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Application of telemetry-based fish habitat models to predict spatial habitat availability and inform ecological restoration

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Abstract

Conservation decisions surrounding which fish habitats managers choose to protect and restore are informed by fish habitat models. As acoustic telemetry has allowed for improvements in our ability to directly measure fish positions year-round, so too have there been opportunities to refine and apply fish habitat models. In an area with considerable anthropogenic disturbance, Hamilton Harbour in the Laurentian Great Lakes, we used telemetry-based fish habitat models to identify key habitat variables, compare habitat associations among seasons, and spatially identify the presence distribution of six fish species. Using environmental data and telemetry-based presence–absence from 2016 to 2022, random forest models were developed for each species across seasons. Habitat variables with the highest relative importance across species included fetch, water depth, and percentage cover of submerged aquatic vegetation. The presence probability of each species was spatially predicted for each season within Hamilton Harbour. Generally, species showed a spatial range expansion with greater presence probability in the fall and winter to include parts of the harbor further offshore, and a range contraction in the spring and summer toward the nearshore, sheltered areas, with summer having the most limited habitat availability. Greater habitat suitability was predicted in western Hamilton Harbour for the majority of species, whereas the east end was less suitable and may benefit from habitat restoration. These types of fish habitat models are highly flexible and can be used with a variety of data, not just telemetry, and should be considered as an additional tool for fish habitat and fisheries managers alike.

KEYWORDS
acoustic telemetry, environmental relations, habitat suitability, machine learning, space use

1 | INTRODUCTION

Habitat is a fundamental ecological concept (Yapp, 1922), yet it is also remarkably difficult to define for mobile aquatic animals such as fishes. In a general sense, habitat is the set of environmental conditions (both physical and environmental—biotic and abiotic) where a given organism completes its life (Morrison et al., 2012). This includes areas occupied during breeding, overwintering, or foraging as well as movement corridors, and any area that allows an organism to survive and complete its life cycle (Krausman, 1999; Fisheries Act, RSC 1985, c F-14). Of course, not all habitats are created equal (Johnson, 2007) such that if a given habitat occupied by an organism fails to provide the necessities of life, an animal must move or face suboptimal conditions (i.e., low habitat quality) that could lead to fitness impairments or even death (Huey, 1991). The habitat requirements of different fishes vary widely with extensive habitat partitioning given differences in environmental tolerances, nutritional requirements, feeding modes, reproductive biology, species interactions, and life history (Benoit et al., 2021; Lane et al., 1996). Even the most basic questions such as how much habitat is enough is actually a rather difficult question to answer (Fahrig, 2001). It is well known that good habitat of sufficient quantity allows fish populations to thrive, whereas similarly degraded habitats lead to reductions in fish populations or changes in community structure and function (Hayes et al., 1996). For decades, researchers have attempted to study fish habitat associations (including fish habitat selection; Rosenzweig, 1981) and develop fish habitat models (Kerckhove et al., 2008; Knudby et al., 2010; Olden & Jackson, 2001). Although predictive models based on known fish habitat requirements identify habitat that suits a fish's fundamental niche, the incorporation of presence data, though time consuming to collect, can provide a more accurate picture of realized fish habitat supply.

Advances in biotelemetry have provided novel, high-resolution information on fish–habitat interactions over diverse temporal and spatial scales. Unlike other methods (e.g., snorkeling, electrofishing, netting), biotelemetry enables researchers to track individual fish through greater time and space enabling them to reconstruct habitat use over ecologically relevant scales (Cooke et al., 2012; Cooke et al., 2016). Notably, biotelemetry can be used in winter, thus providing data on habitat associations during a period for which previously very little was known (Marsden et al., 2021). With improvements in our ability to directly measure fish positions year-round, there have been opportunities to refine fish habitat models (e.g., Brownscombe et al., 2023). Fish habitat models are used by fish habitat managers to understand which habitats to protect and restore and are dependent on robust data to ensure that they are reliable (Kerckhove et al., 2008). Given that functional fish habitat is the foundation for healthy and productive fish populations (Lapointe et al., 2014), developing robust fish habitat models is critical for science-based management.

The North American Laurentian Great Lakes are emblematic of global patterns of freshwater ecosystem degradation and declines in biodiversity (Desforges et al., 2022; Reid et al., 2019) with extensive losses of aquatic habitats and degradation of many remaining systems (Jones et al., 2006; Trebitz et al., 2009). Hamilton Harbour is a large (21.5 km^2) freshwater embayment situated at the western end of Lake Ontario that has experienced considerable anthropogenic disturbance from urban and industrial development (Morrison, 2019). The system has lost 80% of its historic wetlands through infilling (Whillans, 1982), and combined with losses of shoals and contaminated sediments, these changes limit the recovery of fish populations (Boston et al., 2016; Holmes, 1988). Eutrophication and hypolimnetic anoxia are pervasive issues in Hamilton Harbour that result in wind-driven upwellings of oxygen-depleted waters into nearshore areas (Flood et al., 2021). The extent of unmodified shorelines as well as submerged aquatic vegetation (SAV) remains below local targets (Gardner Costa et al., 2019, 2020), so any adjustments in habitat quality from upwellings can further reduce habitat supply. Acoustic telemetry has been critical for elucidating the effects of hypoxia on native fishes in Hamilton Harbour (see Brooks et al., 2022; *in revision*) and has provided important information on fish habitat requirements (Brownscombe et al., 2023) and species-specific spatial ecology (e.g., longnose gar [*Lepisosteus osseus*], Croft-White et al., 2023; walleye [*Sander vitreus*], Brooks et al., 2019) that can be used to inform habitat protection and remediation planning in the Great Lakes (Brooks et al., 2017).

The recovery of fish populations in Hamilton Harbour depends on improvements in the quality and quantity of the aquatic habitat. Understanding habitat associations by fishes of interest as well as habitat availability can identify potential limitations to population recovery related to habitat supply. Recovery of native piscivores is a core objective as they should provide top-down control on less-desirable fishes, including aquatic invasive species (Hoyle & Yuille, 2016). However, recovery of native piscivores remains a challenge with persistently low numbers of northern pike (*Esox lucius*; Larocque et al., 2023), a cool-water nearshore predator, and seemingly spatially limited distributions of largemouth bass (*Micropterus nigricans*; Larocque et al., 2024), a warm-water nearshore predator. In contrast, catch of walleye, a cool-water nearshore and pelagic predator, has increased since 2012 as a result of summer fingerling stocking (OMNRF, 2019). As of yet, however, there is no evidence of increased natural recruitment of this species in the system (J. Midwood, unpublished data). From a different perspective, little is known about the habitat associations of freshwater drum (*Aplodinotus grunniens*), a warm-water, non-piscivore species. As a benthic species, their movement and populations are likely affected by anoxia issues within the harbor. In addition to recovery of native top predators, management of aquatic invasive species in Hamilton Harbour is an ongoing challenge. Whereas declines in the catch of common carp (*Cyprinus carpio*) are a positive sign, increased catch of goldfish (*Carassius auratus*) may pose a challenge to fish population recovery (Boston et al., 2024). A more detailed understanding of the habitat requirements of native and nonnative fishes will help inform recovery opportunities as well as management options, respectively.

Our primary objective was to develop a method to spatially assess telemetry-based fish habitat associations at a scale relevant to management. Specifically, we sought to develop seasonal fish habitat association models in Hamilton Harbour for six fish species (common carp, freshwater drum, goldfish, largemouth bass, northern pike, and walleye), identify key habitat variables, and compare habitat association among seasons. We then applied these models to the system to predict the distribution and habitat supply of each species within the harbor as well as overall "hot spots" for tracked fishes. Finally, to further validate our models, for largemouth bass we used boat electrofishing catch data to assess whether modeled predicted presence aligned with areas of higher catch. It is important to stress that the range of habitat information available for our system was limited, and we were constrained to using static layers for our models. As discussed later, this is not ideal and may limit the broader applicability of the habitat associations presented here. That being said, temporally and spatially comprehensive habitat information is likely to be limited in most settings, so our approach here is closer to what will be achievable for most managers, bearing noted caveats. Despite these caveats, results from this study can still inform habitat remediation efforts within Hamilton Harbour and identify potential population-level limitations related to seasonal habitat supply for the tracked species.

2 | MATERIALS AND METHODS

2.1 | Data collection

Seasonal habitat associations in Hamilton Harbour were modeled for six species (largemouth bass, northern pike, walleye, freshwater drum, common carp, and goldfish) based on 6 years of acoustic telemetry detections from May 2016 to May 2022. A total of 253 fish were tagged with acoustic transmitters (henceforth called tags). The majority of fish ($n = 192$) were tagged with V13 pressure (i.e., depth) sensor tags (V13P tags, InnovaSea, Nova Scotia), but 16 walleye and 13 common carp were tagged with V13 tags (without depth sensors), 29 goldfish were tagged with V9P tags, and 2 walleye and 1 goldfish were tagged with V9 tags (Tables S1 and S2; note power output of all tags was similar at 146 or 147 dB). Capture and surgical tag implantation followed the methods described by Brooks et al. (2019), and procedures were approved and followed the Canadian Council on Animal Care protocol administered by Carleton University (110723) and Fisheries and Oceans Canada (DFO; GLLFAS/WSTD ACC 2079). Fish were tagged during multiple tagging events, and the period of detections varied over the study period (Figure S1).

Tagged fish were tracked in Hamilton Harbour using acoustic receivers (VR2W or VR2AR 69 kHz, InnovaSea, Nova Scotia) distributed among a variety of habitat conditions (e.g., shoals, vegetated areas, deeper open waters, and inlets; Figure 1). In 2016, the array consisted of 32 acoustic receivers and expanded to 59 receivers by 2022 (Figure 1). Note that a few receivers were seasonally deployed (e.g., in Grindstone Creek), lost and replaced, or could not be redeployed due to logistical challenges associated with COVID-19. A timeline of receiver deployments is shown in Figure S2. Receivers in the Piers 5–7 area were highly condensed, and to reduce overlap

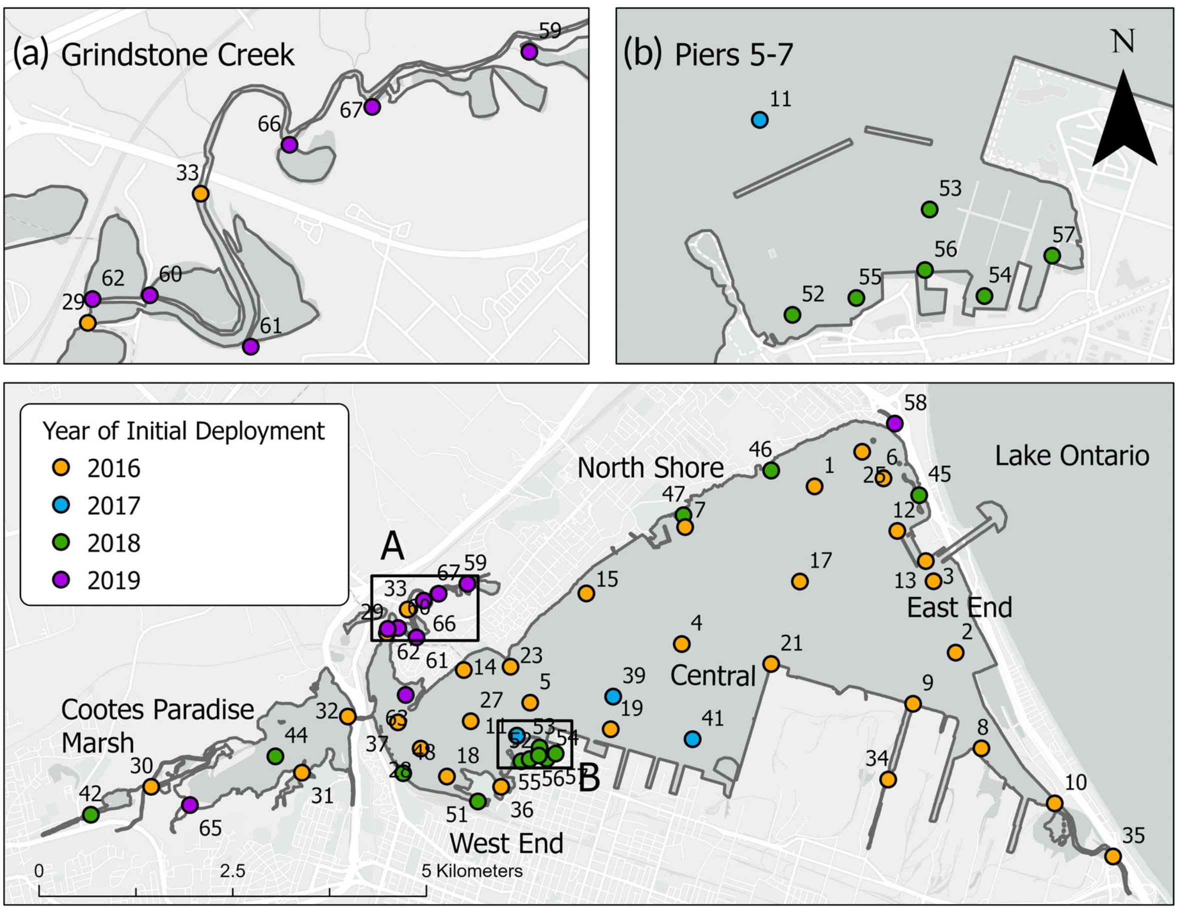

FIGURE 1 Receiver locations in Hamilton Harbour and the expansion of the array over time based on initial year of deployment, with close-ups of (a) Grindstone Creek and (b) Piers 5–7. Numbers indicate the station number. See Figure S1 for the timeline of receiver deployments.

(potential spatial autocorrelation issues) we included only station HAM-053 in the analyses.

Environmental and habitat data used to model habitat associations were bathymetric depth (m), mean wind-weighted fetch (m, to distinguish sheltered vs. more wind-exposed sites; herein referred to as fetch), Secchi depth (m, water clarity), % hard substrate (sum of gravel/rubble/cobble/boulder), and % cover of SAV (Data S1; Figure S3). When detected, tagged fish were assumed to be within 350 m of the receiver based on the average 50% detection range within the open waters of the harbor across stratified and isothermal conditions (Supplementary Data C in Wells et al., 2021). Note that due to differences in detection range year to year, from seiches, vegetation, and stratification, we used an overall detection range of 350 m as we did not have enough data to use a dynamic detection range in different habitats for each season. To determine telemetry-based habitat associations while not knowing the fish's precise location, the mean value of bathymetric depth, Secchi depth, % hard substrate, and % SAV within the 350-m detection range of receivers were calculated using ArcGIS Pro (version 2.8.8, ESRI, Redlands, CA, USA). Fetch was calculated at the receiver station only. This 350-m detection range included only areas within line of sight of the receiver, as islands or land can interfere with detections. To accomplish this, 350-m buffers around each receiver were created in ArcGIS Pro and manually adjusted to correct for line of sight. Environmental values for each receiver were then merged with the detection data. To create model predictions across the entire system, a 50-m grid of the harbor was developed, and mean environmental data were obtained within a 350-m buffer (excluding land) around each grid point to match the methods used at the receiver stations.

Seasons were based on temperature profiles collected using a chain of temperature loggers that were deployed annually at the center of Hamilton Harbour from early spring to late fall (43.288°N, −79.845°W). Season was defined by temperature dynamics and thermocline delineation after Larocque et al. (2020): spring (>5°C and warming isothermal), summer (established thermocline), fall (first full water column mixing), and winter (temperature is no longer declining and <5°C isothermal). Temperature profiles were unavailable in the harbor from 2019 to 2022, and for these years, seasons were based on the mean Julian day of seasonal delineation in the harbor from Larocque et al. (2020): spring: April 25 to June 6, summer: June 7 to October 3; fall: October 4 to November 17, and winter: November 18 to April 24.

2.2 | Data analyses

All data preparation and analyses were conducted in R version 4.3.0 (R Core Team, 2023). Telemetry detections were first submitted to the Great Lakes Acoustic Telemetry Observation System database to undergo basic quality assurance and control, including time synchronization. Data were then filtered to remove fish that were presumed dead. Fish were inferred to be dead if they continuously exhibited constant depth-use profiles and stayed within the same area of the array for the remainder of their detections (potentially detected on multiple receivers all within the same vicinity; Klinard & Matley, 2020). If fish were alive for a period >1 month prior to suspected mortality, then all detections after the 24 h prior to the suspect data were removed. This removed any potential irregular behavior prior to perceived mortality. Fish with <1 month of detections were removed entirely from analyses. Erroneous detections were removed if they met criteria for false-positive detections (i.e., single occurrences with >6000 s between successive detections or 30 times the typical 200-s nominal delay of the tags; Pincock, 2012). Detections were also removed when tags were detected on the same receiver earlier than the minimum ping rate of the tags, and when detections were not spatially possible (e.g., in another lake system). After data preparation, 188 fish were used in our analyses, which included 25 largemouth bass, 32 northern pike, 56 walleye, 13 freshwater drum, 26 common carp, and 36 goldfish. For each species, detection data were used to generate daily presence and absence summaries for each receiver. To ensure sufficient numbers of individuals, only days in which at least five individuals per species were detected in the harbor were included in the analyses (Brownscombe et al., 2023). Environmental variables associated with receivers were not strongly correlated (correlation <0.7), and all variables were used in the analyses.

For each species, a random forest (RF) algorithm (a type of machine-learning algorithm; Breiman, 2001) was fit to species-level daily presence–absence data at each receiver. The habitat conditions associated with each receiver were included as predictors of species presence, including water depth, fetch, Secchi depth, % hard substrate, % SAV, and season. All predictors except season were continuous and were not considered strongly correlated ($r < 0.75$). Season was categorical and was included as we were interested in seasonal changes in habitat associations. For each species, the data were randomly split into 70% training and 30% test datasets. RF models were fit to each species' training data with 1000 trees, and the default number of variables (the square root of the number of predictors) was tried at each split. Models were weighted to account for zero-inflated data and improve accuracy of predicting fish presence (Brownscombe et al., 2021). Presences and absences were numerically weighted using the classwt() argument in the RF model formulation at 1 and 0.95, respectively.

Variable importance was quantified using mean decrease in accuracy (Breiman, 2001), which shows the percentage decrease in model accuracy when a specific variable is omitted. Telemetry-based habitat suitability indices were derived from these models by calculating the partial dependencies ($\hat{y}$, marginal effect of the predictor) of each predictor variable as a two-way interaction with season. RF were fit using the "randomForest" package (Liaw & Wiener, 2002), model fit metrics were calculated using the "caret" package (Kuhn, 2008), and partial dependencies ($\hat{y}$) were calculated using the "pdp" package (Greenwell, 2017).

Spatial autocorrelation was assessed using the test dataset for each species by calculating Moran's I at lag distances of 0.5, 1.0, 2.0, 4.0, and 6.0 km. Moran's I was calculated using the "plot_moran" function in the "spatialRF" package (Benito, 2021). Moran's *I* values range from −1 (indicating perfect negative spatial autocorrelation) to 0 (indicating no spatial autocorrelation) to 1 (indicating perfect positive spatial autocorrelation). All Moran's *I* estimates were near zero (−0.015 to 0.015) for each species and spatial lag, indicating no meaningful residual spatial autocorrelation in fish detections between receivers.

Temporal autocorrelation was assessed using the test dataset for each species. Autocorrelation was inspected for each species using the function "acf," across temporal lags of 1–366 days. Calculated correlations were then plotted using the "ggplot2" package and compared against 95% confidence intervals centered at acf = 0. All species presented evidence of temporal autocorrelation, but RF models are non-parametric and relatively insensitive to autocorrelation (Booher & Walters, 2021; Cutler et al., 2007).

Based on the model, each species' seasonal presence probability ($\hat{y}$) was predicted throughout the harbor based on the environmental variables associated with the 50-m grid points, as described earlier. From these maps, key areas with habitat conditions that each species was associated with could be visualized and the amount of high presence habitat calculated. High presence habitat was deemed as the total area in Hamilton Harbour with a predicted presence probability greater than or equal to 80%. The amount of high presence habitat per season per species was calculated and visually assessed for trends.

To validate the presence probability and habitat suitability model predictions in the harbor, we compared the predicted presence probability of largemouth bass to the mean electrofishing catches in the summers from 2016 to 2021 during local fish community monitoring at depths <2 m (see Brousseau et al., 2005, for details on the standardized electrofishing protocol). Due to the large number of electrofishing survey sites where no adult largemouth bass (total length >250 mm) were captured (zeros), a linear regression could not be performed. Instead, the optimal threshold (optimal.thresholds function in "PresenceAbsence" package using MaxKappa values; Freeman & Moisen, 2008) was calculated to determine what predicted presence probability value from the RF model aligned with the likelihood of capturing an adult largemouth bass during electrofishing surveys (i.e., threshold for presence). A very low threshold would indicate that the model is too generalized, with fish being present at low probabilities, whereas a very high threshold would indicate the model is too specific, with fish present only at high probabilities. The mean catches were also spatially plotted against the predicted presence probability map to visually verify model fit. This analysis could be completed only for largemouth bass because they were more frequently captured in electrofishing surveys than the other species tracked in this study (J. Midwood, unpublished data).

3 | RESULTS

We had sufficient data to model telemetry-based fish habitat associations for six fish species in Hamilton Harbour. Model accuracy was >0.8 for all species (Table 1). For all species, habitat associations varied by season, and season held high importance relative to the other traits (Figures 2–7, panel a). After season, fetch, water depth, and % SAV were the habitat variables with the highest relative importance and improved model accuracy the most across species (Figures 2–7, panel a). Note that the range of values for habitat variables in the models influenced habitat association outputs as models did not extrapolate beyond the range of values associated with the telemetry data. Relative to the conditions that fish can potentially experience within Hamilton Harbour, fetch (0–2.5 km) and water depth (0–20 m) had a wider range of possible conditions compared to % SAV (0%–40%), % hard substrate (0%–6%), and Secchi depth (0–2.5 m). It is important to stress that modeled habitat associations reflect generalized habitat conditions with which fish are associated because telemetry-derived positions were inexact and linked to average habitat conditions within a 350-m buffer.

Largemouth bass and northern pike had similar habitat associations within Hamilton Harbour (Figures 2 and 3). Both inhabited the nearshore as they were more strongly associated with sheltered areas (fetch <1 km) and shallower depths (3–10 m). Largemouth bass and northern pike were associated across all vegetated areas relative to no vegetation (% SAV >0%) and areas with some hard substrate available (2%–6%). Seasonally, largemouth bass expanded their habitat associations with slightly greater depth and Secchi depth in the fall and winter. Northern pike had similar seasonal associations, with a more pronounced preference for greater Secchi depth in the fall and winter (>2 m; Figure 3).

Walleye and freshwater drum had similar habitat associations within Hamilton Harbour (Figures 4 and 5). Both inhabited the offshore and were strongly associated with highly exposed areas (fetch >1 km), deeper waters (water depths 10–25 m), and clearer waters (Secchi depths >1.5 m), with some association with less-vegetated areas (% SAV < 20%) and soft substrates (% hard substrate <2%). Walleye had lower marginal effect values in the summer, which coincided with many tagged walleye leaving Hamilton Harbour and consequently a decline in the proportion of presence near each receiver throughout the harbor. Some freshwater drum also left the harbor during the summer, but there was no decline in marginal effect values compared to other seasons. Walleye exhibited similar habitat associations during spring, fall, and winter, whereas summer showed walleye associated with areas with intermediate Secchi depths (∼1.5 m; Figure 4). Freshwater drum in Hamilton Harbour had the same general offshore habitat associations as walleye, with some seasonal differences in the spring and winter (Figure 5). In the spring, freshwater Drum were associated with all water depths (0–25 m) and Secchi depths (0.5–2.5 m), and moderately exposed areas (fetch ∼1 km; spring and winter seasons).

Common carp and goldfish shared some similar habitat associations across seasons and generally occurred in nearshore habitat similar to largemouth bass and northern pike (Figures 6 and 7). Common carp in Hamilton Harbour were inhabiting the nearshore as they were more strongly associated with sheltered areas (fetch <1.5 km) and low vegetated areas (% SAV <10%), with some association with shallower

TABLE 1 Performance of fish habitat association random forest models for species in Hamilton Harbour.

Species	*n* Size of dataset	Accuracy Overall accuracy of prediction, with confidence intervals	No information rate Likelihood of predicting correctly when no information is given	Sensitivity Likelihood of true presence predicted as presence	Specificity Likelihood of true absence predicted as absence	Positive predictive value Likelihood that a predicted presence is correct	Negative predictive value Likelihood that a predicted absence is correct	Balanced accuracy Average of sensitivity and specificity	*p*-Value Test whether model outperforms no-information null model
Common carp	42,521	0.78 (0.77, 0.79)	0.57	0.77	0.79	0.74	0.82	0.78	0.00
Freshwater drum	30,517	0.83 (0.83, 0.84)	0.55	0.85	0.82	0.79	0.87	0.84	0.00
Goldfish	43,125	0.82 (0.81, 0.82)	0.62	0.88	0.78	0.71	0.91	0.83	0.00
Largemouth bass	42,551	0.84 (0.84, 0.85)	0.71	0.88	0.83	0.68	0.94	0.86	0.00
Northern pike	48,093	0.85 (0.84, 0.85)	0.65	0.87	0.84	0.75	0.92	0.85	0.00
Walleye	56,727	0.84 (0.84, 0.84)	0.61	0.84	0.85	0.90	0.77	0.84	0.00

depths (3–10 m) and no preference for % hard substrate or Secchi depths (Figure 6). Common carp did not exhibit major seasonal variations, aside from associations with a broader range of water depth (3–25 m) in the fall. Goldfish also tended to inhabit the nearshore and had some association with sheltered areas (fetch <1.5 km), at shallower depths (water depths 3–12 m), that were a mix of vegetation (% SAV 1%–35%), with no preference for % hard substrate and mixed preference for Secchi depths (Figure 7). Goldfish had a stronger seasonal change in habitat associations with the fall and winter in which they occurred in both offshore and nearshore habitats and were associated with a greater range of water depths (3–25 m), greater range of exposure (fall only; fetch 0–2.5 km), and greater range of Secchi depths (0.5–2.5 m). In the spring and summer, goldfish were associated with more nearshore (sheltered, shallow), vegetated (% SAV 5%–15%), and turbid environments (Secchi depths <1 m; Figure 7).

The presence probability of each species was spatially predicted for each season within Hamilton Harbour and showed some similar trends across species and seasons. Generally, most species showed a spatial range expansion, with greater presence probability in the fall and winter to include parts of the harbor further offshore and a range contraction in the spring and summer toward the nearshore (Figures 2–7, panel g). The amount of area predicted to have high presence habitat based on a presence probability greater than 80% matched these seasonal spatial trends, with area generally highest for species in fall and lowest in summer (Figure 8). Walleye, followed by freshwater drum and goldfish, had the largest areas of high-quality habitat, particularly in the fall and winter when they were present in offshore areas (Figures 4, 5, and 7, panel g; Figure 8). Largemouth bass, northern pike, and common carp were also the most spatially restricted and had the lowest maximum seasonal area of high presence habitat where the predicted presence was greater than 80% with 2.1, 3.4, and 5.9 km^2, respectively (Figure 8). Notably, high presence habitat was predicted to be available in the western end of Hamilton Harbour for a majority of species, particularly when their spatial ranges contracted in the spring and/or summer (Figures 2–7, panel g). Walleye were an exception to this pattern, with high presence habitat found throughout the system, except during the summer. In the west end of the harbor, in terms of spatial association with the wetlands in the system, largemouth bass, northern pike, and common carp were predicted to be present in Cootes Paradise Marsh, whereas those three species and goldfish were also predicted to be present in Grindstone Creek marshes, particularly in the spring.

Further model validation was conducted by comparing the predicted summer largemouth bass presence probability to an existing dataset of summer electrofishing catches from the same location. The optimal threshold for largemouth bass to be present in electrofishing surveys was at a predicted presence probability of 0.77. Any predicted presence value >0.77 was more likely to have largemouth bass captured during electrofishing surveys, and the model tended to overpredict where largemouth bass would occur relative to actual capture (Figure 9a). Spatially, largemouth bass were primarily captured in the west end of Hamilton Harbour and occasionally along the north and east shoreline, matching the RF model predictions

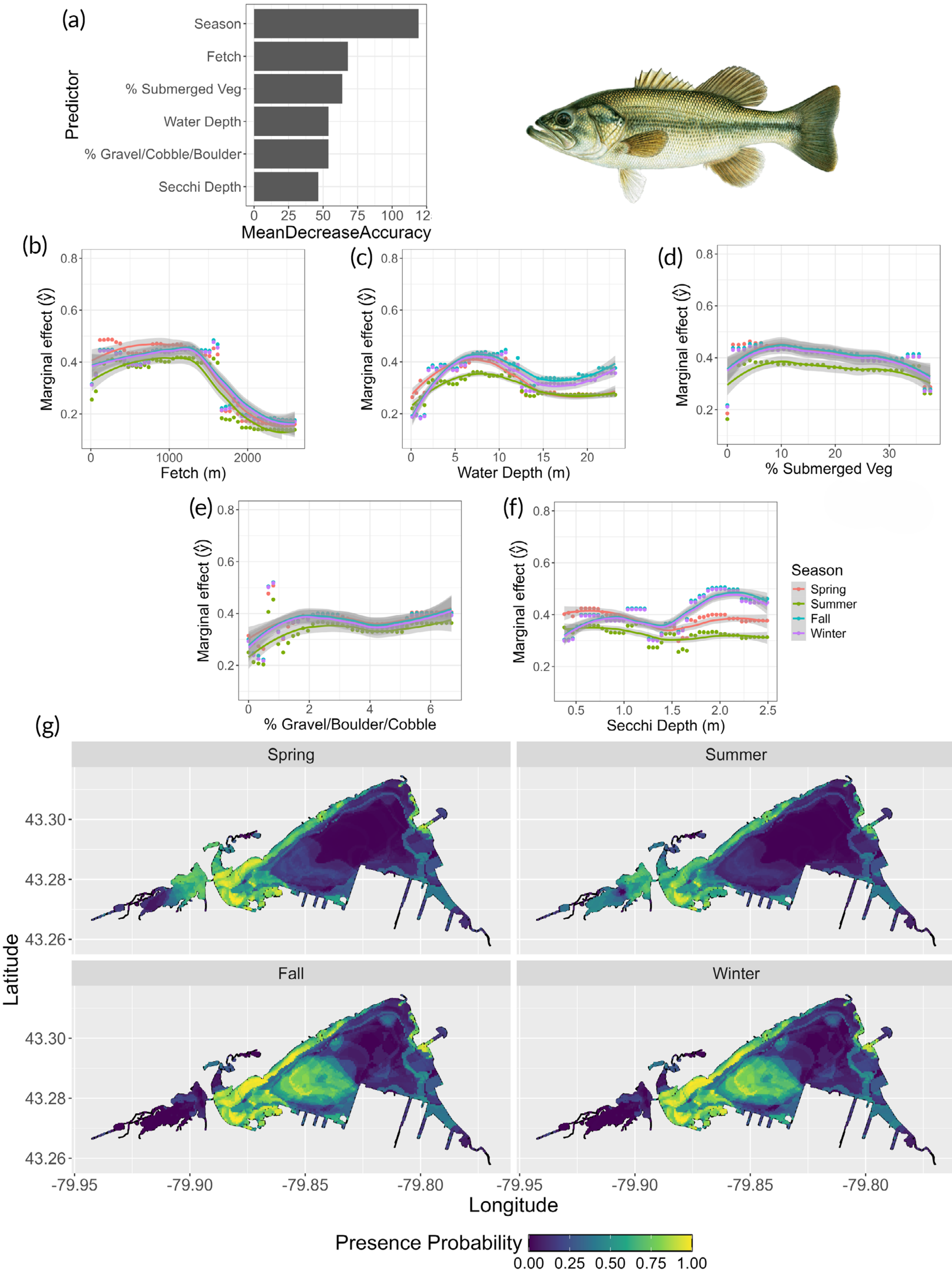

FIGURE 2 Largemouth bass (*Micropterus nigricans*) fish habitat association model in Hamilton Harbour, indicating (a) relative variable importance, (b–f) specific habitat variable associations across seasons, and (g) predicted spatial presence probability throughout the harbor across seasons.

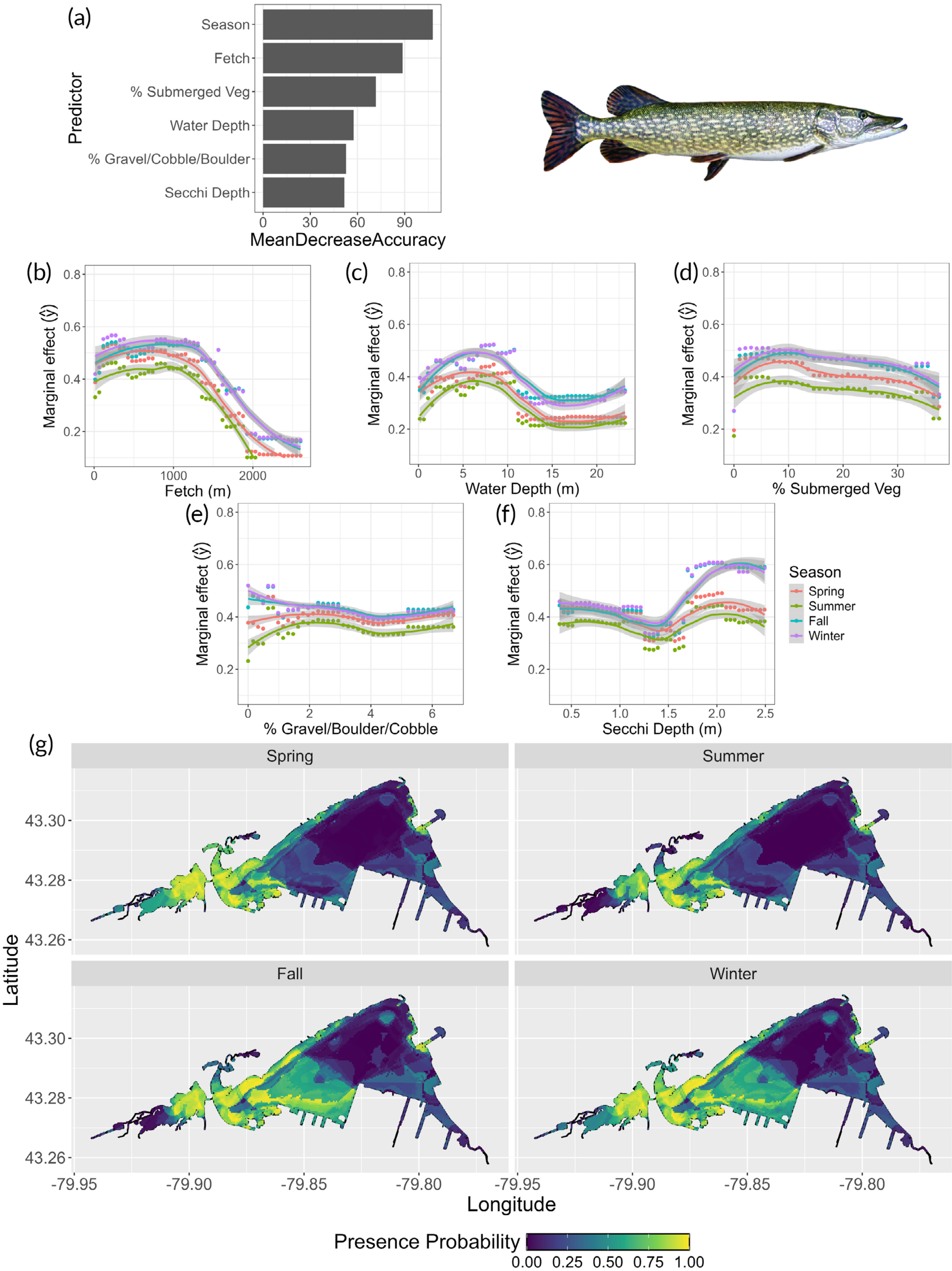

FIGURE 3 Northern pike (*Esox lucius*) fish habitat association model in Hamilton Harbour, indicating (a) relative variable importance, (b–f) specific habitat variable associations across seasons, and (g) predicted spatial presence probability throughout the harbor across seasons.

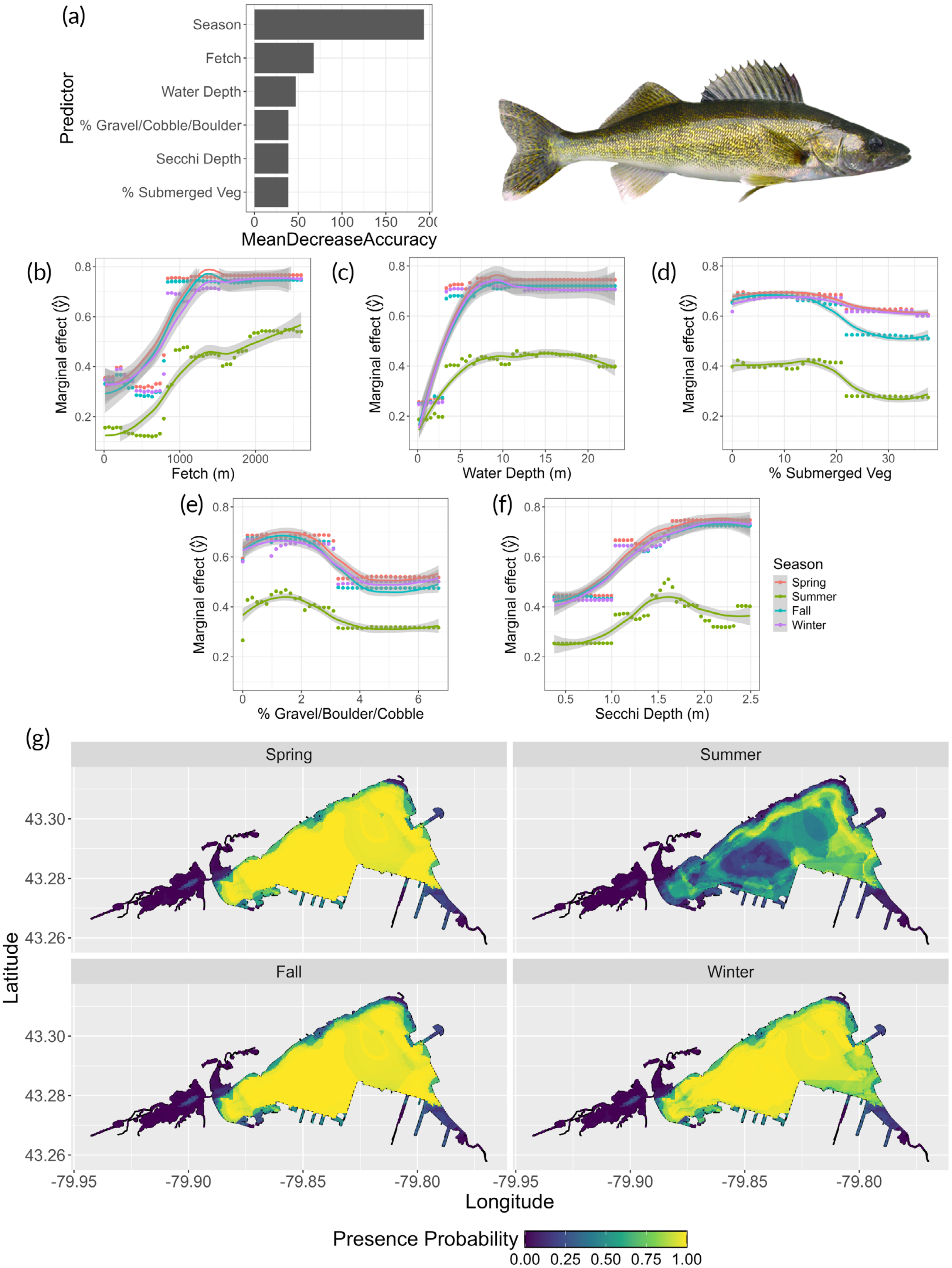

FIGURE 4 Walleye (*Sander vitreus*) fish habitat association model in Hamilton Harbour, indicating (a) relative variable importance, (b–f) specific habitat variable associations across seasons, and (g) predicted spatial presence probability throughout the harbor across seasons.

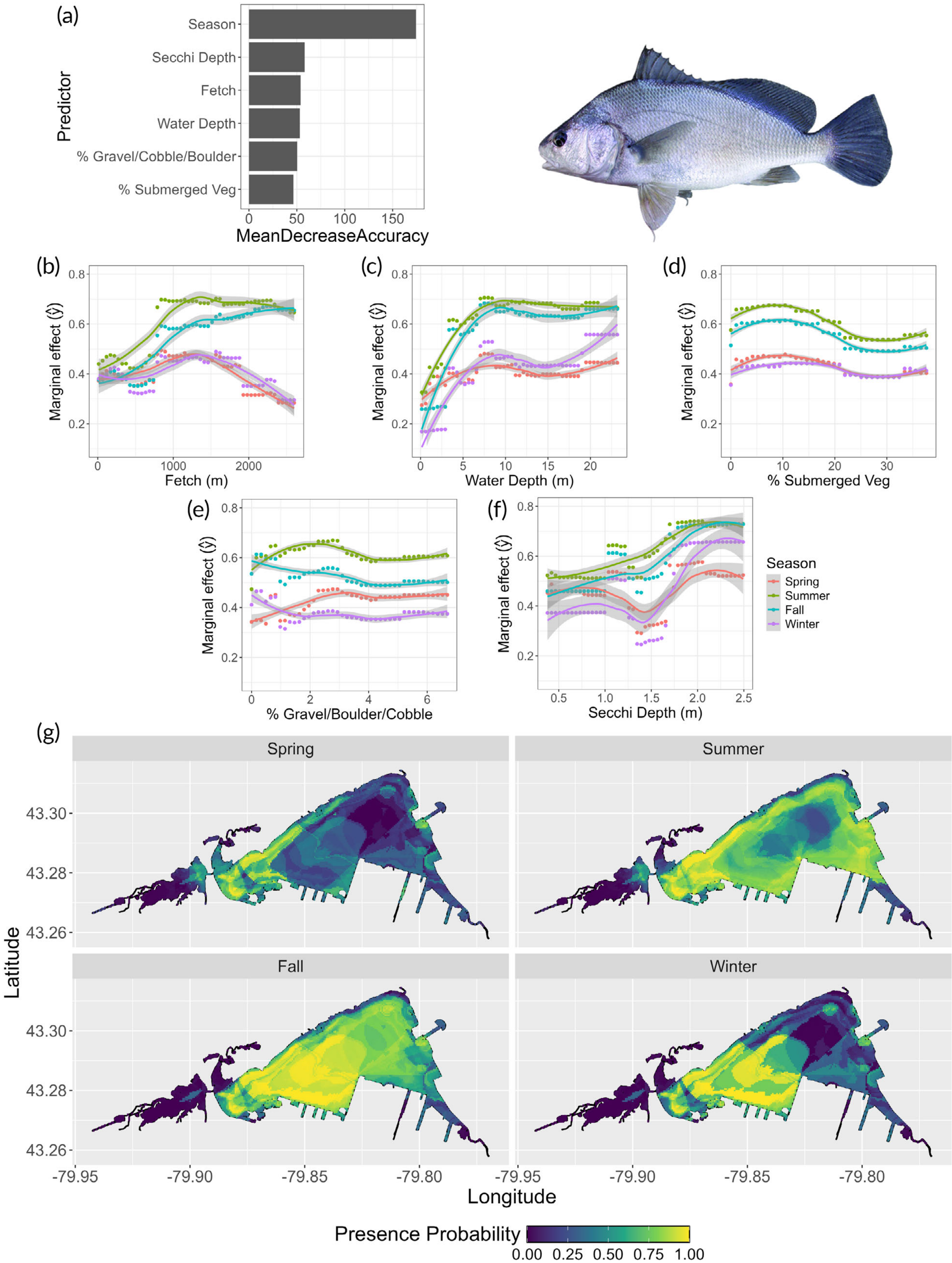

FIGURE 5 Freshwater drum (*Aplodinotus grunniens*) fish habitat association model in Hamilton Harbour, indicating (a) relative variable importance, (b–f) specific habitat variable associations across seasons, and (g) predicted spatial presence probability throughout the harbor across seasons.

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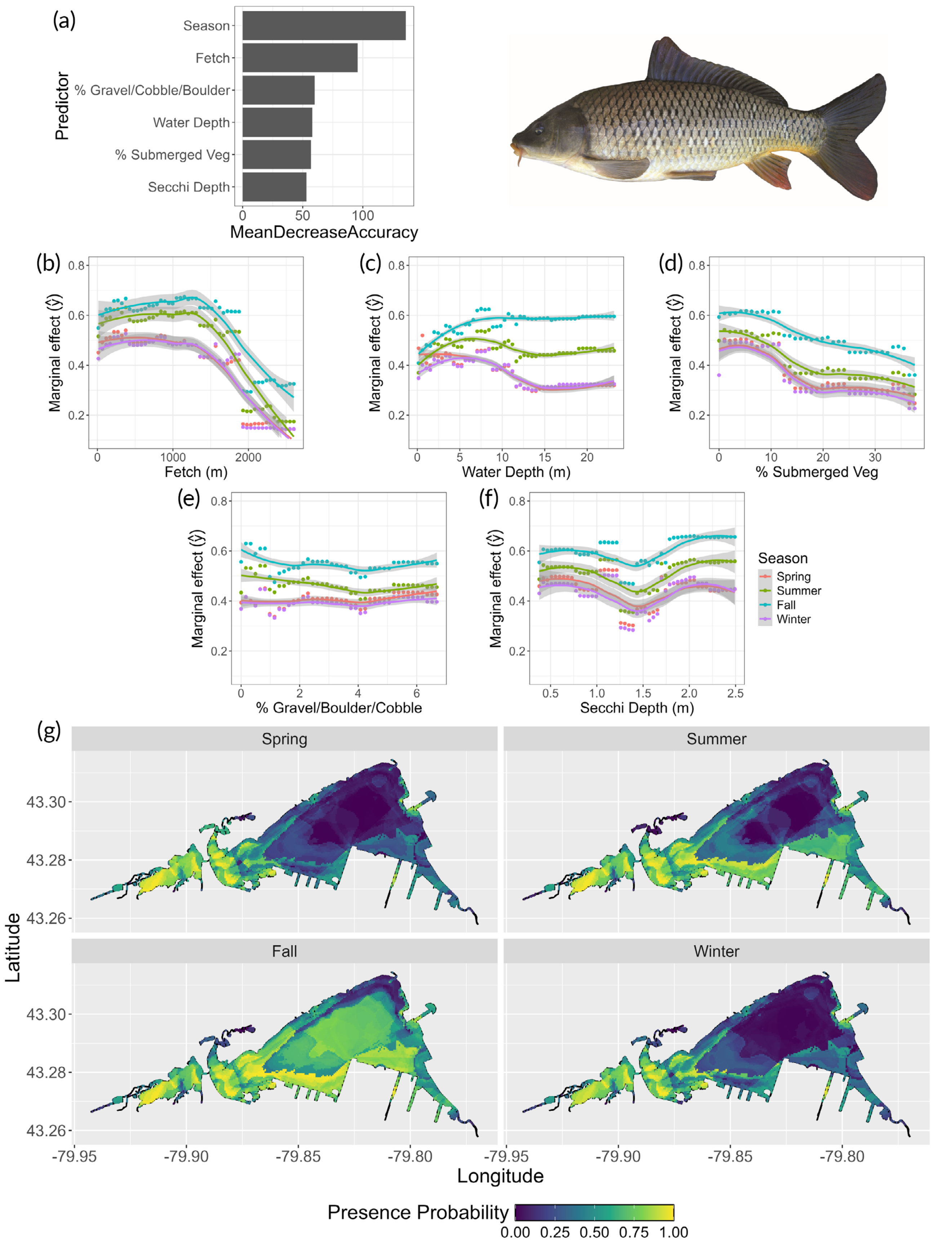

FIGURE 6 Common carp (*Cyprinus carpio*) fish habitat association model in Hamilton Harbour, indicating (a) relative variable importance, (b–f) specific habitat variable associations across seasons, and (g) predicted spatial presence probability throughout the harbor across seasons.

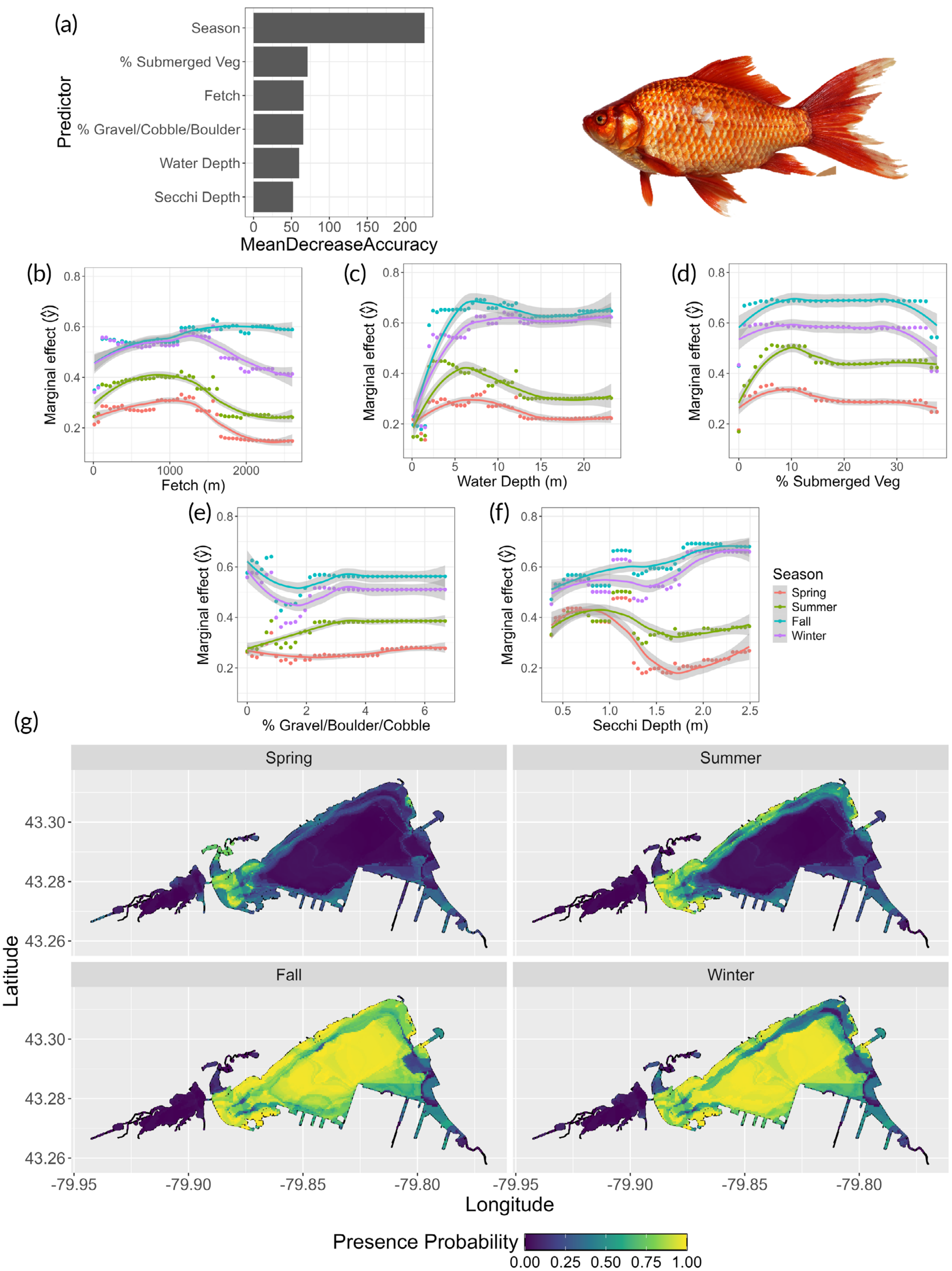

FIGURE 7 Goldfish (*Carassius auratus*) habitat association model in Hamilton Harbour, indicating (a) relative variable importance, (b–f) specific habitat variable associations across seasons, and (g) predicted spatial presence probability throughout the harbor across seasons.

fairly well where electrofishing surveys were able to be conducted (Figure 9b).

4 | DISCUSSION

Seasonal habitat associations and spatially predicted presence distributions (or habitat availability) were defined for six key fish species in Hamilton Harbour, Lake Ontario. Fish presence was primarily related to fetch, water depth, and % SAV in Hamilton Harbour, although the specific habitat that species associated with was variable. Despite differences, across species there were similar seasonal changes in both habitat associations and overall amount of area that fish inhabited, with species tending to use a larger area of the harbor as they moved offshore to deeper waters in the fall and winter. Modeling fish habitat associations for a variety of species highlighted their spatial overlap in the west end of Hamilton Harbour. Model verification with electrofishing catches further bolstered our confidence in the largemouth bass models, and such an approach can help indicate areas for restoration (i.e., low catch and low predicted presence) or future sampling (i.e., no catch information but predicted high presence). Finally, the spatial presence predictions of these fish habitat models provided quantitative estimates of available habitat and, by overlaying output from different species, identified fish "hot spots." Collectively, such outputs can identify habitat-supply-based limitations to fish population recovery and identify areas in need of restoration.

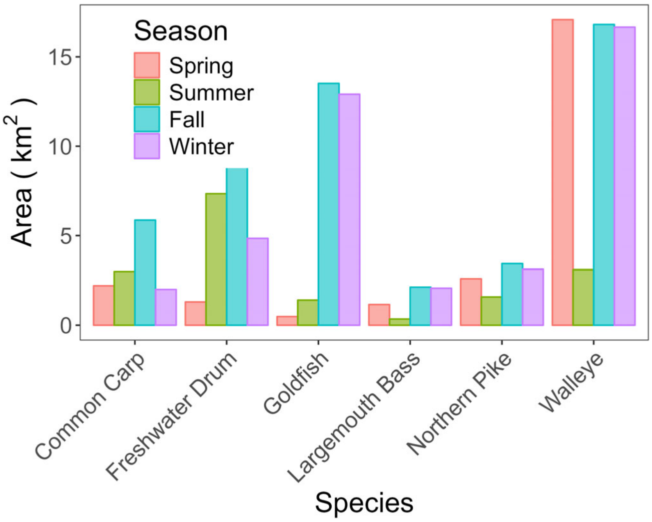

FIGURE 8 The area (km^2) within Hamilton Harbour that had ≥0.80 predicted presence probability for each species across seasons.

When interpreting model results it is important to keep in mind caveats and limitations of the acoustic telemetry and habitat data used in the models. With the acoustic telemetry array in Hamilton Harbour, shallow, nearshore areas had less coverage than offshore areas, particularly in the earlier years of the study. Additionally, the exact position of an individual detected at a receiver was unknown and was assumed to occur within a 350-m radius that reflected the mean 50% detection range (Wells et al., 2021). Not knowing the precise location of fish meant we had to derive habitat variables as the mean conditions within the detection range of the receiver; consequently, habitat conditions for some receivers positioned in shallow nearshore waters included values more indicative of

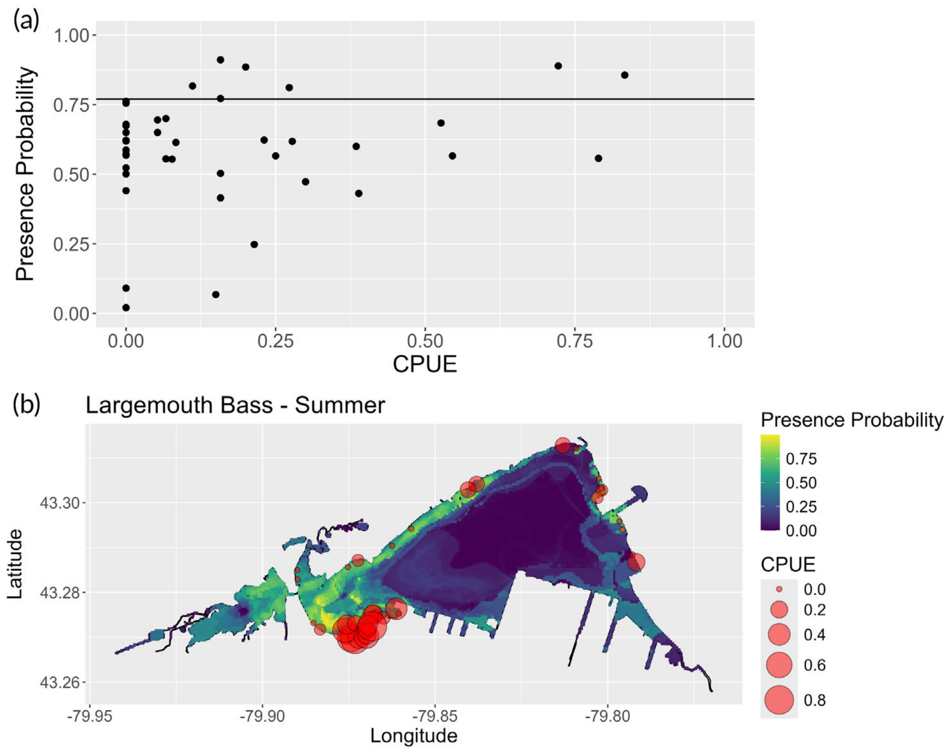

FIGURE 9 Largemouth bass (*Micropterus nigricans*) habitat association model's predicted presence probability and mean catch per unit of effort (CPUE) from electrofishing surveys with (a) the line indicating the 0.77 optimal threshold of the model in which CPUE is >0 and (b) the spatial pattern of predicted presence and CPUE.

offshore areas. Thus, a fish's modeled habitat associations may be deeper, more exposed, or with less vegetation than in reality, particularly because vegetation and hard substrate are localized to shallow areas around the margins of the harbor (Gardner Costa et al., 2019, 2020; Figure S3). Similarly, habitat data were modeled as static values, but the majority of the input variables, including % SAV and water depth, vary seasonally and annually. We did set mean water depths based on the observed mean water levels during the study period, and % SAV was then modeled based on these depths; however, variations from year to year or across seasons could influence how fish interact with habitat features at a receiver. This is particularly true of SAV, where modeled values reflect the summer maxima of extent and cover. Because SAV has largely senesced by the fall and winter, positive associations likely do not reflect the direct use of SAV per se but instead indicate a species' association during these seasons with the conditions that promote the growth and establishment of SAV (i.e., primarily shallower depths [surrogate for sufficient light] and low exposure to wind and wave action; Lacoul & Freedman, 2006). To resolve this type of challenge, future studies of fish habitat association could attempt to use more dynamic habitat variables that capture the seasonal growth and senescence of aquatic vegetation, variation in water depth based on lake water levels, changes in wind direction and speed (our study used fetch based on wind direction only), and variable water clarity driven by riverine inputs and other factors. Such an approach would more tightly align fish presence at a receiver with the recent environmental conditions at that site and would allow other important but more temporally dynamic habitat components like dissolved oxygen (e.g., upwellings of anoxic hypolimnetic waters; Brooks et al., 2022; Flood et al., 2021) or ice cover (e.g., Marcaccio et al., 2022) to be included in the models. Given logistical constraints or lack of data, we limited the analyses to static layers; however, model results from static layers still provide a general indication of fish habitat associations in our system at a temporal scale relevant to managers using a method that is transferable to other systems.

For the most part, despite noted issues of resolution and static habitat inputs, the modeled habitat associations presented here match the literature well (e.g., Lane et al., 1996; Rudolfsen et al., 2021; Scott & Crossman, 1998) and were relatively similar to those derived for fishes inhabiting nearby areas like Toronto Harbour, Lake Ontario (Brownscombe et al., 2023). There were, however, some species-specific differences in habitat associations relative to what has been previously documented. For example, marginal effects for largemouth bass suggested they would select areas with SAV cover (1%–35%) relative to no SAV, whereas past works have indicated a preference for sparse to dense (10%–60%) SAV (Brownscombe et al., 2023; Miranda & Pugh, 1997; Valley et al., 2004). Such a discrepancy is almost certainly related to how habitat variables were derived (as discussed previously) rather than evidence of distinct habitat association in Hamilton Harbour. For example, there are extensive beds of dense SAV along the north shore of the harbor, but the width of these beds is in all instances less than the 350-m receiver detection range (SAV bed width mean ± SD = 175 ± 72 m, maximum = 288 m; Gardner Costa et al., 2019); as such, a species association with % SAV cover will inherently be underestimated in our models.

The modeled habitat associations were indicative of inherent similarities and differences in species' ecology among the tracked fishes. For example, both largemouth bass and northern pike were found to occupy shallow, sheltered areas that can support aquatic vegetation and more structure, which would reflect a more littoral ambush predation behavior with limited movement (Ahrenstorff et al., 2009; Říha et al., 2021). Also, they were the most spatially restricted species in the harbor, which reflects the low movement ambush predation style in these habitats and also indicates this type of habitat is limited in Hamilton Harbour and that this limitation likely contributes to northern pike populations being very low (Larocque et al., 2023). In contrast, walleye and freshwater drum used a larger portion of Hamilton Harbour, consistent with them being more pelagic and benthic species, respectively, that use further offshore, deeper, and more exposed areas with less cover (i.e., SAV or hard substrate; Gorman et al., 2019; Rudolfsen et al., 2021). These two species were more mobile and also had individuals that migrated out of the harbor during the summer, whereas the other study species were more resident. Finally, although there were some differences in habitat associations between common carp and goldfish, with the latter tending to use areas with greater SAV % cover, they both generally preferred nearshore, sheltered areas and showed range expansions in the fall in particular. Predicted areas of suitable habitat for these two nonnative fishes overlapped considerably in the spring and summer with northern pike and largemouth bass, but common carp and goldfish tended to move further offshore into deeper waters in the fall and winter.

There were some consistent seasonal changes in most fish species, with movement toward deeper areas further offshore during the fall and winter and a contraction of the area used in the spring and summer as fish moved closer to shore in sheltered areas. The depth use of these fish species also increased in the fall and winter and decreased in the spring and summer (Larocque et al., 2020), matching the modeled horizontal shifts in this study. Similarly, spatial home ranges of walleye in Hamilton Harbour were also smaller in summer compared to other seasons (Brooks et al., 2019). Summer had the least available habitat for all fish species and could be limiting population recovery for species like northern pike, which are currently in low abundance in the harbor (Budgell et al., 2024; Larocque et al., 2023). In summer, the hypolimnion of Hamilton Harbour is anoxic (Gertzen et al., 2016; Hiriart-Baer et al., 2016; Polak & Haffner, 1978) and can push into nearshore areas during seiche-driven upwelling events (Flood et al., 2021). It has been posited that mobile top predators like walleye may benefit from summer habitat compression associated with anoxia (Brooks et al., in revision) or leave the system during this period (as some individuals migrate to other areas in the summer); however, less-mobile fishes or life phases may be negatively affected and consequently be restricted to less-suitable habitats. Anoxia, among other summer stressors (e.g., algal blooms; Munawar et al., 2017), likely reduces the amount and changes in the type of habitat available for fishes, which would influence their distribution and resulting modeled habitat associations. In other ecosystems, winter may act as the limiting season due to ice cover or water quality factors (e.g., temperature, dissolved oxygen) reducing available habitat (Marsden et al., 2021). In contrast, in Hamilton Harbour, winter was typically second only to fall in the amount of habitat predicted to be available. Evaluating seasonal habitat use showed how different habitat types are important throughout the year and allowed us to identify when habitat supply limitations were occurring across species (typically in summer) and in turn alluded to factors (e.g., anoxia) that may be limiting population recovery in this system.

Across the variety of fishes tagged, spatially, there was stronger association with the west end of the harbor and less association in deeper waters and along the southeastern portion of the harbor (except for walleye). Hamilton Harbour generally has higher fish catches or densities in the west end based on electrofishing (Boston et al., 2016; Maynard et al., 2022) and hydroacoustic surveys (Midwood et al., 2019), which could be related to increased productivity from Cootes Paradise Marsh and Grindstone Creek but also the presence of habitat features such as reduced fetch, reduced depth, and sufficient % SAV cover as determined in our models. Proximity to wetlands or other sheltered areas may promote greater fish presence because they are a source of refuge. In contrast, the east end of the harbor had weaker predicted associations, for more nearshore-oriented fishes in particular. Although habitat remediation efforts at the east end have included the creation of islands with sheltered areas with SAV behind them (Smokorowski et al., 1998), the east end remains more exposed (aligned with the prevailing winds) and is affected by hypolimnetic upwelling of anoxic waters (Flood et al., 2021). In a recent assessment of fish communities within the system, Maynard et al. (2022) found a distinct fish community at the east end of the harbor relative to the north and west and posited that the islands created there provide the only sheltered habitat at the east end of the harbor and thus attract more nearshore-oriented fishes (e.g., pumpkinseed [*Lepomis gibbosus*], yellow perch [*Perca flavescens*], and largemouth bass). That being said, the total amount of sheltered habitat at the east end is much lower than that at the west given the presence of connected wetlands in the latter area, so this remains an area where habitat restoration may be required.

A novel component of the present work was the blending of acoustic telemetry-derived habitat suitability predictions with field-based electrofishing capture rates for largemouth bass. Both methods have limitations; as noted, telemetry detections can be limited by receiver detection range and the scale at which a fish can be positioned within this range. Electrofishing catches can be influenced by site conditions (e.g., conductivity, water clarity, water depth; Brousseau et al., 2005), which can affect species detection and capture, and it is temporally restricted, so sampling must align with the timing of use. Sampling by electrofishing is also spatially restricted to the nearshore (i.e., depths <1.5 m) where largemouth bass will more likely be found and cannot be used to verify absences in deeper, offshore waters. As such, some level of disconnect between telemetry-based predictions and field-based catch rates is to be expected. Taken together, however, these approaches are complementary with electrofishing, confirming the presence of a species within a specific type of habitat and therefore offering an independent means of assessing telemetry-based model predictions; both methods aligned relatively well in this study. Conversely, the application of telemetry-based model predictions back to the system can identify areas where additional field-based sampling efforts should be directed. The latter is particularly important for species with low catch rates in electrofishing-based surveys (e.g., northern pike; Budgell et al., 2024) because apparent absences in catch can be interpreted as low overall population sizes but may instead be related to a misalignment in the timing and location of sampling. If additional sampling confirms the absence of a species of interest in an area predicted to be highly suitable, this would suggest that a habitat component not captured in the model reduces the suitability at that location, and consequently, some form of habitat remediation may be required. For example, some transects with low catches were centrally located along the north shore that were predicted to have high probability of the presence of largemouth bass. Their absence during electrofishing suggests a residual impairment, possibly related to dissolved oxygen or algae covering much of the SAV in this region (J. Brownscombe, personal communication). Although we used an existing electrofishing dataset, model verification can be used with other types of datasets as well. For example, literature-/expert-based habitat suitability models could also be compared to telemetry-derived predictions and better inform areas of congruence and digression, both of which can be informative in our interpretation of habitat use of fishes.

Overall, the analytical approach used here performed well in characterizing the habitat associations of target species and could be expanded to incorporate both telemetry- and field-based occurrence data in future projects. RF models are increasingly employed in habitat selection studies (Kim et al., 2021) due to their resilience to various data distributions and non-linear relationships (Booher & Walters, 2021), and their capacity to incorporate numerous or correlated predictor variables (Cutler et al., 2007). The additional application of marginal effects to determine predicted presence across the range of habitat features provides practical insights into characterizing habitat suitability. This approach has also proven successful in other telemetry (Brownscombe et al., 2021) and riverine (Bzonek et al., in review) datasets. Future work could extend the current application of models such as RFs with marginal effect estimates by incorporating datasets from multiple sampling techniques (i.e., telemetry, boat electrofishing, seining) to broaden the range and resolution of habitat conditions assessed or minimize biases associated with specific sampling techniques. However, careful consideration would be needed to ensure that the biases and assumptions of individual sampling methods were complementary when combined in a composite dataset. As habitat suitability studies continue to yield increasingly informative insights, additional efforts should be applied to improve information accessibility for fisheries managers who use such information for conservation decisions (Cooke et al., 2022). Applications such as online computer dashboards hold promise in furnishing fisheries managers with pertinent habitat suitability information in a practical format, mitigating delays associated with reliance on conventional channels, namely peer-reviewed publications or gray literature.

In general, understanding fish habitat associations across species as well as estimating the amount and visualizing the areas of predicted habitat availability is important for fish habitat and fisheries managers. Acoustic telemetry was used to determine fish–habitat associations in Hamilton Harbour, which in these degraded habitats could vary from literature-based studies that occur in more pristine locations. Thus, it was important to potentially distinguish any differences between telemetry and the literature for additional insights into habitat selection. Using these telemetry-based RF models across seasons, we found that summer has the most limiting amount of habitat in Hamilton Harbour and show visually how the east end of the harbor has lower species presence. The limited habitat supply in summer could imply that water-quality issues related to anoxia may in turn be limiting population recovery of some species, and spatially, the north shore (due to the disconnect with electrofishing) or east end may be a good location for further habitat restoration efforts. Note that unmodeled variables, like dissolved oxygen, may also be limiting habitat use in these areas and should be explored (or identified) to increase the likelihood that habitat remediation efforts are successful. It is important to make these connections between fish habitat associations and how it could be used to assist habitat restoration efforts, and not just imply the importance toward fisheries management and conservation. These RF models are highly flexible and can be used with a variety of data, not just telemetry, and should be considered as an additional tool for fisheries managers. Furthermore, using the RF models to then spatially predict species presence throughout the whole study site provided a powerful visual that fisheries managers can easily interpret. As acoustic telemetry studies continue to be incorporated into fisheries management, year-round telemetry-based fish habitat associations can be assessed to gain further insight into the seasonality of fish movements and habitat selection under a variety of conditions.

AUTHOR CONTRIBUTIONS

Sarah M. Larocque: conceptualization, data generation, methodology, data analysis, manuscript preparation and editing. Paul A. Bzonek: data analysis, manuscript preparation and editing. Jacob W. Brownscombe: conceptualization, methodology, manuscript editing. Gillian K. Martin: data generation, manuscript preparation and editing. Jill L. Brooks: data generation, manuscript editing. Christine M. Boston: data generation, funding. Susan E. Doka: manuscript editing, funding. Steven J. Cooke: manuscript preparation and editing. Jonathan D. Midwood: conceptualization, data generation, methodology, manuscript preparation and editing, funding.

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REFERENCES

Ahrenstorff, T. D., Sass, G. G., & Helmus, M. R. (2009). The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*). *Hydrobiologia*, *623*, 223–233.

Benito, B. M. (2021). spatialRF: Easy spatial regression with random forest. R package version 1.1.3. https://blasbenito.github.io/spatialRF/

Benoit, D. M., Jackson, D. A., & Chu, C. (2021). Partitioning fish communities into guilds for ecological analyses: An overview of current approaches and future directions. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*, 984–993.

Booher, E. C. J., & Walters, A. W. (2021). Biotic and abiotic determinants of finescale dace distribution at the southern edge of their range. *Diversity and Distributions*, *27*, 696–709.

Boston, C. M., Larocque, S. M., Tang, R. W. K., Brooks, J. L., Bowman, J. A., Cooke, S. J., & Midwood, J. D. (2024). Life outside the fishbowl: Tracking an introduced population of goldfish (*Carassius auratus*) in an embayment on the Laurentian Great Lakes. *Journal of Great Lakes Research*, *50*, 102253.

Boston, C. M., Randall, R. G., Hoyle, J. A., Mossman, J. L., & Bowlby, J. N. (2016). The fish community of Hamilton harbour, Lake Ontario: Status, stressors, and remediation over 25 years. *Aquatic Ecosystem Health & Management*, *19*, 206–218.

Breiman, L. (2001). Random forests. *Machine Learning*, *45*, 5–32.

Brooks, J. L., Boston, C., Doka, S., Gorsky, D., Gustavson, K., Hondorp, D., Isermann, D., Midwood, J. D., Pratt, T. C., Rous, A. M., Withers, J. L., Krueger, C. C., & Cooke, S. J. (2017). Use of fish telemetry in rehabilitation planning, management, and monitoring in areas of concern in the Laurentian Great Lakes. *Environmental Management*, *60*, 1139–1154.

Brooks, J. L., Midwood, J. D., Gutowsky, L. F. G., Boston, C. M., Doka, S. E., Hoyle, J. A., & Cooke, S. J. (2019). Spatial ecology of reintroduced walleye (*Sander vitreus*) in Hamilton harbour of Lake Ontario. *Journal of Great Lakes Research*, *45*, 167–175.

Brooks, J. L., Midwood, J. D., Smith, A., Cooke, S. J., Flood, B., Boston, C. M., Semecsen, P., Doka, S. E., & Wells, M. G. (2022). Internal seiches as drivers of fish depth use in lakes. *Limnology and Oceanography*, *67*, 1040–1051.

Brousseau, C. M., Randall, R. G., & Clark, M. G. (2005). Protocol for boat electrofishing in nearshore areas of the lower Great Lakes: Transect and point survey methods for collecting fish and habitat data, 1988 to 2002. *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, *2702*, 89.

Brownscombe, J. W., Midwood, J. D., & Cooke, S. J. (2021). Modeling fish habitat–Model tuning, fit metrics, and applications. *Aquatic Sciences*, *83*, 1–14.

Brownscombe, J. W., Midwood, J. D., Doka, S. E., & Cooke, S. J. (2023). Telemetry-based spatial–temporal fish habitat models for fishes in an urban freshwater harbour. *Hydrobiologia*, *850*, 1779–1800.

Budgell, E., Reddick, D. T., Boston, C. M., & Midwood, J. D. (2024). Autumn sampling for evidence of northern pike (*Esox lucius*) recruitment in Hamilton harbour watersheds. *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, *3270*, 24.

Cooke, S. J., Docker, M. F., Mandrak, N. E., Young, N., Heath, D. D., Jeffries, K. M., Howarth, A., Brownscombe, J. W., Livernois, J., Semeniuk, C. A. D., Venturelli, P. A., Danylchuk, A. J., Lennox, R. J., Jarić, I., Fisk, A. T., Vandergoot, C. S., Britton, J. R., Muir, A. M., & Muir, A. M. (2022). Technoscience and the modernization of freshwater fisheries assessment and management. *Environmental Technology and Innovation*, *28*, 102865.

Cooke, S. J., Hich, S. G., Lucas, M. C., & Lutcavage, M. (2012). Biotelemetry and biologging. In A. Zale, D. Parrish, & T. Sutton (Eds.), *Fisheries Techniques* (3rd ed., pp. 819–860). American Fisheries Society.

Cooke, S. J., Martins, E. G., Struthers, D. P., Gutowsky, L. F. G., Power, M., Doka, S. E., Dettmers, J. M., Crook, D. A., Lucas, M. C., Holbrook, C. M., & Krueger, C. C. (2016). A moving target—Incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations. *Environmental Monitoring and Assessment*, *188*, 239.

Croft-White, M. V., Larocque, S. M., Reddick, D. T., Smith, P. D., Cooke, S. J., & Midwood, J. D. (2023). Diversity of movement patterns of longnose gar tracked in coastal waters of western Lake Ontario. *Environmental Biology of Fishes*. https://doi.org/10.1007/s10641-023-01491-1

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random forests for classification in ecology. *Ecology*, *88*, 2783–2792.

De Kerckhove, D. T., Smokorowski, K. E., & Randall, R. G. (2008). A primer on fish habitat models Canadian technical report of fisheries and aquatic sciences 2817. *Canadian Technical Report of Fisheries and Aquatic Sciences*, *2817*, 65.

Desforges, J. E., Clarke, J., Harmsen, E. J., Jardine, A. M., Robichaud, J. A., Serré, S., Chakrabarty, P., Bennett, J. R., Hanna, D. E. L., Smol, J. P., Rytwinski, T., Taylor, J. J., Martel, A. L., Winegardner, A. K., Marty, J., Taylor, M. K., O'Connor, C. M., Robinson, S. A., Reid, A. J., … Cooke, S. J. (2022). The alarming state of freshwater biodiversity in Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, *79*, 352–365.

Fahrig, L. (2001). How much habitat is enough? *Biological Conservation*, *100*, 65–74.

Flood, B., Wells, M., Midwood, J. D., Brooks, J., Kuai, Y., & Li, J. (2021). Intense variability of dissolved oxygen and temperature in the internal swash zone of Hamilton harbour, Lake Ontario. *Inland Waters*, *11*, 162–179.

Freeman, E. A., & Moisen, G. (2008). PresenceAbsence: An R package for presence absence analysis. *Journal of Statistical Software*, *23*, 1–31.

Gardner Costa, J., Rémillard, C. Y., Doolittle, A., & Doka, S. E. (2020). Hamilton harbour shoreline survey—2006. *Canadian Technical Report of Fisheries and Aquatic Sciences*, 3381, vii + 37.

Gardner Costa, J., Tang, R. W. K., Leisti, K. E., Midwood, J. D., & Doka, S. E. (2019). Submerged aquatic vegetation survey in Hamilton harbour, Lake Ontario, 2016. *Canadian Technical Report of Fisheries and Aquatic Sciences*, 3343.

Gertzen, E. L., Doka, S. E., Tang, R. W., Rao, Y. R., & Bowlby, J. N. (2016). Long-term dissolved oxygen and temperature monitoring in Hamilton harbour, Lake Ontario (2006-2013). *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, *3092*, 29.

Gorman, A. M., Kraus, R. T., Gutowsky, L. F. G., Vandergoot, C. S., Zhao, Y., Knight, C. T., Faust, M. D., Hayden, T. A., & Krueger, C. C. (2019). Vertical habitat use by adult walleyes conflicts with expectations from fishery-independent surveys. *Transactions of the American Fisheries Society*, *148*, 592–604.

Greenwell, B. M. (2017). Pdp: An R package for constructing partial dependence plots. *R Journal*, *9*, 421–436.

Hayes, D. B., Ferreri, C. P., & Taylor, W. W. (1996). Linking fish habitat to their population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 383–390.

Hiriart-Baer, V. P., Boyd, D., Long, T., Charlton, M. N., & Milne, J. E. (2016). Hamilton harbour over the last 25 years: Insights from a long-term comprehensive water quality monitoring program. *Aquatic Ecosystem Health and Management*, *19*, 124–133.

Holmes, J. A. (1988). Potential for fisheries rehabilitation in the Hamilton harbour-cootes paradise ecosystem of Lake Ontario. *Journal of Great Lakes Research*, *14*, 131–141.

Hoyle, J. A., & Yuille, M. J. (2016). Nearshore fish community assessment on Lake Ontario and the St. Lawrence river: A trap net-based index of biotic integrity. *Journal of Great Lakes Research*, *42*, 687–694.

Huey, R. B. (1991). Physiological consequences of habitat selection. *The American Naturalist*, *137*, S91–S115.

Johnson, M. D. (2007). Measuring habitat quality: A review. *Condor*, *109*, 489–504.

Jones, M. L., Shuter, B. J., Zhao, Y., & Stockwell, J. D. (2006). Forecasting effects of climate change on Great Lakes fisheries: Models that link habitat supply to population dynamics can help. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 457–468.

Kim, Z., Shim, T., Ki, S. J., Seo, D., An, K. G., & Jung, J. (2021). Evaluation of classification algorithms to predict largemouth bass (*Micropterus salmoides*) occurrence. *Sustainability*, *13*, 9507. https://doi.org/10.3390/su13179507

Klinard, N. V., & Matley, J. K. (2020). Living until proven dead: Addressing mortality in acoustic telemetry research. *Reviews in Fish Biology and Fisheries*, *30*, 485–499.

Knudby, A., Brenning, A., & LeDrew, E. (2010). New approaches to modelling fish-habitat relationships. *Ecological Modelling*, *221*, 503–511.

Krausman, P. R. (1999). Some basic principles of habitat use. In K. L. Launchbaugh, K. D. Sanders, & J. L. Mosley (Eds.), *Grazing Behaviour of Livestock and Wildlife, Idaho Forest, Wildlife and Range Exp. Sta. Bull. No. 70* (pp. 85–90). University of Idaho.

Kuhn, M. (2008). Building predictive models in R using the caret package. *Journal of Statistical Software*, *28*, 1–26.

Lacoul, P., & Freedman, B. (2006). Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews*, *14*, 89–136.

Lane, J. A., Portt, C. B., & Minns, C. K. (1996). Adult habitat characteristics of Great Lakes fishes. *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, *2358*, 43.

Lapointe, N. W. R., Cooke, S. J., Imhof, J. G., Boisclair, D., Casselman, J. M., Curry, R. A., Langer, O. E., McLaughlin, R. L., Minns, C. K., Post, J. R., Power, M., Rasmussen, J. B., Reynolds, J. D., Richardson, J. S., & Tonn, W. M. (2014). Principles for ensuring healthy and productive freshwater ecosystems that support sustainable fisheries. *Environmental Reviews*, *22*, 110–134.

Larocque, S. M., Boston, C. M., Brooks, J. L., Jacob, W., Cooke, S. J., Doka, S. E., & Midwood, J. D. (2024). Telemetry-derived seasonal fish-habitat associations and spatial use in the Hamilton harbour area of concern in western Lake Ontario. *Canadian Technical Report of Fisheries and Aquatic Sciences*, *3593*, 193.

Larocque, S. M., Boston, C. M., & Midwood, J. D. (2020). Seasonal daily depth use patterns of acoustically tagged freshwater fishes informs nearshore fish community sampling protocols. *Canadian Technical Report of Fisheries and Aquatic Sciences*, *3409*, 38.

Larocque, S. M., Piczak, M. L., Turner, N. A., Jennifer, E., Boston, C. M., & Midwood, J. D. (2023). Mark-recapture population estimates of piscivores in the Hamilton harbour area of concern. *Canadian Technical Report of Fisheries and Aquatic Sciences*, *3506*, vii + 31.

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, *2*, 18–22.

Marcaccio, J. V., Gardner Costa, J., Brooks, J. L., Boston, C. M., Cooke, S. J., & Midwood, J. D. (2022). Automated coastal ice mapping with SAR can inform winter fish ecology in the Laurentian Great Lakes. *Canadian Journal of Remote Sensing*, *48*, 19–36.

Marsden, J. E., Blanchfield, P. J., Brooks, J. L., Fernandes, T., Fisk, A. T., Futia, M. H., Hlina, B. L., Ivanova, S. V., Johnson, T. B., Klinard, N. V., Krueger, C. C., Larocque, S. M., Matley, J. K., McMeans, B., O'Connor, L. M., Raby, G. D., & Cooke, S. J. (2021). Using untapped telemetry data to explore the winter biology of freshwater fish. *Reviews in Fish Biology and Fisheries*, *31*, 115–134.

Maynard, D., Boston, C. M., & Midwood, J. D. (2022). Fish community structure varies by location and presence of artificial islands: A case study in Hamilton harbour, Lake Ontario. *Environmental Biology of Fishes*, *105*, 1557–1573.

Midwood, J. D., Leisti, K. E., Milne, S. W., & Doka, S. E. (2019). Assessing seasonal changes in pelagic fish density and biomass using hydroacoustics in Hamilton harbour, Lake Ontario in 2016. *Canadian Technical Report of Fisheries and Aquatic Sciences*, 3299, x + 63 p.

Miranda, L. E., & Pugh, L. L. (1997). Relationship between vegetation coverage and abundance, size, and diet of juvenile largemouth bass during winter. *North American Journal of Fisheries Management*, *17*, 601–610.

Morrison, B. P. (2019). Chronology of Lake Ontario ecosystem and fisheries. *Aquatic Ecosystem Health and Management*, *22*, 294–304.

Morrison, M. L., Marcot, B., & Mannan, W. (2012). *Wildlife-habitat relationships: Concepts and applications*. Island Press.

Munawar, M., Fitzpatrick, M., Niblock, H., Kling, H., Rozon, R., & Lorimer, J. (2017). Phytoplankton ecology of a culturally eutrophic embayment: Hamilton harbour, Lake Ontario. *Aquatic Ecosystem Health and Management*, *20*, 201–213.

Olden, J. D., & Jackson, D. A. (2001). Fish–habitat relationships in lakes: Gaining predictive and explanatory insight by using artificial neural networks. *Transactions of the American Fisheries Society*, *130*, 878–897.

OMNRF. (2019). *Lake Ontario fish communities and fisheries: 2018 annual report of the Lake Ontario management unit*. Ontario Ministry of Natural Resources and Forestry (OMNRF), Picton, Ontario, Canada (p. 218).

Pincock, D. G. (2012). False detections: What they are and how to remove them from detection data. *Amirix Document DOC-004691 Version 03*. Vemco, Halifax, Nova Scotia, Canada, 11 p.

Polak, J., & Haffner, G. D. (1978). Oxygen depletion of Hamilton harbour. *Water Research*, *12*, 205–215.

R Core Team. (2023). R: A language and environment for statistical computing. https://www.r-project.org/.

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*, 849–873.

Říha, M., Gjelland, K., Děd, V., Eloranta, A. P., Rabaneda-Bueno, R., Baktoft, H., Vejřík, L., Vejříková, I., Draštík, V., Šmejkal, M., Holubová, M., Jůza, T., Rosten, C., Sajdlová, Z., Økland, F., & Peterka, J. (2021). Contrasting structural complexity differentiate hunting strategy in an ambush apex predator. *Scientific Reports*, *11*, 1–20.

Rosenzweig, M. L. (1981). A Theory of Habitat Selection. *Ecology*, *62*, 327–335.

Rudolfsen, T. A., Watkinson, D. A., Charles, C., Kovachik, C., & Enders, E. C. (2021). Developing habitat associations for fishes in Lake Winnipeg by linking large scale bathymetric and substrate data with fish telemetry detections. *Journal of Great Lakes Research*, *47*, 635–647.

Scott, W. B., & Crossman, E. J. (1998). *Freshwater fishes of Canada*. Galt House Pub.

Smokorowski, K. E., Stoneman, M. G., Cairns, V. W., Minns, C. K., Randall, R. G., & Valere, B. (1998). Trends in the nearshore fish Community of Hamilton Harbour, 1988 to 1997, as measured using an index of biotic integrity. *Canadian Technical Report of Fisheries and Aquatic Sciences*, *2230*, 97.

Trebitz, A. S., Brazner, J. C., Danz, N. P., Pearson, M. S., Peterson, G. S., Tanner, D. K., Taylor, D. L., West, C. W., & Hollenhorst, T. P. (2009). Geographic, anthropogenic, and habitat influences on Great Lakes coastal wetland fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 1328–1342.

Valley, R. D., Cross, T. K., & Radomski, P. (2004). The role of submersed aquatic vegetation as habitat for fish in Minnesota lakes, including the implications of non-native plant invasions and their management. *Minnesota Department of Natural Resources*, *160*, 25.

Wells, M. G., Li, J., Flood, B., Kuai, Y., Brooks, J. L., Cooke, S. J., Semcesen, P., & Midwood, J. D. (2021). Speed of sound gradients due to summer thermal stratification can reduce the detection range of acoustic fish tags: Results from a field study in hamilton harbour, ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*, 269–285.

Whillans, T. H. (1982). Changes in marsh area along the Canadian shore of Lake Ontario. *Journal of Great Lakes Research*, *8*, 570–577.

Yapp, A. R. H. (1922). The concept of habitat published by British Ecological Society. *Journal of Ecology*, *10*, 1–17.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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