between Winter Flounder movement and water temperature, tide cycles, salinity, and dissolved oxygen (Burrows et al. 1994; Berghahn 2000; Stierhoff et al. 2006; Taylor et al. 2016). Finally, we included atmospheric weather data to incorporate any relationships attributable to the association among wind speed, turbidity, and trophic relationships (Lunt and Smee 2014; Bever et al. 2018), or to the association between freshwater input, mixing, and salinity (Gillson 2011; Ilarri et al. 2022).

To include historical weather, we compiled daily observations of air temperature, precipitation, and wind speed from all NOAA weather stations in Washington County, Rhode Island, for the years 1998–2024 (NOAA 2024). Weather station data were assigned to fyke survey stations based on their proximity to the sampling location and data availability for each sampling day of the fyke survey. Various metrics (average, maximum, minimum, and range) of air temperature were calculated, along with daily precipitation and wind speed, which we summarized over the soak period for each fyke sample. We also calculated the mean lunar illumination over the soak period using the *lunar* R package (Lazaridis 2022).

Many candidate predictors were summary statistics of catch and environmental data, which we generated to mitigate missing data and summarize different aspects of the collected environmental parameters. For example, the fyke survey sampling protocol calls for water temperature observations to be made when the nets are set and hauled. However, only 81% of samples included both water temperature observations. To mitigate this, we calculated a summary statistic termed 'water temperature' that used the average of the two observations where available and either the set or haul observation if only one observation was available. We used a similar approach with salinity and dissolved oxygen.

We also calculated summary statistics for the years 2019–2024, when 15-minute water quality observations were available from *in situ* data loggers. In addition to traditional summary statistics such as the mean and range of temperature observations, we also included statistics describing the distribution shape such as kurtosis, skewness, and bimodality (Table S6). Distribution shapes, like rates of change and extreme values, are sometimes more informative than mean conditions in predicting ecological data. For example, the skewness, kurtosis, and rate of change of sea surface temperature time series were more predictive of coral cover than degree heating weeks in the Western Indian Ocean (McClanahan and Azali 2021). Similarly, the skewness and kurtosis of functional trait distributions in dryland plant communities had a stronger impact on multifunctionality than species richness and aridity (Gross et al. 2017).

After compiling the environmental data and generating summary statistics, we tested for correlation among the prospective covariates using Spearman's correlation coefficient with a threshold value of $\rho \geq 0.7$ (Myers and Sirois 2014).There is some evidence that the variable importance measures used in random forest modeling are biased against highly correlated variables, although correlation itself is not problematic (Genuer et al. 2015; Fox et al. 2017). We removed air temperature from both datasets as it was highly correlated with water temperature ($\rho = 0.80$ for the all years dataset and $\rho = 0.78$ for the five-year dataset) (Table S6). We hypothesized water temperature to be a stronger predictor of fish behavior than air temperature. We also removed minimum and maximum water temperature observations from the five-year dataset as they were both highly correlated with the mean water temperature and with each other (Table S6). The mean is a more robust statistic than the maximum or minimum, but its inclusion in the model does not suggest that relatively extreme temperature conditions (either maxima and minima or quantiles) have no relationship with Winter Flounder behavior and/or abundance. We also removed variables with ≥ 15% missing observations. This procedure left us with 11 candidate variables for the all years dataset and 19 candidate variables for the five-year dataset (Tables 1, S7).

2.4 Modeling

Four RFMs were developed to understand the relationship between Winter Flounder fyke net catch and the sampling conditions: one classification model and one regression model for each dataset prepared as described in section 2.3 ("all years," i.e., 1998–2024 and "five-year," i.e., 2019–2024). Given the characteristic breeding ecology of Rhode Island Winter Flounder, we assumed that the true total abundance within each pond remained the same throughout a survey year, and that no emigration or immigration occurred during the spawning season. The effect of survey year on the catch was thus considered to be a true indicator of abundance, while all other effects were interpreted as catchability. Classification RFMs predict a binary response based on the presence or absence of Winter Flounder in each fyke net sample (occurrence); regression RFMs predict a continuous response based on the number of Winter Flounder caught in each sample (abundance) (Breiman 2001). Each model type thus indicates distinct but complementary aspects of fish behavior given that the factors influencing whether fish occur may be related or unrelated to those that affect their abundance. Occurrence and abundance tend to be closely related in species that are evenly dispersed (Brown 1984; Estrada and Arroyo 2012). However, species that aggregate, as Winter Flounder do when they breed, often exhibit decoupling between occurrence and abundance (Estrada and Arroyo 2012).

We followed the same variable selection and prediction procedure for all four models. We used the *VSURF* R package to select predictor variables for the RFMs (Genuer et al. 2022). *VSURF* has increased prediction accuracy and parsimony when compared with other RFM variable selection methods (Speiser et al. 2019). It uses random forest variable importance to generate two lists of variables: a minimal list of variables required for accurate prediction, and an identical or slightly expanded list that includes additional variables that are informative for interpretation but not strictly necessary for model performance (Genuer et al. 2015). *VSURF*'s variable selection process is designed to be conservative such that it will possibly result in false negatives but not false positives (Genuer et al. 2015). In random forest modeling, trimming superfluous variables decreases computation time and aids interpretation, but does not significantly affect model performance (Fox et al. 2017). Because VSURF did not select any of the variables only available in the five-year dataset (Table S7), we do not present the five-year RFMs here.

Once predictor variables were selected, we implemented the two RFMs using the *randomForest* R package (Liaw and Wiener 2002). We used bootstrapped training datasets that were sampled with replacement to be the same size as the original datasets (1055 fyke sets). We then used the out-of-bag samples as testing datasets. After tuning the number of variables tried at each tree and running each RFM with the selected variables, we extracted two measures of variable importance for each model. For the classification model, these were the mean decrease in accuracy when a variable is removed and the decrease in Gini coefficient attributed to a variable's inclusion (Liaw and Wiener 2002). For the regression model, we used the percent increase in mean squared error when a variable was removed and the increase in node purity when it was included (Liaw and Wiener 2002).

We presented most model predictions by plotting the accumulated local effects (ALE) of each predictor using the iml R package (Molnar 2018). However, we also include a partial dependence (PD) plot generated using the randomForest R package to produce a revised abundance index for Rhode Island Winter Flounder (Liaw and Wiener 2002). PD plots are used more frequently than ALE plots in presenting RFM's, but they can mislead interpreters where they generate model predictions over unrealistic ranges of the plotted or unplotted variables or in cases of correlation among predictors (Friedman 2001; Apley and Zhu 2020). ALE plots overcome these challenges by showing effects rather than absolute numbers and predicting over local means for each predictor value rather than generalized values for the entire dataset (Apley and Zhu 2020). In the case of the abundance index, the PD plot is preferred because it predicts real numbers rather than centering predictions on 0. For all PD and ALE plots, we also include a rug displaying the distribution of training data to aid interpretation. Regions of each rug with a higher density of observations should be interpreted as more reliable, and regions with low density should be interpreted with caution (Molnar 2022). Because RFMs are nonparametric, they do not estimate confidence intervals (Breiman 2001). Instead, model predictions are usually presented as line or bar plots, often with predictor distribution data included (Cutler et al. 2007; Vezza et al. 2015; Galligan and McClanahan 2024).

3. Result

Between 1999–2024, RI DMF conducted 1055 fyke net hauls in three coastal ponds (Figure S1; Tables S1–3). Survey-induced mortality was 3.9%. The mean ± standard error (SE) length for all Winter Flounder was 31.2 ± 0.1 cm (Figure S2). Over the survey period, 2,404 fish were tagged (all ≥ 30 cm) and 286 were recaptured (Table S4). Ten fish were recaptured more than once (Table S4). All individuals recaptured by the fyke survey were found in the ponds where they were tagged (Table S5). Winter Flounder returned by the public mostly followed the same pattern, but in seven instances, fish tagged in one pond were recaptured in another pond (Table S5). No live returns from another pond took place during the breeding season. Two individuals tagged in Ninigret Pond were captured in Point Judith Pond in mid-May; two individuals tagged in Point Judith Pond were recaptured in Potter Pond, one in late April and the other in mid-May; and two individuals tagged in Potter Pond were recovered in Point Judith Pond, one in June and the other in early October. One individual tagged in Point Judith Pond was recovered in Potter Pond in January, but was already dead. Winter Flounder spent a mean ± SE of 265 ± 18 days at large (Figure S3). The longest period between tag deployment and live recapture was 1,545 days for an individual tagged in Ninigret Pond in 2014 and caught in Block Island Sound in 2018. The shortest time at large was two days for four fish captured and recaptured in Point Judith Pond. Approximately 8% of all recaptures occurred within one week of tag deployment, and 10% occurred within two weeks.

Both models predicted Winter Flounder capture with > 80% accuracy for training data and > 45% accuracy for testing data (Table 2). In classification, ‘accuracy’ refers to the percentage of correct classifications (presence/absence) (Breiman 2001). In regression, it refers to the proportion of total variance explained by the model (Breiman 2001). The all years models included year, station, day of year, and pond (both models); set occurrence (classification only); and water temperature and soak period (regression only) (Figure 2). The five-year models included day of year, station, and set occurrence (both models); pond (classification only); and year (regression only). None of the additional environmental variables included in the five-year dataset were selected for model prediction (e.g., salinity, water temperature curve shapes, dissolved oxygen; Table S7), so we do not present those models here. Both all years models found strong interannual effects and identified sampling variables (e.g., location, day of year, and set occurrence) as influential (Figure 2). Because the classification (occurrence) and regression (abundance) models predict different response variables, they are both presented as complementary indicators of Winter Flounder behavior.

3.1 Fixed Gear Catchability

Winter Flounder catch rates were predicted by sampling variables and water temperature (Figure 2). Both models showed a peak in Winter Flounder capture occurring in January and early February, followed by a decrease through the spring (Figure 3). However, the model predictions diverged in April and May, when abundance began to increase again, and occurrence continued to decrease (Figure 3). The classification model predicted decreased occurrence associated with a higher number of gear redeployments in the same spot within a sampling station within each respective year (set occurrence) (Figure 3). Limited variation in abundance was attributed to the soak period, with an increase in abundance associated with soak periods of > 4 days (Figure 3). Station and pond were deemed influential by both models (Figure 2), with varying effects on occurrence and abundance (Figure 4). Notably, Potter Pond had no sites with a positive effect on occurrence or abundance, and Ninigret Pond displayed the strongest positive effects (Figure 4).

Water temperature was the only environmental variable selected by either model (Figure 2). Higher water temperature was associated with increased abundance, but not occurrence, of Winter Flounder in the survey catch (Figure 3). Abundance of Winter Flounder increased with water temperature until ~8 °C and then decreased to a neutral effect at ~13 °C (Figure 3). Fyke sets at 9 °C captured 3–4 more individuals than sets at 1 °C (Figure 3). We believe this relationship is ecologically independent of seasonality because Winter Flounder capture also peaked in colder months (Figure 3). In most cases, water temperature fluctuated by ≤ 5 °C over a soak period, but ~21% of samples had a larger range, and a six-day sample from March 2021 displayed a range of 14.7 °C (Table 1). Most temperature observations were well within the environmental preferences of Winter Flounder (Table 1; Klein-MacPhee 2002). No other environmental variables predicted Winter Flounder abundance or occurrence, including salinity, dissolved oxygen, wind speed, precipitation, and lunar illumination (Table S7).

3.2 Abundance Index

The abundance index predicted by the regression RFM showed strong effects of year on abundance (Figures 2, 5). The index showed a sharp decrease in abundance from 1999–2003, a stable period from 2003–2006, and then a continuous slow decline through the remainder of the survey period (Figure 5). Survey effort was not distributed evenly across years, with lower effort in 2016–2019 (Figures 5, S1). Higher sampling effort took place from 2020–2024 (Figure S1). Despite these variations, however, the predicted abundance index was consistent across all years, and removed the exaggerated variation found in the raw survey data (Figure 5).

4. Discussion

Although Winter Flounder occurrence and abundance are understood to be consistent in inshore breeding habitats through the winter, catch rates in this fixed gear survey were not (Klein-MacPhee 2002; Ziegler et al. 2019). Notably, catch rates were most affected by sampling rather than environmental parameters, suggesting that Winter Flounder exhibit behavioral rigidity in the face of rapidly shifting environmental conditions in their southern Rhode Island breeding habitat (Oczkowski et al. 2015). The most pronounced effects on catch rates were attributed to seasonality (Figure 3). Increased catch rates in January and early February suggest a period of increased movement before and during the beginning of the spawning period (Fairchild et al. 2013; Ziegler et al. 2019; Balouskus et al. 2024), perhaps associated with male territorial behavior and/or courtship as described in other flounder species (Konstantinou and Shen 1995; Manabe et al. 2000; Carvalho et al. 2003). Correlating January peak catch rates with sex and spawning status could help elucidate this relationship, as could direct behavioral observations through catch-and-release, telemetry, or visual methods (Fairchild et al. 2009, 2013; Grothues et al. 2012; Ziegler et al. 2019). The decrease in occurrence through the remainder of the spring spawning period could either indicate a shift in spawning behavior or learned gear avoidance over the course of a survey season as suggested by the negative relationship between set occurrence and the occurrence of Winter Flounder in the catch (Figure 3). The comparatively reduced negative effect on Winter Flounder abundance found in the late spring that co-occurs with the opposite trend in occurrence likely indicates a patchy distribution of Winter Flounder activity in space and time (Figure 3). This could reflect a higher number of sampling events with no catch and with abundant catches co-occurring at the end of the survey season when most breeding adults are leaving their inshore habitat (Phelan 1992; Klein-MacPhee 2002; Ziegler et al. 2019). In this case, the modeled relationship would include a true abundance effect linked to emigration in addition to the catchability effect.

The strong effect of seasonality does not necessarily mean that the timing of Winter Flounder breeding has not changed since 1999. Notably, temporal changes have been observed in Point Judith Pond, with a narrower spawning window in more recent years (Balouskus et al. 2024). Primary production in the coastal ponds is not strongly regulated by seasonality (Conover 1961; Nixon et al. 2009), and is thus unlikely to be related to the timing of Winter Flounder spawning aggregations. The survey could benefit from increased coverage of earlier months as the effect of seasonality shows that Winter Flounder are already present in the ponds before the first fyke nets are hauled (Figure 3).

The repeated use of a survey location was associated with a reduced likelihood of Winter Flounder occurrence (Figure 3). This result may reflect learned gear avoidance as fish become more experienced with a particular gear location over the course of a survey year (Underwood et al. 2015; Diaz Pauli and Sih 2017). It may also suggest some kind of social learning as set occurrence was associated with flounder absence, but not changes in relative abundance. A soak period of > 4 days was associated with a slight increase in Winter Flounder abundance (Figure 3), after which gear saturation is likely reached (Prchalová et al. 2011; Kuriyama et al. 2019). Future survey efforts should include a minimum soak period of four days in sampling protocols.

No environmental variables predicted Winter Flounder occurrence, and water temperature was the only environmental variable that predicted abundance (Figure 3). The relationship we found between water temperature and abundance is consistent with previous work showing strong effects of temperature on behavior and recruitment for this species (Bell et al. 2018; Dolan et al. 2021; Langan et al. 2022). Below an ~8 °C threshold, warmer temperatures were associated with increased abundance (Figure 3). This trend is consistent with observations of burrowing and/or inactivity at cooler temperatures, which would make Winter Flounder less available to fixed gears (Grothues et al. 2012; Ziegler and Frisk 2019). Above ~8 °C, the positive effect of temperature on abundance declined until reaching 0 (Figure 3). It is possible that this relationship represents a true effect on abundance, and not just on catchability, because Winter Flounder sometimes move in response to warm temperatures. In Narragansett Bay, RI, juvenile Winter Flounder avoided areas where water temperatures exceeded 25 °C (Taylor et al. 2016), and in Mattituck Creek, NY, migratory breeding adults began to leave the estuary when the average water temperature was ~12 °C (Ziegler et al. 2019). If relatively warmer temperatures provide a cue for movement in the breeding aggregations studied here, the decrease in abundance above ~8 °C could indicate migration out of the ponds. Notably, the warmest temperatures observed in this study, and all temperatures ≥ 10 °C (8.5% of all fyke sets) were observed after March 15. It is also possible that temperature preferences and response behaviors are influenced by factors such as age, sex, and/or membership in either the estuarine resident or seasonal migrant group (Klein-MacPhee 2002; Siskey et al. 2020). Winter Flounder display diverse temperature preferences throughout their range, and respond to shifts in temperature by managing depth, activity level, and burrowing behaviors (Klein-MacPhee 2002). We also note the possible amplification of long-term warming in the study location, which could further influence Winter Flounder behavior (Grothues et al. 2012; Oczkowski et al. 2015; Ziegler et al. 2019).

Other environmental parameters observed in this study are also thought to influence Winter Flounder behavior, including dissolved oxygen and salinity (Meng et al. 2000, 2005; Meise et al. 2003; Stierhoff et al. 2006; Taylor et al. 2016; Dolan et al. 2021). However, we found no relationships between these variables and catch rates. This is likely because salinity and dissolved oxygen remained within the environmental preferences of Winter Flounder in almost all cases, even in the small number of samples during which salinity or dissolved oxygen significantly changed over a soak period (Meng et al. 2000; Klein-MacPhee 2002). Likewise, we found no effect of lunar cycle (illumination) or observed tidal range on catch rates (Table S7). It is possible that tidal dynamics influence Winter Flounder behavior on shorter timescales than the ~4 day soak periods used in this study (Tyler 1971).

Our revised abundance index for all three subpopulations shows a slow but continuing decline since 2007 that is not apparent in the raw survey data. Whereas the previous, uncorrected abundance index shows more volatility over the last 20 years, and a period of apparent rebuilding beginning in 2022, our revised index shows greater consistency from year to year and no evidence of rebuilding. Like our index, the 2022 stock assessment for SNE/MA Winter Flounder showed a significant drop in spawning stock abundance in the early 2000's, with 10,005 mt in the year 2000 and 4,648 mt in 2005 (NEFSC 2022). However, the assessment's increase in spawning stock biomass from 2005–2013 and the subsequent decrease to ~3,500 mt are not reflected in our index (NEFSC 2022). This discrepancy may suggest that the decrease observed in Rhode Island in the early 2000's was driven by stockwide dynamics, whereas the factors influencing subsequent stockwide trends were no longer influencing these three subpopulations after the year 2005.

While other catchability studies have compared multiple abundance indices (e.g., McManus et al. 2020) or used cameras to observe gear efficiency (e.g., Bacheler and Shertzer 2020), our study drew on the breeding ecology of Rhode Island Winter Flounder to assume no intra-annual change in abundance within each coastal pond. While this is a helpful assumption for modeling purposes, it is probably not the case, and disentangling intra-annual abundance changes from catchability factors presents a significant challenge for this study. Survey-induced depletion and/or winter predation could provide additional explanations for the decline in catch rates associated with day of year and set occurrence. Given the low mortality observed in this survey (3.9%), we consider survey-induced depletion to be unlikely, but it has occurred in other small, isolated subpopulations (Tettelbach et al. 2017). On the other hand, both avian and pinniped predators target adult Winter Flounder in their breeding habitat, and these pressures may be increasing (Toth et al. 2018; Aarts et al. 2019; Balouskus et al. 2024). While it is possible that predation affects the abundance of adult Winter Flounder on the short time-scales necessary to influence our results, top-down controls are more salient for this species at earlier life stages (Taylor 2003; Manderson et al. 2006; Langan et al. 2022), and no strong correlations exist between the abundance of predators and of Winter Flounder in Point Judith Pond (Balouskus et al. 2024).

A third, and potentially more significant confounding factor for this study is the possibility that Winter Flounder travel among ponds during the spawning season and that each pond does not represent a truly closed subpopulation. If this is true of Rhode Island Winter Flounder, then the intra-annual changes in catch rates observed by this survey could represent a mix of catchability and abundance effects, rather than catchability alone. A telemetry study on Long Island observed approximately 10% of Winter Flounder captured in Shinnecock Bay entering adjacent inshore breeding areas, although these were mostly observed outside the breeding season (Sagarese and Frisk 2011). Nonetheless, movement among breeding locations would be consistent with, although not necessary for, the genetic connectivity observed for Winter Flounder on Long Island (Dolan et al. 2024). Such movement would be possible for the Rhode Island subpopulations given the proximity of the three ponds included here. Notably, Point Judith Pond and Potter Pond are connected by a short tidal channel < 1 km. However, out of the 286 tagged Winter Flounder recovered in this survey, no live fish were found in a different pond during the breeding season. Microsatellite data likewise suggest a highly structured population (Buckley et al. 2008). We thus consider our assumption of no migration during the breeding season to be plausible for southern Rhode Island, even though it cannot be generalized to other nearby systems. Additional telemetry, mark-recapture, and genetic studies would be needed to further evaluate this assumption.

The Rhode Island coastal pond survey is unique in that it directly samples specific Winter Flounder subpopulations in their spawning habitat. Correcting survey data for catchability allowed us to predict abundance trends at a finer spatial and stock structure resolution than was previously available, and using multiple response variables (occurrence and abundance) allowed us to better elucidate different types of multivariate relationships (Siskey et al. 2020; NEFSC 2022). These models can be updated after the completion of each survey season to further improve abundance predictions and provide insight into current (sub)population trends. The similarity of subpopulation and stockwide abundance trends before 2005 serves to highlight the role of regional drivers of Winter Flounder abundance, such as sea surface temperature, predation, and competition (Howell et al. 2016; Bell et al. 2018; Frisk et al. 2018; Langan et al. 2022, 2023). However, the divergence between our index and the SNE/MA stock assessment also demonstrates the importance of restoring and maintaining high quality spawning habitat at the local level (Howell et al. 2016; Ayvazian et al. 2020; McManus et al. 2021b; Langan et al. 2023; Barrett et al. 2024).

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Conflict of Interest Statement

The authors report no conflict of interest.

Data Availability Statement

Data and code are publicly available on Zenodo at https://doi.org/10.5281/zenodo.14224683.

Ethics Statement

There were no ethical guidelines applicable to this study.

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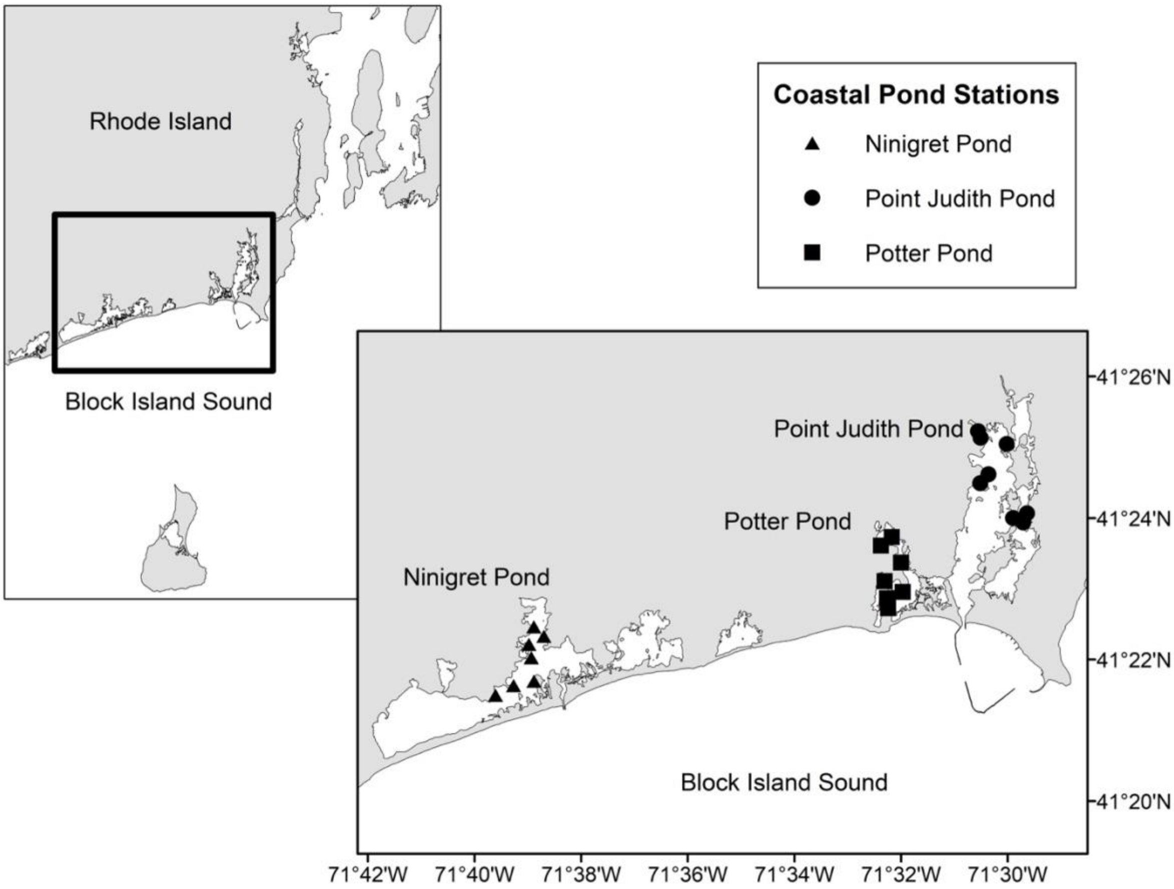

Figure 1 Fyke net sampling stations from 1999–2024.

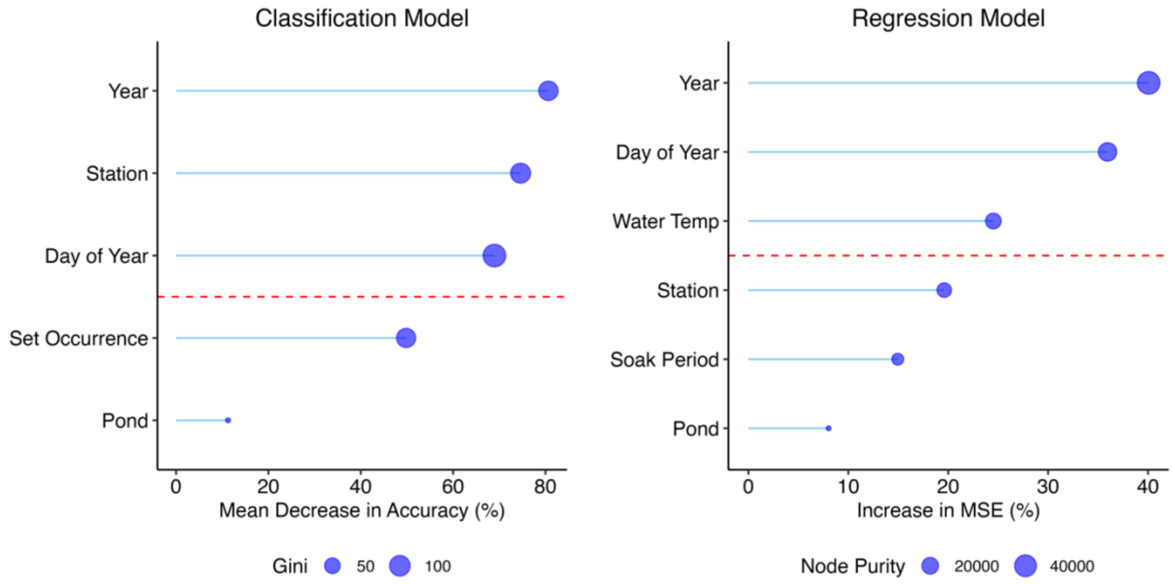

Figure 2 Two measures of variable importance for both random forest models (RFMs). The x-axis for the classification model is the mean decrease in classification accuracy (%) when a variable is removed. The x-axis for the regression model is the increase in mean squared error (%) when a variable is removed. Variables above the red dashed line are required for model performance, and those below are recommended for interpretation. Less important variables have been trimmed from both models.

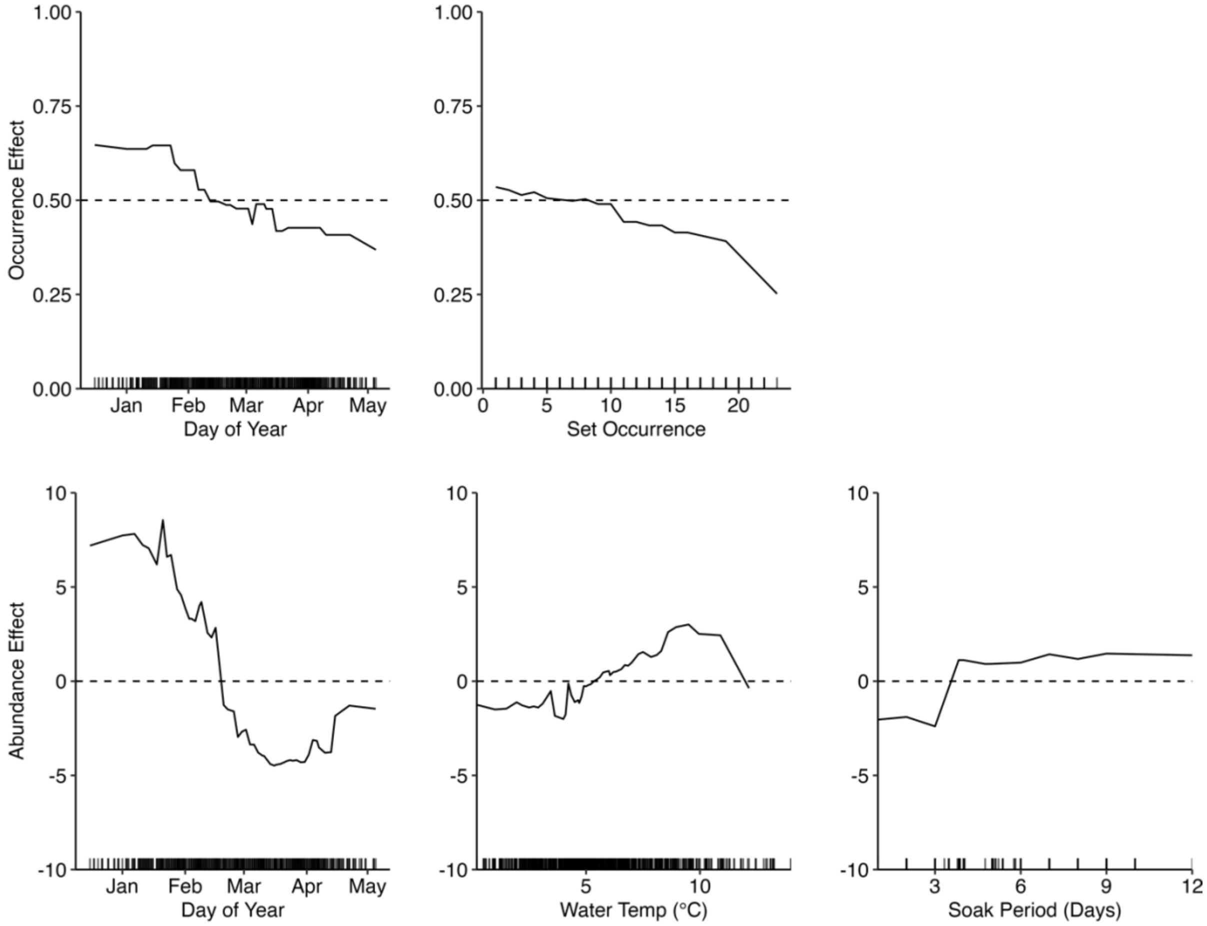

Figure 3 Accumulated local effects (ALE) of selected variables on Winter Flounder occurrence (classification) and abundance (regression). The rug on each plot represents the distribution of training data for each predictor, indicating over what ranges the model predictions are most reliable. Specific descriptions of each predictor (x-axes) can be found in Table 1.

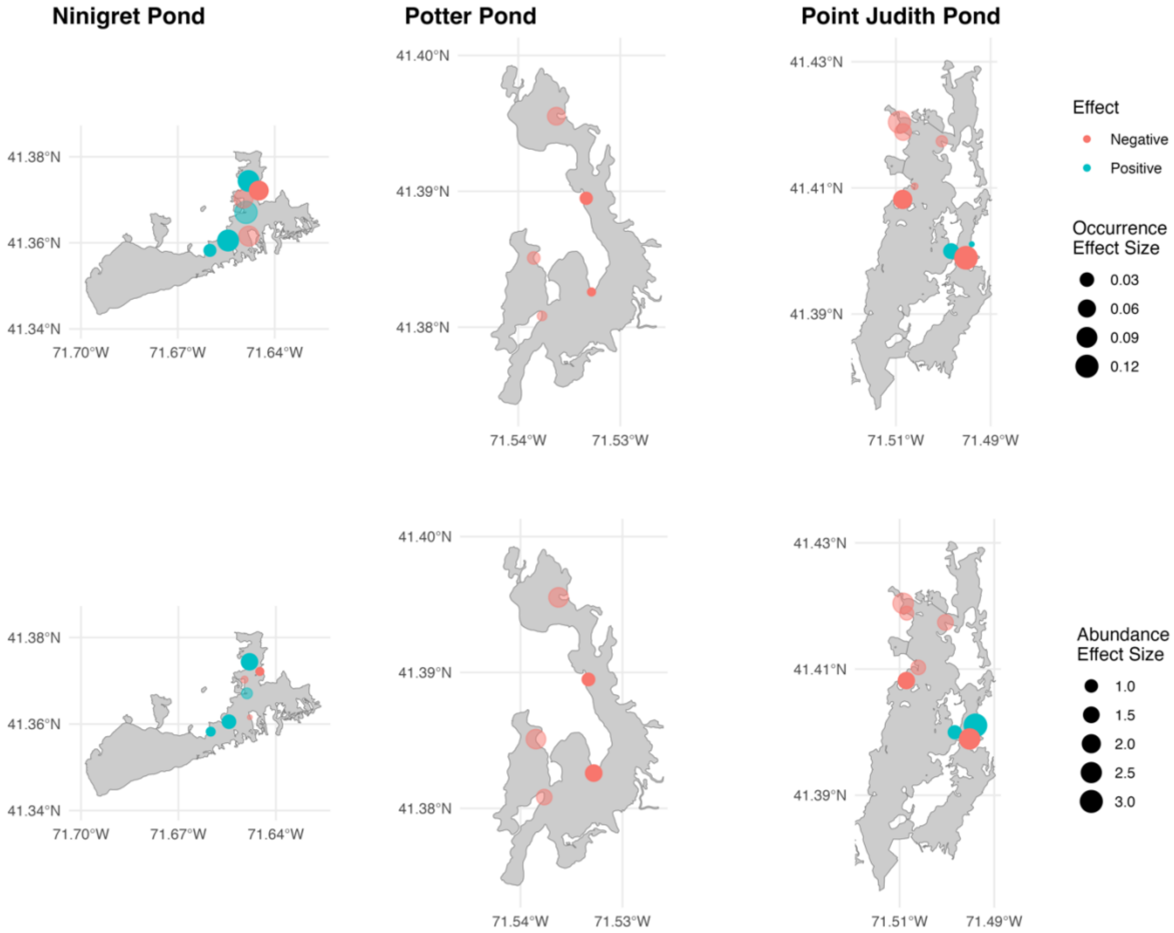

Figure 4 ALE of survey station on Winter Flounder occurrence (classification) and abundance (regression) in the catch. Stations with small sample sizes (fewer than 30 fyke net hauls) are greyed out.

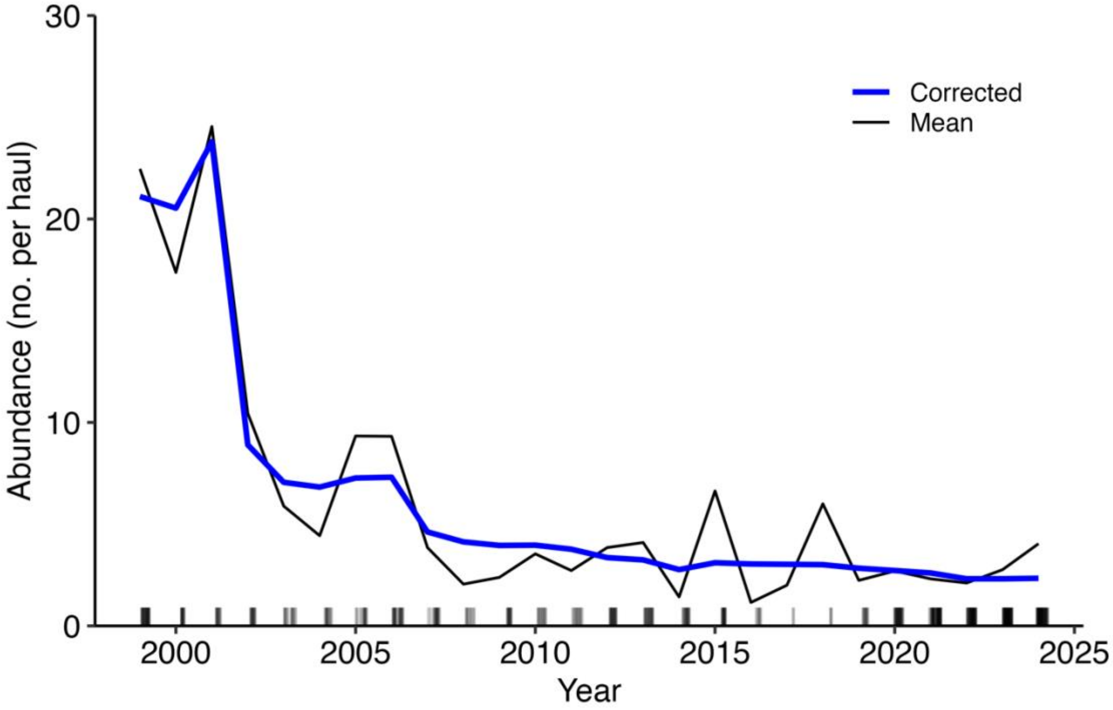

Figure 5 Fishery-independent abundance index for Rhode Island Winter Flounder subpopulations. The black line represents the arithmetic mean of the survey data for each year. The blue line is a partial dependence plot of Winter Flounder abundance on year.

Table 1 Variables used by random forest models to predict Winter Flounder catch rates.

Variable Category	**Variable**	**Mean ± SE**	**Range (min–max)**	**Description**
Sampling	Year	N/A	1999–2024	Survey year in which the fyke net was hauled. The year indicated corresponds to the calendar year for January–May of a November–May survey year.

Sampling	Pond	N/A	N/A	One of three sampling locations assumed to indicate subpopulations: Ninigret Pond, Point Judith Pond, or Potter Pond.
Sampling	Station	N/A	N/A	One of 22 sampling locations within three ponds.
Sampling	Day of year	N/A	December 15 – May 4	Day of the sampling season on which fyke net was hauled, modeled as a modified Julian day beginning on November 1.
Sampling	Soak period (days)	4.6 ± 0.1	1–12	Number of nights between set and haul of fyke net.
Sampling	Set occurrence	6.3 ± 0.2	1 – 23	The nth time sampling has occurred at this station in a given survey year.
Environmental	Water temperature (°C)	5.7 ± 0.1	0.0 – 16.1	Water temperature over the soak period. 81% of values are the average of observations made at the beginning and end of the soak period, 14% of values are

observations when gear was hauled at the end of the soak period, 3% of values are observations when gear was set at the beginning of the soak period, and 2% of values are missing.

Table 2 Description of RFMs and their performance. For classification models, performance is measured by accuracy of model classifications. For regression models, performance is the proportion of variance explained.

Model	**Predictors**	**Performance (training set)**	**Performance (test set)**
Classification (Occurrence)	5	92.1%	81.1%
Regression (Abundance)	6	81.1%	45.5%