Increasing Occurrence of Atlantic Bluefin Tuna on Atlantic Herring Spawning Grounds: A Signal of Escalating Pelagic Predator–Prey Interaction?

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Abstract
Predation can be a significant source of natural mortality for small pelagic fish species, rivaling or exceeding fishery removals. Failure to account for changes in natural mortality can introduce uncertainty in the assessment and management of these stocks. In this study, a 10-year span of hydroacoustic data was used to detect Bluefin Tuna Thunnus thynnus on two major fall spawning grounds of Atlantic Herring Clupea harengus, an economically and ecologically valuable forage fish species in the southern Gulf of St. Lawrence (sGSL). Average Bluefin Tuna detections increased 22-fold from 2002 to 2012 on both spawning grounds independently of Atlantic Herring density or aggregation size. This increase is directionally consistent but larger than changes in other Bluefin Tuna population indices. Preliminary estimates of annual Atlantic Herring consumption doubled across the time series, reaching values of 4,300–20,000 metric tons in recent years. This would suggest that Bluefin Tuna are among the most important consumers of Atlantic Herring in the sGSL. These findings are key for an ecosystem-based approach to the assessment and management of both Atlantic Herring and Bluefin Tuna in the sGSL.

Predation can be a significant source of natural mortality for small pelagic fish species, rivaling or exceeding fishery removals (Overholtz and Link 2007). Consequently, accounting for this source of natural mortality is important to facilitate accurate assessment and management of these fish stocks. Fisheries management is often based on the assumption that natural mortality is constant or varies around a mean value, yet numerous examples show that predator–prey interactions are dynamic and can cause a sustained directional change (i.e., increase or decrease) in natural mortality (Lee et al. 2011; Thorson et al. 2015; Skern-Mauritzen et al. 2016; Jacobsen and Essington 2018; Siple et al. 2018). In a stock assessment, failure to account for trends in natural mortality due to changes in predator–prey interactions can result in biased estimates of population parameters and vital rates (Legault and Palmer 2015; Jacobsen et al. 2019). Therefore, identifying changes in predator–prey interactions and advising

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decision makers of the potential impacts of these changes on pelagic species are important challenges facing fisheries science.

Estimating the effects of predators on prey populations is challenging, particularly when predatory interactions vary over time and across large spatial scales, as is expected in marine ecosystems. There are multiple factors that influence predator–prey interactions, including diet composition, habitat overlap, and the timing of interactions (Tunney et al. 2012; McMeans et al. 2015; Bartley et al. 2019). Although increases in population abundance of a predator can be associated with increased predation on prey species, it is important to assess multiple lines of empirical evidence that link predator increases to predation on prey populations (Grubbs et al. 2016). As one line of evidence, predators and prey must be present in the same place at the same time in order for predation to occur. Therefore, an important part of determining the potential for a change in the abundance of a predator to affect pelagic forage species in marine ecosystems is establishing that predators are found in the same locations at the same time as prey species. The nature of the relationship between the spatial distribution of predators and the spatial distribution of prey affects the foraging success of predators and the mortality rate of prey. Predators should seek out areas with high prey density to increase foraging success, whereas prey should move away from areas with a high density of predators to reduce the risk of mortality (Sih 1984, 2005). The strength of predators’ effects will be greater when prey are constrained spatially, such as in overwintering and spawning grounds (Sih 2005).

The Atlantic Herring Clupea harengus is a vital prey species for many predators in the southern Gulf of St. Lawrence (sGSL), including grey seals Halichoerus grypus (Hammill and Stenson 2000; Hammill et al. 2007, 2014), seabirds (Cairns et al. 1991), cetaceans (Fontaine et al. 2019; Bartley et al. 2019). Although increases in population abundance of a predator can be associated with increased predation on prey species, it is important to assess multiple lines of empirical evidence that link predator increases to predation on prey populations (Grubbs et al. 2016). As one line of evidence, predators and prey must be present in the same place at the same time in order for predation to occur. Therefore, an important part of determining the potential for a change in the abundance of a predator to affect pelagic forage species in marine ecosystems is establishing that predators are found in the same locations at the same time as prey species. The nature of the relationship between the spatial distribution of predators and the spatial distribution of prey affects the foraging success of predators and the mortality rate of prey. Predators should seek out areas with high prey density to increase foraging success, whereas prey should move away from areas with a high density of predators to reduce the risk of mortality (Sih 1984, 2005). The strength of predators’ effects will be greater when prey are constrained spatially, such as in overwintering and spawning grounds (Sih 2005).

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Bluefin Tuna migrate into the sGSL to feed from July to December, where they are targeted by lucrative commercial and recreational fisheries. Bluefin Tuna abundance has varied greatly in the last few decades. The western Atlantic Bluefin Tuna stock biomass declined in the 1970s to its lowest level, where it remained for more than two decades; biomass then began a gradual increase from 2004 to reach 60% of the 1974 biomass in 2013 (ICCAT 2014b). Bluefin Tuna CPUE in Canada is higher than CPUE in the United States (ICCAT 2014a, 2014b), and this was deemed to be largely a reflection of a perceived northward shift in the abundance of large Bluefin Tuna (ICCAT 2017). However, there is also evidence from genetic studies that an increasing fraction of these fish are from the eastern management unit (ICCAT 2014b; Hanke et al. 2017). The annual proportion of successful tuna fishing trips has also followed a similar increasing trend (Vanderlaan et al. 2014), and based on catches, the sGSL now represents the core distribution range for Bluefin Tuna in Canadian waters (COSEWIC 2011).

Limited diet sampling suggests that Bluefin Tuna feed primarily on two pelagic fish species: Atlantic Herring and Atlantic Mackarel Scomber scombrus (Chase 2002; Wilson et al. 2010; Pleizier et al. 2012). Consequently, higher Bluefin Tuna abundance in the sGSL may result in increased Atlantic Herring removals due to predation, thereby potentially increasing their natural mortality. However, the changes in Bluefin Tuna abundance and how these changes translate into potential predation and consumption of small pelagic species (e.g., Atlantic Herring) in the sGSL are currently not well understood.

The main objective of this study was to investigate the co-occurrence of Atlantic Herring and Bluefin Tuna on herring fall spawning grounds in the sGSL and how this has varied through time. To achieve this objective, our study addressed two specific components. First, we used acoustic data to quantify the relative Bluefin Tuna occurrence on Atlantic Herring spawning grounds through time. Second, we tested whether the number of Bluefin Tuna detections observed was related to the characteristics of different spawning aggregations. This habitat overlap could be particularly important in controlling changes in the strength of the predator–prey interaction, as Atlantic Herring are spatially constrained during the spawning period due to their spawning site fidelity and the fact that the
fall spawning grounds have been consistent throughout the time series. If a change in the co-occupation of Bluefin Tuna and Atlantic Herring has occurred, we wanted to assess how the change could modify the potential for Bluefin Tuna predation and consumption of Atlantic Herring. We produced estimates of Bluefin Tuna consumption to identify changes in the number of Atlantic Herring potentially being consumed by Bluefin Tuna in the sGSL. These preliminary estimates are intended to establish a scale of the potential consumption by Bluefin Tuna and how it compares to other important predators. This information can then be used to identify new scenarios of natural mortality that could be incorporated into future assessments of Atlantic Herring in the sGSL.

METHODS

Survey

Hydroacoustic surveys were conducted biannually from 2002 to 2012 between August and October on two major fall herring spawning grounds in the sGSL (Fisherman’s Bank, Prince Edward Island; and Miscou, New Brunswick; Figure 1). The two spawning grounds represent the northwestern and southeastern geographic range of fall-spawning Atlantic Herring in the sGSL, and they show opposite trends in SSB (Figure 2; McDermid et al. 2018). A single gill-net fishing vessel collected hydroacoustic data on each spawning ground during regular nightly fishing activities. Seven different vessels served as platforms over the 10-year period. Each vessel was equipped with a Femto DE9320 digital echosounder and a 120-kHz, 14° beam angle, single-beam transducer, calibrated as described by Clay and Claytor (1998). Acoustic backscatter, latitude, and longitude were recorded every second along the vessel’s track. Data were collected during every night of fishing; however, sampling effort varied between regions and years as a result of weather dependence, weekend fishery closures, equipment or vessel malfunctions, or the fishery attaining the total allowable catch before the end of the spawning season (Table 1).

Data

Acoustic data editing and processing were carried out using Echoview version 8.0. Atlantic Herring aggregations were delineated in the echogram in order to calculate the total amount of time that each vessel spent above herring aggregations during the night (survey effort). Echo counting was used to quantify the number of Bluefin Tuna targets in the vicinity of the Atlantic Herring aggregations. Targets were visually inspected and selected if (1) the acoustic trace signature (curved shape and relative size) and (2) the target strength fell within the range reported in the literature for Bluefin Tuna (between −33 and −14 dB; Josse and Bertrand 2000; ICCAT 2014a; Melvin 2016). In this study, observations on 121 confirmed Bluefin Tuna targets (based on size, shape, position, and targets within the vicinity of other Bluefin Tuna targets) redefined the upper and lower target strength thresholds to −38.5 and −11.5 dB, respectively (Figure 3). This is a broader range than was found by Melvin (2016), which can be explained by the fact that we inspected 121 targets (versus the 34 targets examined by Melvin 2016), thus increasing our chance of encountering extreme values (larger and smaller fish; fish on the margin of the acoustic cone).

It is extremely difficult to discern large individual targets, such as Bluefin Tuna, within a densely aggregated fish school on acoustic echograms. Hence, only targets on the periphery of Atlantic Herring schools were considered. Furthermore, to avoid acoustic signal contamination produced by the interaction of the boat and the water surface, targets had to be located below a depth of 5 m. Potential target confusion resulting from similarly sized predators (seals and pilot whales) was considered negligible, as their echogram characteristics are distinct from those of Bluefin Tuna (Melvin 2016).
The target acquisition period was limited to the period of active fishing (i.e., prior to hauling the nets back) so as to avoid counting Bluefin Tuna that were feeding on fish that fell from the nets as they were retrieved. This behavior was noted by Melvin (2016) and fish harvesters and is easily identifiable on the echograms by the large numbers of Bluefin Tuna aggregated closely under the boat at the end of the fishing night in the absence of any Atlantic Herring aggregation under the vessel. The pre-haulback period was used for the study to eliminate the human interaction with Bluefin Tuna predatory behavior. Sampling effort was weighted and controlled for potential interannual, interregional, and nightly variation in survey effort by using the number of Bluefin Tuna detections per hour during even years between 2002 and 2012 for the complete data set ($n = 165$).

We considered two alternative forms of the data: (1) a complete acoustic survey data set ($n = 165$) and (2) a reduced acoustic survey data set ($n = 154$) for which both Atlantic Herring school area and herring acoustic density analyzed by LeBlanc (2013; Table 1) were available. Ten samples of acoustic data from 2010 and 2012 were not analyzed by LeBlanc (2013). The first data set allowed for estimation of the number of Bluefin Tuna targets observed per hour, region, year, and Julian day. The second data set allowed for estimation of the number of Bluefin Tuna targets observed per hour, region, year, and Julian day relative to herring school area and herring acoustic point density.

### Model Selection and Validation

Bluefin Tuna occurrence in the complete data set ($n = 165$ surveys) was modeled as a function of the factors Year (2002–2012) and Region (Fisherman’s Bank or Miscou) and
the continuous variable Julian Day (220–279). Bluefin Tuna occurrence in the reduced data set \((n = 154\) surveys) was modeled as a function of the factors Year (2002–2012) and Region (Fisherman’s Bank or Miscou) and the continuous variables Julian Day (220–279), Herring School Area (0.0160–3.2930), and Herring Acoustic Density (0.1–20.4).

Additional models were also fitted using absolute Bluefin Tuna counts as the dependent variable and including search time as an offset term (Zuur et al. 2013). Results from these models did not differ from the results of models using detection rate as the response variable.

Data exploration was performed in accordance with Zuur et al. (2010), while model selection and validation were conducted using the methods of Zuur et al. (2013). Bluefin Tuna occurrence was modeled using both Poisson and negative binomial general linear models with a log link function. The log link function ensures positive fitted values, and the negative binomial distribution is typically used for count or rate data (Zuur et al. 2013). Model fits were tested for statistical overdispersion, and sources of overdispersion considered were missing covariates, missing interaction terms, outliers, nonlinear patterns, and variation larger than the Poisson distribution allows. We ultimately used the negative binomial distribution because the Poisson fits were overdispersed. Model assumptions were verified by plotting the residuals against the fitted values and by plotting the Pearson’s residuals against each of the covariates. Independence was assessed by plotting the Pearson’s residuals against the variable Year. Autocorrelation was estimated to be weak (<3% for the reduced data set with Atlantic Herring covariates; <8% for the complete data set), and an autocorrelation term did not improve the generalized least-squares model. Hence, no autocorrelation term was added to the model. The MASS package (Venables and Ripley 2002) in R (R Core Team 2018) was used to fit the models.

Nested models were compared using residual deviance and Akaike’s information criterion corrected for small sample size \((AIC_c)\). Full models based on the complete and reduced data sets were defined as follows:

\[
BFT_{ij} \sim NB(\mu_{ij}, 0),
\]

\[
E(BFT_{ij}) = \mu_{ij},\quad V(BFT_{ij}) = \mu_{ij} + \frac{\mu_{ij}^2}{\theta_{ij}},
\]

\[
\log(\mu_{ij}) = \eta_{ij},
\]

\[
\eta_{ij} = \beta_1 + \beta_2 f_{\text{Year}_{ij}} \times \beta_3 f_{\text{Region}_{ij}} + \beta_4 f_{\text{Jday}_{ij}} + \beta_5 f_{\text{Harea}_{ij}} + \beta_6 f_{\text{Hdensity}_{ij}},
\]

where \(BFT_{ij}\) is Bluefin Tuna nightly detections per hour spent on Atlantic Herring aggregations for the \(i\)th observation from the \(i\)th year; \(f_{\text{Year}_{ij}}\) is a categorical variable for the fixed year effect (even years from 2002 to 2012); \(f_{\text{Region}_{ij}}\) is a categorical variable for the fixed region effect (Miscou or Fisherman’s Bank); and \(f_{\text{Jday}_{ij}}\) is the Julian day of the year. For the reduced data set only, \(f_{\text{Harea}_{ij}}\) is the area occupied by the Atlantic Herring school, and \(f_{\text{Hdensity}_{ij}}\) is the herring acoustic density.

**Consumption Estimation**

Annual consumption of Atlantic Herring by Bluefin Tuna in the sGSL was roughly estimated using a daily ration estimate, residency time, and estimates of Bluefin Tuna numbers at age (NAA) and weight at age. We used a methodology similar to that described by Benoît and Rail (2016). The average reported daily ration for Bluefin Tuna based on general allometric relationships, bioenergetic modeling, and empirical observations is 3.0% of body mass and ranges from 1.0% to 4.7% of body mass (see Overholtz 2006; Butler et al. 2010; Mariani et al. 2017). We used a 4-month residency time for Bluefin Tuna in the sGSL (122 d from July to December; Hanke et al. 2013). Based on the few published studies, the Bluefin Tuna’s diet consists of 50% Atlantic Herring on average (Chase 2002; Pleizier et al. 2012).

A virtual population analysis (VPA) called “Base Case High Maturity” from the Atlantic Bluefin Tuna stock assessment (ICCAT 2017) was used to estimate yearly Bluefin Tuna NAA in the sGSL for each year from 1994 to 2015:

\[
\text{NAA}_{\text{sGSL}} = \text{NAA}_{\text{total}} \times \frac{\text{CAA}_{\text{sGSL}}}{\text{CAA}_{\text{total}}},
\]

where \(\text{NAA}_{\text{sGSL}}\) is Bluefin Tuna NAA in the sGSL; \(\text{NAA}_{\text{total}}\) is Bluefin Tuna NAA for the western area (west of 45.0°W); \(\text{CAA}_{\text{sGSL}}\) is the Bluefin Tuna catch at age in the sGSL; and \(\text{CAA}_{\text{total}}\) is the Bluefin Tuna catch at age in the western area. This approach assumes that the proportion of the western catch that was caught in the sGSL is equal to the proportion of the western area population in the sGSL. While imperfect,
this is the only way to currently estimate Bluefin Tuna NAA in the sGSL. It reflects the constant fraction in regional quota allocations, accounting for spatial non-uniformity in fishing effort. The annual Bluefin Tuna NAA in the sGSL were then multiplied by the annual weight at age for the western area to obtain biomass at age for the sGSL. The daily prey consumption at age was then obtained by multiplying the biomass at age by the daily ration estimates (1.0, 3.0, and 4.7% of body mass). The daily prey consumption at age was summed over ages and multiplied by the sGSL residency time and the average proportion of herring in the diet to obtain the total yearly consumption of Atlantic Herring by Bluefin Tuna in the sGSL.

RESULTS

The best model was selected based on the lowest AICc value and as the most parsimonious model among those with AICc difference (ΔAICc) values less than 2 (Burnham and Anderson 2002; Arnold 2010). For both the complete data set and the reduced data set, the best model was the model with only the Year covariate. For the reduced data set, the models with the Year × Region interaction and the Herring Acoustic Density covariate had ΔAICc values greater than 2. All other models in the reduced data set had ΔAICc values less than 2. The model that included Year + Region and the Year-only model had equally low AICc values; hence, the most parsimonious model (the model with only the Year covariate) was selected as the best model (Table 2). For the complete data set, the model with the Year × Region interaction and models with the Julian Day covariate had ΔAICc values greater than 2. The other model with the Year + Region covariates in the complete data set had a ΔAICc value less than 2; however, the AICc value was lower for the Year-only model and it was the most parsimonious model. Thus, the Year-only model was identified as the best model (Table 2). We favored the model based on the complete data set over the reduced data set for providing annual Bluefin Tuna occurrence rate estimates for two reasons: (1) it offered more tuna occurrence data for the years 2010 and 2012 (Table 2); and (2) the additional covariates used in the reduced data set (Herring School Area and Herring Acoustic Density) were uninformative, as shown by the model selection process. Poisson models were overdispersed, while negative binomial models had dispersion parameters closer to 1 (final complete data set model dispersion = 1.23). The θ parameter of the negative binomial distribution was estimated to be 1.04 for the complete data set. Diagnostic plots from the best-fit negative binomial model showed no evidence of patterns in the residuals based on fits of the residuals to each of the covariates (see Supplementary Material, Figure S1 available in the online version of this article).

Acoustic survey-based index estimates indicated that the average Bluefin Tuna occurrence increased 22-fold from 2002 to 2012 on both of the herring fall spawning grounds in the sGSL (Miscou and Fisherman’s Bank; Table 1). Similarly, the maximum number of observed Bluefin Tuna detections in 1 h increased from 10 tuna/h in 2002 to 62 tuna/h in 2010 and 89 tuna/h in 2012 (Figure 4). The number of Bluefin Tuna detections estimated by the complete data set model ranged from 1.1 tuna/h (95% CI = 0.7–1.8) to 5.5 tuna/h (95% CI = 3.8–7.9) between 2002 and 2008 and then increased to 24.2 tuna/h (95% CI = 15.4–37.9) in 2010 and 23.7 tuna/h (95% CI = 14.9–37.7) in 2012 (Figure 4; Table 3).

The spatial distribution of Atlantic Herring aggregations sampled varied only slightly between years (Figure 5) within the Miscou and Fisherman’s Bank regions. Bluefin Tuna were detected within many of these Atlantic Herring aggregations during each year, and the number of aggregations with detections exhibited a marked increase in 2010 and 2012. Herring school areas were similar between Fisherman’s Bank and Miscou in 2002 but diverged thereafter, with school sizes at Miscou increasing over the time series and school sizes at Fisherman’s Bank decreasing (Table 1). The trends in density of Atlantic Herring aggregations also showed differing patterns (Table 1). In Fisherman’s Bank, Atlantic Herring density was fairly consistent across the time series, with a mean of 2.5 kg/m² (range = 1.1–5.1 kg/m²). In Miscou, the acoustic density of Atlantic Herring schools declined across the time series from a high of 3.5 kg/m² to a low of 0.5 kg/m² (mean = 1.8 kg/m²).

The total number of Bluefin Tuna in the sGSL was estimated by the VPA to vary between 16,610 in 1994 and 31,305 in 2015. Bluefin Tuna found in the sGSL are large, with a modal and mean mass of approximately 300 kg (Hanke et al. 2013). The estimated Atlantic Herring consumption by Bluefin Tuna based on the VPA-generated Bluefin Tuna NAA increased between 1994 and 2015 (Figure 6). Using the average daily ration of 3.0% of body mass and a 50% herring diet, the annual consumption of Atlantic Herring by Bluefin Tuna was estimated at an average of 7,729 metric tons between 1994 and 2000 (1.0% of body mass: 2,577 metric tons; 4.7% of body mass: 12,110 metric tons). Annual consumption in 2002 was estimated at 7,071 metric tons (1.0% of body mass: 2,357 metric tons; 4.7% of body mass: 11,079 metric tons). The estimated annual consumption then increased to 13,620 metric tons in 2012 (1.0% of body mass: 4,346 metric tons; 4.7% of body mass: 20,427 metric tons). Estimated annual consumption values remained high between 2012 and 2015, with values of 13,192 metric tons in 2015 (1.0% of body mass: 4,397 metric tons; 4.7% of body mass: 20,668 metric tons).

DISCUSSION

Predator–prey interactions are dynamic and play an important role in shaping marine ecosystems. Prey select
habitat on the basis of resource availability and predation risk, whereas predators select habitats on the basis of prey abundance and the different demographic or functional response parameters in those habitats (Abrams 2007). An important factor in determining the potential impact of a predator on pelagic forage species in marine ecosystems is establishing that predators are found in the same locations at the same time as prey species. Life history events, such as spawning, often constrain the spatial distribution of prey to particular areas. This spatial constraint might be easily predicted and accessed by predators (Sih 1984, 2005). For example, several studies found strong spatial matching between murres Uria spp. and Capelin Mallotus villosus in the Barents Sea during Capelin spawning; however, there was only weak spatial overlap during the Capelin feeding migration (see Fauchald 2009).

Fall-spawning Atlantic Herring in the sGSL demonstrate spawning site fidelity, returning to one of six spawning grounds (Wheeler and Winters 1984; McQuinn 1997; Brophy et al. 2006; McDermid et al. 2018). Bluefin Tuna

| Model | Residual deviance | AICc | ΔAICc |
|-------|-------------------|------|-------|
| Reduced data set (n = 154) | | | |
| BFT ~ (Year × Region) + Herring School Area + Julian Day + Herring Acoustic Density | 172.1 | 812.2 | 4.8 |
| BFT ~ Year + Region + Herring School Area + Julian Day + Herring Acoustic Density | 172.4 | 810.6 | 3.2 |
| BFT ~ Year + Region + Herring School Area + Julian Day | 172.4 | 808.5 | 1.1 |
| BFT ~ Year + Region + Herring School Area | 172.5 | 807.7 | 0.3 |
| BFT ~ Year + Region | 172.4 | 807.4 | 0.0 |
| BFT ~ Year | 173.3 | 807.4 | 0.0 |
| Complete data set (n = 165) | | | |
| BFT ~ (Year × Region) + Julian Day | 185.9 | 892.9 | 6.9 |
| BFT ~ Year + Region + Julian Day | 186.6 | 888.3 | 2.3 |
| BFT ~ Year + Region | 186.5 | 887.3 | 1.3 |
| BFT ~ Year | 187.3 | 886.0 | 0.0 |

FIGURE 4. Bluefin Tuna (BFT) detections per hour spent on Atlantic Herring fall spawning grounds (cyan boxplots = Miscou; red boxplots = Fisherman’s Bank) for even years between 2002 and 2012 (left panel). The black center line in each box shows the median value, the box indicates the 25th and 75th percentiles, the whiskers show the variability outside the quartiles, and the points indicate outliers. Mean values (±95% CI) estimated by the negative binomial model are presented in the right panel.

TABLE 3. Estimated average (with 95% CI) nightly count of Bluefin Tuna per hour spent on Atlantic Herring spawning aggregations (Miscou and Fisherman’s Bank) in the southern Gulf of St. Lawrence based on the Year-only negative binomial generalized linear model for the complete data set (see Table 2).
are known predators of Atlantic Herring and occur in the sGSL during the summer and fall (Chase 2002; Wilson et al. 2010; Pleizier et al. 2012; Hanke et al. 2013; Vanderlaan et al. 2014). This presents a unique opportunity to investigate the co-occurrence of Bluefin Tuna and Atlantic Herring when herring are spatially constrained on their spawning grounds. Using targeted hydroacoustic studies on Atlantic Herring fall spawning grounds, we were able to demonstrate that Bluefin Tuna co-occur with Atlantic Herring in their core Canadian distribution. Furthermore, we identified a substantial 22-fold increase in Bluefin Tuna on Atlantic Herring fall spawning grounds over the 10-year time series. This large increase occurred on both of the fall spawning grounds examined, despite (1) the spawning grounds occurring at opposite ends of the geographic range in the sGSL and (2) the divergent trends in

FIGURE 5. Map of Atlantic Herring school locations (red dots) and Bluefin Tuna locations (black dots) at (A) Miscou and (B) Fisherman’s Bank for even years between 2002 and 2012 based on acoustic data collected by harvesters while conducting their fishing activities.
herring SSB in these areas. This spatial overlap and the increasing number of Bluefin Tuna on Atlantic Herring fall spawning grounds are likely to have important consequences for the predator–prey dynamics in this system. Spring-spawning Atlantic Herring also occur in the sGSL; however, corresponding hydroacoustic data for spring spawning grounds do not exist. Nevertheless, it is not expected that such a data set would detect these levels of co-occurrence between Bluefin Tuna and spawning herring since spring spawning occurs from April to June, whereas Bluefin Tuna typically enter the sGSL in July. Spring Atlantic Herring may still be consumed by Bluefin Tuna outside of the spawning grounds while aggregated in feeding or migrating schools.

The model selection process showed that the number of Bluefin Tuna detections on a given day was independent of the region or the day of the year. This indicates that the increase in Bluefin Tuna was similar between the two regions annually. In addition, there was no observed increase or decrease in Bluefin Tuna occurrence on Atlantic Herring spawning grounds within a year. This may not be surprising, as the time period covered by the surveys within each year was limited to the fall herring fishing season, which aims for the peak of Atlantic Herring abundance on spawning grounds. Bluefin Tuna detections were also independent of the density and spatial extent of the Atlantic Herring aggregations. The final models only retained year as the significant variable for Bluefin Tuna abundance. The increase in Bluefin Tuna detections between years was characterized by a period of relative stability, followed by a sharp increase during the last 2 years of the time series. Detects of Bluefin Tuna increased dramatically from as low as 1 tuna/h in 2002 to a maximum of 89 tuna/h in 2012. Interestingly, the magnitude of this increase on Atlantic Herring spawning aggregations exceeds the increases in other Bluefin Tuna abundance indices for the sGSL during the same time period (see Supplementary Material, Figure S2). The standardized CPUE index from the sGSL Bluefin Tuna fishery showed a 7.5-fold increase in relative abundance (Hanke and Chevarie 2018), and the fishery-independent sGSL acoustic index (which uses a target-counting technique similar to that used in our study) demonstrated a fourfold increase (Melvin et al. 2018; Minch 2020) for the same time period. The increase in Bluefin Tuna detections from the present study does not serve as a GSL-wide index of Bluefin Tuna abundance but rather as an index of the change in Atlantic Herring–Bluefin Tuna interactions. However, the difference in Bluefin Tuna abundance increases between indices is of great importance in an ecosystem-based approach to stock assessment because the changes in these values may lead to alternate interpretations of the predator’s effect on the prey.

Our second objective was to investigate a bottom-up driven prediction for the distribution of Bluefin Tuna based on Atlantic Herring density or the size of herring spawning aggregations. Bluefin Tuna are considered largely opportunistic feeders (Chase 2002; Estrada et al. 2005; Pleizier et al. 2012; Olafsdottir et al. 2016), but they target herring aggregations on the eastern U.S. shelf (Schick and Lutcavage 2009; Golet et al. 2013), and existing diet data suggest that they feed almost exclusively on Atlantic Herring and Atlantic Mackerel in the sGSL (Pleizier et al. 2012). In addition, many of the Atlantic Herring in the diets were gravid, which is consistent with feeding on spawning aggregations (Pleizier et al. 2012). As the increase in Bluefin Tuna detections from this study is of greater magnitude than the increase in other non-herring-specific indices of Bluefin Tuna abundance, this study supports the idea that Bluefin Tuna actively target Atlantic Herring aggregations in the sGSL. However, neither herring acoustic density nor herring school area explained the variation in the number of Bluefin Tuna occurring nightly on the Atlantic Herring spawning grounds in this study. Atlantic Herring populations in the two regions studied here exhibited dramatically opposite trends in SSB, with increasing SSB values at Miscou and decreasing SSB values at Fisherman’s Bank (Figure 2; McDermid et al. 2018). However, both regions showed similar increases in the number of Bluefin Tuna detections. From 2002 to 2012, Atlantic Herring SSB demonstrated an increasing trend in the northern region of the sGSL (including Miscou), reaching just under 100,000 metric tons in 2012. At the same time, Atlantic Herring SSB in the southern region (including Fisherman’s Bank) was rapidly
The spatial size of Atlantic Herring schools also declined over the 2002–2012 time frame at Fisherman’s Bank, whereas the Atlantic Herring school size at Miscou increased threefold. Nevertheless, the density of herring in the schools remained fairly constant at Fisherman’s Bank and declined slightly at Miscou over time. The observation of similar increases in Bluefin Tuna occurrence in regions with different Atlantic Herring biomass trends is intriguing and also supports the idea that Bluefin Tuna are targeting the spawning grounds of Atlantic Herring. In this study, we did not detect a relationship between herring aggregation characteristics and Bluefin Tuna abundance. This does not preclude the potential for bottom-up processes; it may be that the two Atlantic Herring populations studied here still occur at sufficient densities or school in large enough aggregations that they continue to present attractive foraging opportunities. There may be a threshold at which Bluefin Tuna would alter their feeding behavior through means such as prey switching or habitat (location) switching to support their energy demands with respect to prey density. Future research could consider (1) whether the Bluefin Tuna-specific Atlantic Herring mortality rate is density dependent or independent, (2) whether a numerical (linear) or a Holling functional (nonlinear) relationship with Atlantic Herring abundance is to be expected, and (3) the type of nonlinear response (type I, II, or III). As Atlantic Herring aggregate to spawn, a type III functional response may occur, wherein a disproportionately greater number of prey is killed when the predator abundance increases (Accolla et al. 2015). Interactions between Bluefin Tuna and their other preferred prey in the sGSL, Atlantic Mackerel (Pleizier et al. 2012), as well as competing predators could also be investigated.

Our third objective was to establish the magnitude of annual Atlantic Herring consumption by Bluefin Tuna in the sGSL through time. Top predators like tuna can have large impacts on small pelagic fish, including sudden recruitment failure due to high consumption (Mariani et al. 2017). Bluefin Tuna have standard metabolic rates that are among the highest of any teleost fish species (Dickson and Graham 2004; Blank et al. 2007), resulting in elevated prey consumption. The methods for how to scale up observations from the local scale to ecosystem dynamics are challenging (Bailey et al. 2010). The scale of predator–prey interactions is often estimated systemwide by using annual or seasonal consumption rates, which assume spatial homogeneity (Bailey et al. 2010), as was done in this study. We opted to calculate Atlantic Herring consumption by Bluefin Tuna using the population estimate data from the Bluefin Tuna stock assessment VPA results (ICCAT 2017) and the sGSL-specific indices rather than using the abundance information from our study to calculate predation rates. Although the present study shows a more dramatic increase in Bluefin Tuna than other sGSL indices, the surveys were biased to herring aggregations on spawning grounds and thus do not accurately reflect consumption outside of the Atlantic Herring spawning season. The VPA data on Bluefin Tuna abundance and weight at age provided a rough estimate of Atlantic Herring consumption throughout the time of Bluefin Tuna presence in the sGSL. With this data, the biomass of Atlantic Herring consumed in the sGSL nearly doubled to reach estimates of 4,300–20,000 metric tons in 2012. These consumption data should be interpreted with caution, as predator abundance and diet data are often scarce. Nevertheless, this level of consumption would put Bluefin Tuna among the greatest known annual consumers of Atlantic Herring in recent years, along with grey seals (11,220 metric tons), Atlantic white-sided dolphins Lagenorhynchus acutus (10,000 metric tons), other cetaceans (6,000 metric tons), and seabirds (9,866 metric tons; Benoît and Rail 2016). This simple approach shows a doubling of Atlantic Herring consumption by Bluefin Tuna; however, our study identified a far greater increase of Bluefin Tuna on fall herring spawning grounds (Figure S2), indicating that consumption on spawning grounds—and, thus, overall consumption—may be greater than estimated here. Bluefin Tuna may now be a major source of Atlantic Herring natural mortality in the sGSL, rivaling fishing mortality. This is important information for the assessment of Atlantic Herring stocks and should act as an incentive to gather additional data and refine the consumption estimates so as to better inform and evaluate the estimated natural mortality dynamics of herring in their future assessments.

The need to consider species interactions and related processes, such as predator top-down control, in fisheries management has been well documented for marine ecosystems (Hollowed et al. 2000; Jurado-Molina and Livingston 2002; Worm and Myers 2003), for forage fish species (Tyrrell et al. 2011; Jacobsen and Essington 2018; Siple et al. 2018), and for Atlantic Herring in particular (Overholtz et al. 2008). Overholtz et al. (2008) argued that a dynamic mortality rate due to consumption by major predators should be included in analyses of prey fish dynamics when predator biomass changes substantially over time. In the Canadian Pacific, Siple et al. (2018) recently found that long-term shifts in natural mortality explained changes in age structure, biomass declines, and failure to reach management thresholds for two Pacific Herring Clupea pallasii stocks in Puget Sound. Under these conditions, the assumption of constant natural mortality will usually be invalid and related reference points (e.g., maximum sustainable yield, yield per recruit, and SSB per recruit) will be misleading and overly optimistic.

Predation can have large impacts on the stock dynamics of marine fish, particularly forage fish (Jacobsen and Essington 2018). Moreover, when combined with fishing
these impacts can be amplified (Beverton 1990; Essington et al. 2015). An example of the significant impact that predation can have on prey fish population dynamics has been documented in the case of Atlantic Cod in the sGSL (Neuenhoff et al. 2019). Estimated predation mortality on adult Atlantic Cod increased sharply during their collapse and has comprised the majority of their mortality since the 1990s. Although predation appeared to play only a minor role in the collapse of Atlantic Cod, it could be one of the main factors preventing this species’ recovery (Neuenhoff et al. 2019) and the recovery of other collapsed groundfish stocks in the sGSL ecosystem (Swain and Benoit 2015). As Atlantic Herring stock components are either collapsed or declining in the sGSL, increased predation might become increasingly detrimental to their ability to recover.

Interaction among marine species can change, and these changes can influence the dynamics of species that are harvested by fisheries, thus generating challenges for stock assessment and fisheries management (Legault and Palmer 2015; Jacobsen et al. 2019). Here, we used acoustic-based monitoring of the presence of predators on prey aggregations that indicated an escalating predator–prey relationship for fall-spawning Atlantic Herring stocks in the sGSL. The increase in Bluefin Tuna occurrence was independent of spawning grounds, Atlantic Herring density, or aggregation size, and Bluefin Tuna could now be the most important predators of herring in the sGSL. In the interest of assessing and managing sGSL Atlantic Herring, future studies should aim to incorporate informed estimates of the herring biomass consumption by Bluefin Tuna and other major predators and investigate the nature of the interaction between the species to better understand top-down control by Bluefin Tuna and bottom-up control by Atlantic Herring.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.