



# Ontogenetic shifts in isotope-inferred trophic ecology of Atlantic bluefin tuna *Thunnus thynnus* in Atlantic Canada

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**ABSTRACT:** Upper trophic level predators can greatly influence the dynamics and productivity of forage fish species. Quantifying this influence requires information on prey consumption; however, establishing feeding habits of highly mobile predators is particularly challenging. Stable isotopes of carbon and nitrogen ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) have been applied to characterize the trophic ecology of Atlantic bluefin tuna *Thunnus thynnus* (ABFT) in several important regions; however, applications in Canada are lacking. Here, we used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of ABFT muscle tissue collected in 2014–2018 on 2 important foraging grounds along the coast of Atlantic Canada to evaluate the temporally integrated trophic ecology of this ecologically and commercially important species. Populations of some small pelagic fish species in these areas have been depleted, and predation by ABFT is considered a potentially important contributor. Isotopic diet reconstructions found that Atlantic mackerel were the dominant prey in the southern Gulf of St. Lawrence, and a combination of Atlantic herring and sandlance were the most dominant prey consumed on the Scotian Shelf. Diet reconstructions identified an ontogenetic shift in prey consumption, with more sandlance consumed by smaller ABFT and a shift to higher consumption of Atlantic mackerel and Atlantic herring as fish increased in size. Isotopic niche overlap indicated relatively high overlap for adults among years, suggesting that ABFT did not show substantial inter-annual variation in their trophic ecology. Overall, the study provides insight into the trophic ecology of ABFT along the Atlantic Coast of Canada that can be integrated into investigations of predator impacts on depleted mackerel and herring populations.

**KEY WORDS:** Trophic ecology · Diet · Commercial fish · Predator · Ecosystem-based fisheries management ·  $\delta^{13}\text{C}$  ·  $\delta^{15}\text{N}$

## 1. INTRODUCTION

Information on the trophic ecology of a species is essential for understanding its prey requirements, interactions with other species and overall role in an ecosystem (Frisch et al. 2014, Brodeur et al. 2017). With a move towards ecosystem-based approaches to fisheries management, a comprehensive understand-

ing of fish diet and trophic niche improves our ability to draw links between species within an ecosystem and can help better ensure sustainable fisheries management (Link 2002, Pauly et al. 2002). The impact of predators on the productivity and dynamics of their prey depends, in part, on how prey choice and consumption vary spatially, temporally and with prey abundance (Holling 1959, Koen-Alonso 2007, Hun-  
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sicker et al. 2011). Furthermore, given apparent intra-specific spatial, temporal and ontogenetic variation in fish diets (Winemiller 1990, Sánchez-Hernández et al. 2019), it is important to characterize the trophic ecology of a species across these dimensions.

Traditional stomach content analyses are an effective way to characterize diet, generalist versus specialist prey consumption and trophic niche (Amundsen et al. 1996). However, the method is not temporally integrated, only capturing a snapshot of prey consumed prior to capture, and thus is subject to biases associated with differential digestion rates and species identification (Amundsen & Sánchez-Hernández 2019, Burbank et al. 2019, da Silveira et al. 2020, Brown-Vuillemin et al. 2023). For highly mobile, active predators, a snapshot of diet may miss important prey, provide relatively poor characterization of diet and either overestimate or underestimate consumption based on the time of capture as a result of seasonal shifts in prey availability and consumption. This may be especially challenging for endothermic predators with rapid digestion rates. For example, Varela et al. (2013) examined the diet of pre-spawning Atlantic bluefin tuna *Thunnus thynnus* (ABFT) in the Strait of Gibraltar and concluded stomach content analysis provided poor information on diet, as many stomachs were empty or contained high proportions of digested and unidentifiable material.

By contrast, stable isotopes of carbon and nitrogen ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) in muscle tissue can provide an effective, temporally integrated depiction of diet (Newsome et al. 2007), as turnover rates are in the range of months as opposed to hours (Olson et al. 2010, Weidel et al. 2011).  $\delta^{15}\text{N}$  has been used extensively to characterize the trophic positions occupied by consumers and their prey within food webs (Post 2002, Quezada-Romegialli et al. 2018), while  $\delta^{13}\text{C}$  provides insight into the habitat type from which food is sourced (France 1995, Phillips & Gregg 2001, Harrison et al. 2017, Burbank et al. 2022) and is useful for distinguishing between foraging in pelagic and benthic habitats. Together,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values can be used in isotope mixing models to characterize the relative proportion of prey consumed by a predator (Phillips & Gregg 2003, Moore & Semmens 2008, Stock et al. 2018). Furthermore, isotope values provide insight into the isotopic niche size of a population by incorporating information on diet and habitat, and isotopic niche overlaps can be computed to conceptualize how populations, or groups within a population, interact and exploit similar habitat and dietary resources over time (Layman & Post 2007, Newsome et al. 2007, Jackson et al. 2011, Swanson et al. 2015). Together, isotopic-based diet reconstructions along

with niche size and overlap estimates can provide temporally integrated insight into the trophic ecology of a species.

ABFT are a commercially important, highly mobile predator that often feed on schooling forage fish (Butler et al. 2010, Varela et al. 2020, Turcotte et al. 2023). For some depleted NW Atlantic forage fish populations, notably Atlantic herring *Clupea harengus* in the southern Gulf of St. Lawrence (sGSL) and the northern contingent of the Atlantic mackerel *Scomber scombrus* population, predation by ABFT could be a potentially important contributor to mortality, along with fishing (Benoît & Rail 2016, Turcotte et al. 2021a, Rolland et al. 2022, Van Beveren et al. 2024). Tagging studies suggest that ABFT forage along the Atlantic coast of Canada from around early June until late November before migrating back to spawning grounds in the Gulf of Mexico and the Mediterranean Sea (Block et al. 2019). Two important foraging grounds in Canadian waters that support an ABFT fishery are located on the Scotian Shelf south of Nova Scotia and in the sGSL off the coast of Prince Edward Island. Information on the trophic ecology of ABFT during their summer and fall residency along the coast of Atlantic Canada mainly comprises stomach content analyses that have identified Atlantic herring (Pleizier et al. 2012, Varela et al. 2020) and Atlantic mackerel (Turcotte et al. 2023) as dominant prey items. These studies are useful for understanding feeding ecology but only provide a snapshot of prey consumption and have at times identified notable proportions of unidentifiable fish (Pleizier et al. 2012). Given that ABFT are highly active predators, stable isotope analyses offer a valuable approach to providing a temporally integrated characterization of diet during their time foraging along Atlantic Canada. Stable isotopes have been successfully applied to characterize the diet and trophic ecology of ABFT in several instances, such as in the Strait of Gibraltar (Varela et al. 2013) and along the east coast of the USA (Estrada et al. 2005, Logan et al. 2015). However, applications in Canada have been limited to one 3 yr study in the southern Gulf of St. Lawrence in which no prey isotope values were collected and no diet reconstructions were attempted (Varela et al. 2020).

Here, we used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of ABFT muscle tissue and prey collected on 2 important ABFT foraging grounds along the coast of Atlantic Canada to evaluate and characterize the temporally integrated trophic ecology of this ecologically and commercially valuable species. We evaluated isotope inferred diet and niche of ABFT in the sGSL and Scotian Shelf over 5 yr (2014–2018) and examined changes in prey consump-

tion and trophic niche with fish size. We hypothesized that Atlantic herring and Atlantic mackerel would prove to be the dominant prey item at all sizes but that the relative proportion of prey consumed would change with fish size and that the isotopic niche size would be larger for adults than for juveniles.

## 2. MATERIALS AND METHODS

### 2.1. Sample collection and stable isotope analyses

Atlantic bluefin tuna were captured by rod and reel in 2014–2018 by harvesters during September and October in the sGSL and on the Scotian Shelf (Fig. 1). Individuals were measured for curved fork length (CFL, cm) and a small piece of red muscle tissue from the dorsal musculature in the head was collected and stored at  $-20^{\circ}\text{C}$  until further analysis. Red muscle tissue was used rather than white muscle tissue because red muscle tissue has a higher turnover rate (Graham et al. 1983), thereby characterizing prey consumption

likely reflective of summer foraging in the sGSL or Scotian Shelf. Within the context of this study, ABFT of  $<200$  CFL (cm) were considered juveniles and those  $\geq 200$  CFL (cm) were considered adults. To facilitate isotope-based diet reconstructions, putative prey samples were collected opportunistically throughout the sampling time series in each region (see Table 1 and Section 2.2 for species included in each region), and a small dorsal muscle tissue sample, taken from just posterior to the dorsal fin, was collected and stored at  $-20^{\circ}\text{C}$  until further analysis. For some smaller putative prey collected, such as Euphausiidae, the entire organism was taken and processed without the shell for use in stable isotope analyses.

For stable isotope analyses, the dorsal muscle tissue of ABFT and putative prey species (e.g. Atlantic herring, Atlantic mackerel) were dried in a standard laboratory drying oven at  $50^{\circ}\text{C}$  for a minimum of 48 h before being homogenized with a mortar and pestle. The dried, ground homogenate was weighed (target weight: 0.3 mg) into tin capsules ( $8 \times 5$  mm; Elemental Microanalysis) using an analytical balance (XP205

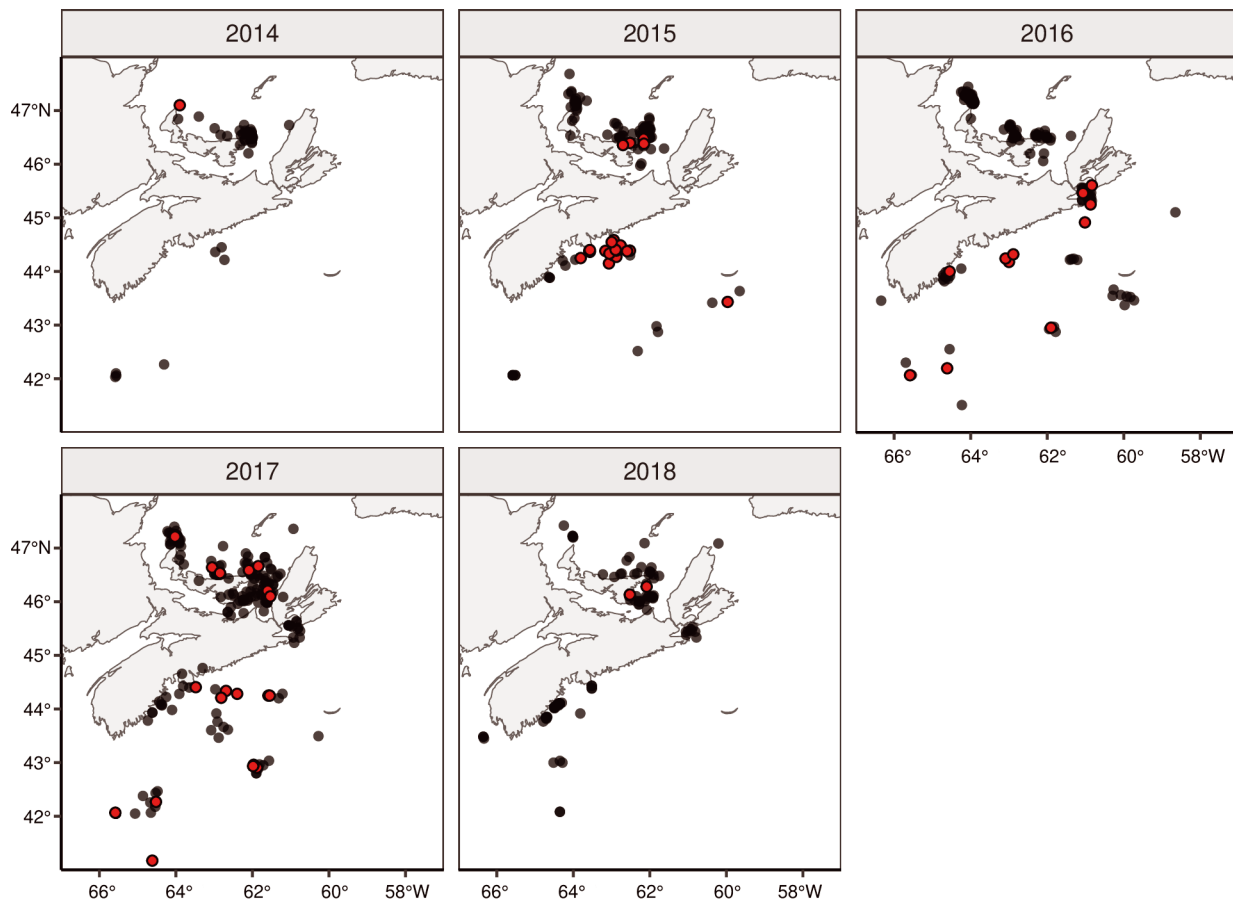


Fig. 1. Reported capture locations of adult (black circles) and juvenile (red circles) Atlantic bluefin tuna used in this study for captures where GPS locations were available

DeltaRange, Mettler-Toledo) and analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios at the University of Waterloo's Environmental Isotope Lab using a Delta Plus Continuous Flow stable isotope ratio mass spectrometer (Thermo Finnigan) coupled to a 4010 Elemental Analyser (CNSO 4010, Costech Analytical Technologies). Analytical results were expressed as ‰ deviations from the international standard reference materials of Vienna PeeDee Belemnite for C (Craig 1957) and atmospheric nitrogen for N (Mariotti 1983). Duplicates were run for every 10<sup>th</sup> sample for quality assurance (i.e. precision). Internal laboratory standards inserted at the beginning, middle and end of sample runs were used to assess measurement accuracy, with internal standards having been cross-calibrated against International Atomic Energy Agency standards for C (CH3, CH6) and N (N1, N2). Reference materials were used in data normalization and to ensure measurement precision and accuracy, with quality control and assurance checks indicating an error for reportable data of no more than 0.2 and 0.3‰, respectively, for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .  $\delta^{13}\text{C}$  values of all ABFT muscle tissue samples and all prey species within a given location with C:N ratios of >4 were lipid-corrected using equations presented in Logan et al. (2008).

## 2.2. Bayesian isotope mixing models

Bayesian isotope mixing models were constructed using the mixSIAR package (Stock & Semmens 2016, Stock et al. 2018) in R v.4.2.2 (R Core Team 2020) to estimate the relative temporally integrated proportion of each prey group in ABFT diets. The isotope mixing models were run with uninformative priors for the proportions, using year as a fixed factor and CFL as a continuous factor to examine changes in relative prey proportions across years and fish size. All models were run using Markov chain Monte Carlo (MCMC) methods with 3 chains of 1 000 000 runs with a burn-in of 500 000. Following model runs, the Gelman-Rubin and Geweke tests were used to assess convergence of Bayesian isotope mixing model estimates (Stock & Semmens 2016). Models were formulated with both residual and process errors (Stock et al. 2018). We incorporated diet-tissue discrimination factors of  $1.88 \pm 0.3\text{‰}$  for  $\delta^{13}\text{C}$  and  $1.9 \pm 0.4\text{‰}$  for  $\delta^{15}\text{N}$  into the mixing models based on Madigan et al. (2012). Separate Bayesian iso-

tope mixing models were run for fish captured in the sGSL and Scotian Shelf, as they were assumed to have access to different suites of prey with different prey isotope values. In the isotope mixing models, we included prey that ABFT are known to consume in notable amounts within the regions of interest based on Pleizier et al. (2012), and later confirmed by Turcotte et al. (2023) and Varela et al. (2020), and for which suitable samples were collected in the field during the ABFT sample collection period. Prey used for the sGSL model included Atlantic cod *Gadus morhua*, Atlantic herring, capelin *Mallotus villosus*, Atlantic mackerel, sandlance *Ammodytes* spp. and shortfin squid *Illex illecebrosus*. Atlantic cod and shortfin squid were combined as a group for the mixing model as they have very similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (see Fig. 2A). Prey sources used for the Scotian Shelf model included Atlantic cod, Atlantic herring, Euphausiidae, Atlantic mackerel and sandlance (Table 1). Prey sources were limited to 5 to ensure that the models converged, to improve model inference and to avoid erroneous conclusions from models (Stock et al. 2018).

## 2.3. Isotopic niche size and overlap

We used the 'NicheRover' package in R (Swanson et al. 2015) to estimate and compare the isotopic niche size of adult and juvenile ABFT. The package estimates the niche region in bivariate  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  space within which individuals of a given group have a 95% probability of occurring based on 10 000 MCMC chains (Swanson et al. 2015, Burbank et al. 2019). In the context of this study, groups equated to either juvenile or adult ABFT, and the estimated niche region was used as a proxy for isotopic niche

Table 1. Mean ( $\pm$ SD)  $\delta^{13}\text{C}$  (‰) and  $\delta^{15}\text{N}$  (‰) values and number of individuals of each prey species collected in the southern Gulf of St. Lawrence (sGSL) and Scotian Shelf that were used in the Bayesian isotope mixing models

Location	Species	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
sGSL	Atlantic cod	13	$-19.68 \pm 0.36$	$13.45 \pm 0.59$
	Atlantic herring	15	$-17.99 \pm 0.34$	$12.79 \pm 0.32$
	Capelin	15	$-20.34 \pm 0.31$	$11.90 \pm 0.39$
	Mackerel	15	$-19.47 \pm 0.36$	$11.27 \pm 0.43$
	Sandlance	15	$-22.03 \pm 0.59$	$10.77 \pm 0.49$
	Shortfin squid	4	$-20.30 \pm 0.31$	$13.16 \pm 0.35$
Scotian Shelf	Atlantic cod	4	$-18.08 \pm 1.22$	$12.93 \pm 0.75$
	Atlantic herring	25	$-20.31 \pm 0.70$	$11.73 \pm 0.43$
	Euphausiidae	18	$-16.09 \pm 0.65$	$7.79 \pm 0.80$
	Mackerel	8	$-18.96 \pm 0.16$	$12.87 \pm 0.24$
	Sandlance	21	$-21.20 \pm 0.35$	$10.98 \pm 0.50$

size. The package was also employed to estimate bidirectional isotopic niche overlap. Bayesian techniques facilitate the computation of 95% directional pairwise probabilities to quantify the probability that the juvenile group would occur within the niche region of the adult group and vice versa. We quantified the isotopic niche size and overlap of adults and juveniles in the sGSL and Scotian Shelf with all years pooled to quantify changes in trophic ecology across life stages within each area. We also quantified isotopic niche size and overlap of adults among years to examine potential temporal shifts in niche size and overlap within each area. Comparisons by year were not possible for juveniles due to the limited sample sizes. All analyses were conducted in R v.4.2.2 (R Core Team 2020).

### 3. RESULTS

A total of 377 and 280 Atlantic bluefin tuna captured between 2014 and 2018 in the sGSL and Scotian Shelf, respectively, were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . The mean ( $\pm$ SD)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of all adults pooled across all years were  $-17.93 \pm 0.44\text{‰}$  and  $13.01 \pm 0.76\text{‰}$ , respectively, in the sGSL and  $-18.02 \pm 0.42\text{‰}$  and  $13.07 \pm 0.72\text{‰}$ , respectively, in the Scotian Shelf. For juveniles, the equivalent  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measures were  $-18.40 \pm 0.29\text{‰}$  and  $12.54 \pm 0.67\text{‰}$ , respectively, in the sGSL and  $-18.39 \pm 0.44\text{‰}$  and  $12.74 \pm 0.84\text{‰}$ , respectively, in the Scotian Shelf (Table 2). In the sGSL, the average  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of adults across the 5 yr ranged from  $-18.08 \pm 0.41\text{‰}$  in 2018 to  $-17.75 \pm 0.38\text{‰}$  in 2014 and  $12.85 \pm 0.76\text{‰}$  in 2016 to  $13.14 \pm 0.74\text{‰}$  in 2014, respectively

(Table 2, Fig. 2A). In the Scotian Shelf, the average isotope values of adults ranged from  $-18.27 \pm 0.47\text{‰}$  in 2016 to  $-17.64 \pm 0.33\text{‰}$  in 2014 for  $\delta^{13}\text{C}$  and  $12.90 \pm 0.79\text{‰}$  in 2015 to  $13.53 \pm 0.51\text{‰}$  in 2014 for  $\delta^{15}\text{N}$  (Table 2, Fig. 2B). The range of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (CR and NR) of adults were wider in the sGSL (CR: 3.92‰; NR: 5.37‰) than in the Scotian Shelf (CR: 2.67‰; NR: 4.11‰; Table 2). Conversely, for juveniles, the CR and NR were wider for the Scotian Shelf (Table 2).

The relative proportions of each prey consumed by ABFT in the sGSL based on Bayesian isotope mixing models were largely consistent through time (Table 3), with a coefficient of variation (CV) of 16% across years. The median posterior estimates of the relative proportions of each prey indicated that Atlantic mackerel was the dominant prey item in the sGSL, ranging from 0.66 in 2018 to 0.76 in 2015. The next most prominent diet items were sandlance, with a range of 0.15 in 2015 to 0.23 in 2018, followed by Atlantic herring, with a range of 0.066 in 2015 to 0.093 in 2014. Capelin and the 'other' groups, comprising Atlantic cod and squid, were found to have a high likelihood of making negligible contributions to ABFT diets. Ontogenetic shifts in the relative proportions of select prey consumed in the sGSL were also apparent (Fig. 3). The Bayesian isotope mixing model results indicate that similar relative proportions of Atlantic mackerel and sandlance are consumed at smaller CFLs (~50%). As CFL increased, the relative proportion of sandlance decreased while that of Atlantic mackerel increased to a peak before decreasing at very large sizes. By contrast, the relative proportion of Atlantic herring increased across the size range, approaching that of mackerel at the largest CFLs to

Table 2. Capture location, stage, year, number of individuals, mean ( $\pm$ SD)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , range of  $\delta^{13}\text{C}$  values (CR) and range of  $\delta^{15}\text{N}$  values (NR) of Atlantic bluefin tuna used in this study. sGSL: southern Gulf of St. Lawrence; CFL: curved fork length

Capture location	Stage	Year	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	CR (‰)	NR (‰)	
sGSL	Juvenile < 200 CFL (cm)	All years pooled	14	$-18.40 \pm 0.29$	$12.54 \pm 0.67$	0.99	2.76	
		Adult $\geq$ 200 CFL (cm)	2014	30	$-17.75 \pm 0.38$	$13.14 \pm 0.74$	1.54	3.06
			2015	71	$-17.85 \pm 0.44$	$13.08 \pm 0.82$	2.49	4.76
			2016	70	$-17.98 \pm 0.38$	$12.85 \pm 0.76$	1.72	4.41
			2017	158	$-17.96 \pm 0.47$	$13.02 \pm 0.72$	3.54	4.35
			2018	34	$-18.08 \pm 0.41$	$13.08 \pm 0.83$	1.54	3.59
			All years pooled	363	$-17.93 \pm 0.44$	$13.01 \pm 0.76$	3.92	5.37
	Scotian Shelf	Juvenile < 200 CFL (cm)	All years pooled	43	$-18.39 \pm 0.44$	$12.74 \pm 0.84$	2.67	4.82
Adult $\geq$ 200 CFL (cm)			2014	6	$-17.64 \pm 0.33$	$13.53 \pm 0.51$	0.88	1.43
			2015	36	$-17.87 \pm 0.39$	$12.90 \pm 0.79$	1.54	3.29
			2016	59	$-18.27 \pm 0.47$	$13.03 \pm 0.63$	2.37	2.74
			2017	99	$-17.94 \pm 0.36$	$13.00 \pm 0.71$	2.17	3.55
			2018	37	$-18.06 \pm 0.44$	$13.43 \pm 0.74$	2.00	3.68
			All years pooled	237	$-18.02 \pm 0.42$	$13.07 \pm 0.72$	2.67	4.11

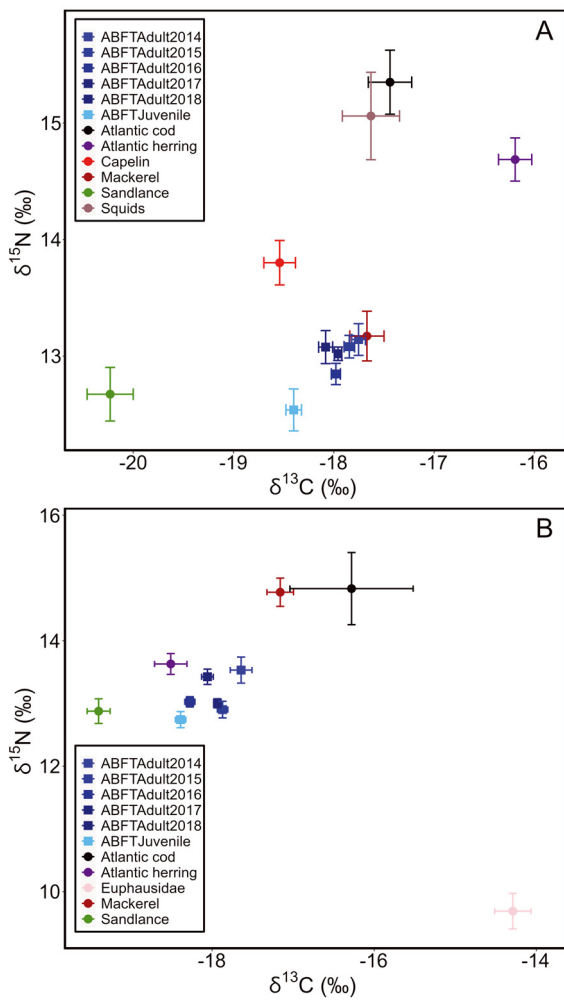


Fig. 2. Mean ( $\pm$ SE)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of Atlantic bluefin tuna (ABFT) adults examined in each year, ABFT juveniles across years and all potential prey considered in this study from (A) the southern Gulf of St. Lawrence and (B) the Scotian Shelf. Diet–tissue discrimination factors were incorporated to adjust the position of prey within the isotopic biplots

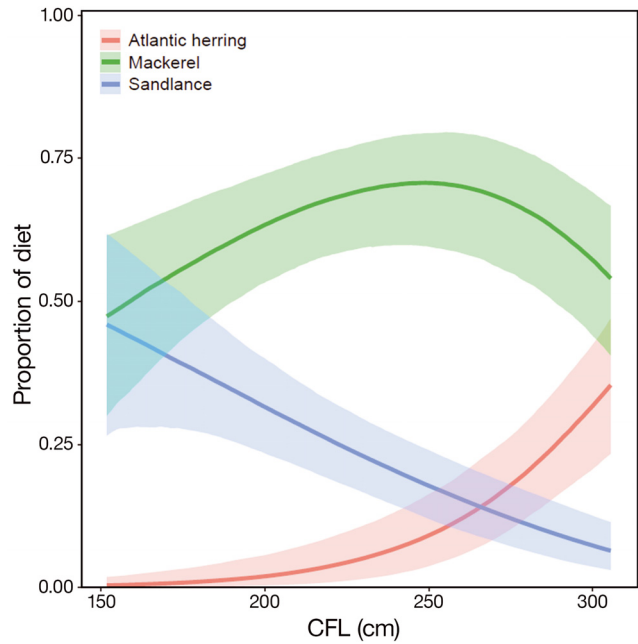


Fig. 3. Median (solid line) estimated proportion of diet items consumed by Atlantic bluefin tuna in the southern Gulf of St. Lawrence in relation to curved fork length (CFL) pooled across 2014–2018 based on Bayesian isotope mixing model results. Shaded areas: 95% credible intervals

become the second most consumed prey (Fig. 3). As these ontogenetic trends were similar across years, they are presented here with years pooled.

The relative proportions of each prey consumed by ABFT on the Scotian Shelf based on Bayesian isotope mixing models were more variable through time (CV: 35% across years) compared to the sGSL and were more evenly distributed across prey species (Table 3). The median posterior estimates of the relative proportions of prey consumed indicated that sandlance and Atlantic herring were the most dominant prey items

Table 3. Median posterior estimate of the annual relative proportion of each prey item consumed by Atlantic bluefin tuna in 2014–2018 in the southern Gulf of St. Lawrence (sGSL) and Scotian Shelf based on Bayesian isotope mixing models. ‘Other’ group in the sGSL: Atlantic cod and squid

Capture location	Prey item	Median proportion of prey consumption (95% credible intervals)				
		2014	2015	2016	2017	2018
sGSL	Atlantic herring	0.093 (0.030–0.19)	0.066 (0.016–0.15)	0.074 (0.025–0.14)	0.072 (0.023–0.14)	0.085 (0.028–0.17)
	Capelin	0.009 (0–0.075)	0.008 (0–0.062)	0.009 (0–0.070)	0.009 (0–0.070)	0.010 (0–0.077)
	Mackerel	0.71 (0.57–0.83)	0.76 (0.63–0.86)	0.70 (0.59–0.80)	0.71 (0.59–0.81)	0.66 (0.52–0.77)
	Other	0.005 (0–0.038)	0.004 (0–0.030)	0.005 (0–0.034)	0.005 (0–0.035)	0.005 (0–0.039)
	Sandlance	0.17 (0.094–0.24)	0.15 (0.088–0.22)	0.20 (0.13–0.27)	0.19 (0.13–0.26)	0.23 (0.15–0.31)
Scotian Shelf	Atlantic cod	0.042 (0.001–0.23)	0.036 (0.001–0.19)	0.029 (0.001–0.14)	0.041 (0.001–0.18)	0.040 (0.001–0.23)
	Atlantic herring	0.28 (0.12–0.54)	0.31 (0.057–0.56)	0.29 (0.061–0.51)	0.26 (0.057–0.47)	0.47 (0.10–0.69)
	Euphausiidae	0.12 (0.057–0.19)	0.16 (0.11–0.20)	0.10 (0.064–0.13)	0.10 (0.023–0.17)	0.084 (0.040–0.12)
	Mackerel	0.15 (0.009–0.40)	0.10 (0.010–0.20)	0.090 (0.007–0.21)	0.11 (0.008–0.26)	0.11 (0.007–0.28)
	Sandlance	0.37 (0.18–0.54)	0.37 (0.20–0.55)	0.48 (0.28–0.63)	0.43 (0.28–0.57)	0.28 (0.13–0.53)

on the Scotian Shelf, with sandlance proportions ranging from 0.28 in 2018 to 0.48 in 2016 and Atlantic herring proportions ranging from 0.26 in 2017 to 0.47 in 2018. The median relative proportion estimate for Atlantic mackerel was much lower on the Scotian Shelf than in the sGSL, ranging from 0.090 in 2016 to 0.15 in 2014. Median relative proportion estimates for Euphausiidae ranged from 0.084 in 2018 to 0.16 in 2015 and those for Atlantic cod ranged from 0.029 in 2016 to 0.042 in 2014. Ontogenetic shifts in prey consumption were evident on the Scotian Shelf but less clear and more uncertain compared to the sGSL (Fig. 4). The Bayesian isotope mixing model results suggest that across years, with increasing fish length, the relative proportion of sandlance consumed decreased and the relative proportion of Atlantic herring and mackerel consumed increased, with more Atlantic herring consumed than sandlance at large sizes. This trend was particularly evident in 2018, when Atlantic herring were the most prominent item in the diet. As trends were more variable across years in samples from the Scotian Shelf compared to the sGSL, size-based relative prey consumption estimates are presented separately for each year (Fig. 4).

The median ( $\pm$ SE) isotopic niche breadth of adults in the sGSL, pooled across all years ( $6.24 \pm 0.33\text{‰}^2$ ), was significantly larger ( $t$ -test,  $t_{12532} = 295.78$ ,  $p < 0.001$ ) than the isotopic niche of juveniles ( $3.33 \pm 0.92\text{‰}^2$ ). On the Scotian Shelf, the reverse was found (juveniles:  $6.52 \pm 1.00\text{‰}^2$ , adults:  $5.89 \pm 0.38\text{‰}^2$ ;  $t_{12838} = -58.86$ ,  $p < 0.001$ ) (Fig. 5). The isotopic niche of adults pooled across years was significantly higher in the sGSL than on the Scotian Shelf ( $t_{19448} = 69.61$ ,  $p < 0.001$ ), whereas the isotopic niche of juveniles was significantly higher on Scotian Shelf ( $t_{19876} = 230.25$ ,  $p < 0.001$ ) (Fig. 5). The isotopic niche of adults in the sGSL was variable among years (CV: 13.4%) and always higher than the isotopic niche of juveniles, with a high of  $6.58 \pm 0.78\text{‰}^2$  in 2015 and a low of  $5.09 \pm 0.96\text{‰}^2$  in 2014 (Fig. 6). Similarly, the adult isotopic niche was variable among years on the Scotian Shelf (CV: 14.5%). In 2014, only 6 individuals were available for analysis on the Scotian Shelf, which is below the recommended analytical threshold of 10 for the method (Swanson et al. 2015). Excluding 2014, the isotopic niche of adults on the Scotian Shelf ranged from a low of  $4.76 \pm 0.48\text{‰}^2$  in 2016 to a high of  $5.72 \pm 0.94\text{‰}^2$  in 2018 and was

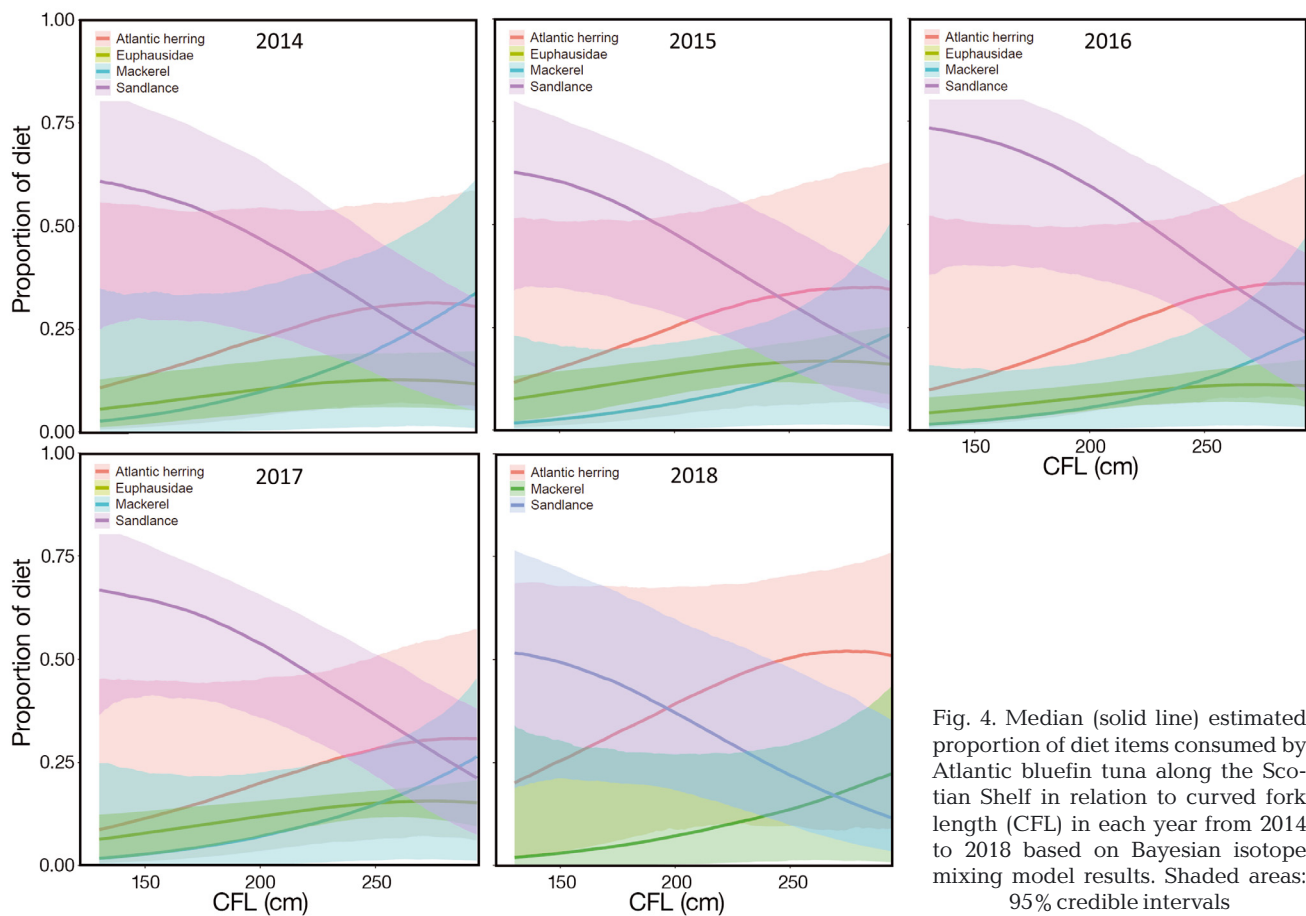


Fig. 4. Median (solid line) estimated proportion of diet items consumed by Atlantic bluefin tuna along the Scotian Shelf in relation to curved fork length (CFL) in each year from 2014 to 2018 based on Bayesian isotope mixing model results. Shaded areas: 95% credible intervals

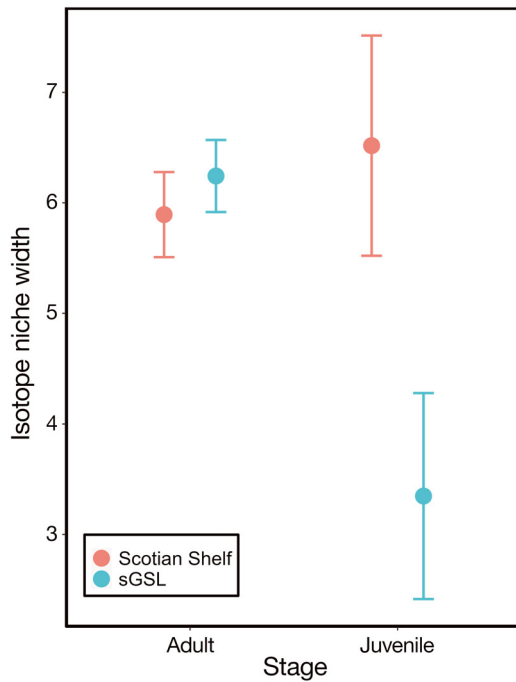


Fig. 5. Isotopic niche width of adult and juvenile Atlantic bluefin tuna pooled across years in the southern Gulf of St. Lawrence (blue) and Scotian Shelf (red)

always lower than that of juveniles (Fig. 6). Additionally, the isotopic niche of adult ABFT captured in the sGSL and Scotian Shelf was similar in 2016 and 2018 but was substantially higher in the sGSL in 2015 and 2017.

In the sGSL, the median probability that the isotopic niche of juveniles overlapped with the niche of adults pooled across years was 93.1% (95% credible interval: 78–99%), and the probability that the isotopic niche of adults pooled across years overlapped with the niche of juveniles was substantially lower at 49.6% (32–74%) (Table 4). On the Scotian Shelf, the median probability the isotopic niche of juveniles overlapped with the niche of adults pooled across years (84.8%, 73–93%) and vice-versa (87.5%, 75–96%) were both high (Table 4). When examining isotopic niche overlap of adults among years, the probability that the isotopic niche of adults in one year overlapped with adults in another year was high in the sGSL (all probabilities of overlap:  $\geq 84.9\%$ ) and was high on the Scotian Shelf with the exception of 2014 (all probability of overlap:  $\geq 80.8\%$ ) (Table 5).

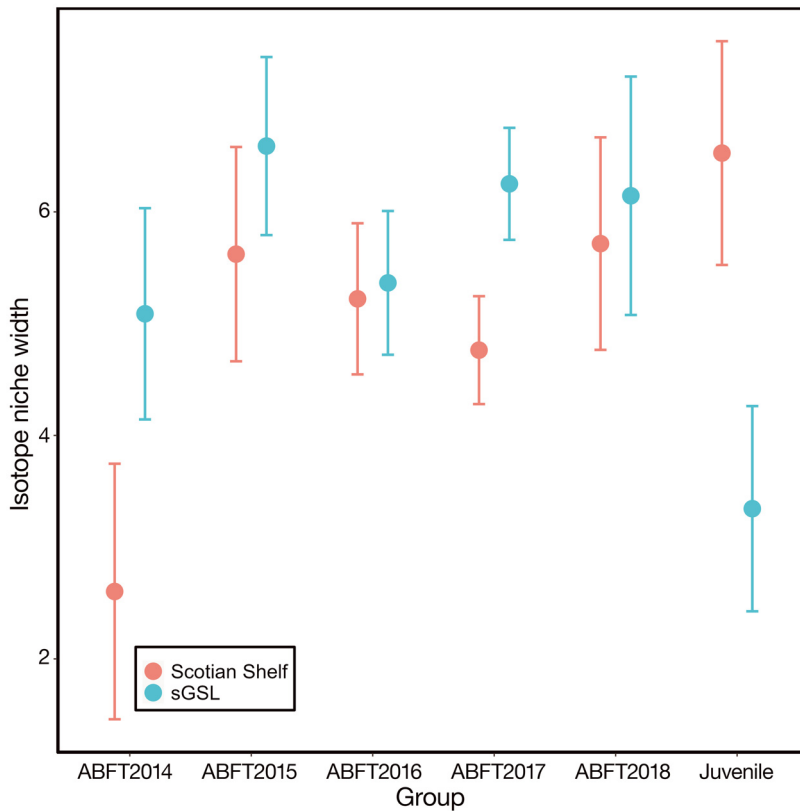


Fig. 6. Isotopic niche width of Atlantic bluefin tuna adults in 2014–2018 and juveniles pooled across years in the southern Gulf of St. Lawrence (blue) and Scotian Shelf (red)

#### 4. DISCUSSION

Overall, our study characterized the temporally integrated trophic ecology, including the diet and isotopic niche size and overlap, of ABFT in 2 important foraging grounds along the Atlantic coast of Canada: the sGSL and Scotian Shelf. Isotopic diet reconstructions estimated Atlantic mackerel as the dominant prey in the sGSL, supporting findings from Turcotte et al. (2023), and a combination of Atlantic herring and sandlance as the dominant prey consumed by ABFT on the Scotian Shelf. Diet reconstructions identified an ontogenetic shift in prey consumption, with more sandlance being consumed by smaller ABFT and a shift to higher consumption of Atlantic mackerel and Atlantic herring as ABFT increased in size. Isotopic niche width was variable through time and was higher in adults than in juveniles in the sGSL but higher in juveniles than in adults on the Scotian Shelf. Isotopic niche overlap indicated relatively high overlap among the 5 yr, suggesting



Table 4. Mean, median and 95% credible interval of estimated directional overlap of isotopic niche among juveniles and adult Atlantic bluefin tuna pooled across years in the southern Gulf of St. Lawrence (sGSL) and Scotian Shelf. Values are given as probabilities (%) that the isotopic niche of group A overlaps the isotopic niche of group B

Capture location	Group B	Group A	Stable isotope overlap probability		
			Mean	Median	95% credible interval
sGSL	Adult	Juvenile	92	93	78–99
	Juvenile	Adult	50	50	32–74
Scotian Shelf	Adult	Juvenile	84	85	73–93
	Juvenile	Adult	87	88	75–96

ABFT did not show substantial inter-annual variation in trophic ecology for the period considered.

The Bayesian isotope mixing models employed in this study suggest that Atlantic mackerel had the highest relative contributions to the diet of ABFT in the sGSL (~70% across years) followed by sand lance and Atlantic herring, with limited interannual variation in dietary contributions (Table 3). Examining CFL as a continuous covariate indicated apparent shifts in diet as fish grow (Fig. 3), with smaller individuals consuming higher proportions of sand lance and increasing their reliance on mackerel with size to a maximum at around 255 CFL (cm). Relative contributions of Atlantic herring to the diet also increased with size, with the herring constituting approximately 30% of the diet of the largest individuals. These temporally integrated estimates of the relative contributions of prey to ABFT diet were similar to the diet estimates completed in the sGSL in 2015 and 2018–2021 (Varela et al. 2020, Turcotte et al. 2023). Turcotte et al. (2023) estimated ABFT diet in the sGSL consisted of approximately 66% Atlantic mackerel based on ABFT stomach contents by weight in 2018, 86% in 2019, 84% in 2020 and 74% in 2021. Similarly, Varela et al. (2020) employed stomach content analysis of ABFT captured in the sGSL and found that Atlantic mackerel constituted 76% of ABFT diet by weight in 2015, with contributions declining to 21 and 27% by weight in 2016 and 2017, respectively. Furthermore, Varela et al. (2020) found that as reliance on Atlantic mackerel declined, there was an increase in consumption by weight of Atlantic herring (57 and 65% in 2016 and 2017, respectively). In 2016, Atlantic mackerel were found in more stomachs, with a frequency of occurrence of 41% compared to 37% for Atlantic herring, but this was not the case in 2017. Varela et al.'s (2020) conclusions, based on stomach content observations, that the use of Atlantic mackerel as prey by ABFT declined in 2016 and 2017 are not consistent with our

findings that suggest Atlantic mackerel was still the dominant prey item. We also estimated higher proportions of sand lance (15–23%) than previous studies that have noted typically below 1% by weight (Pleizier et al. 2012, Varela et al. 2020, Turcotte et al. 2023).

Discrepancies in study findings may be linked to the methods used for making dietary inferences, the timing of ABFT sampling and the size of individuals included in each investigation. The use of stomach contents provides a snapshot of diet, and if, for example,

ABFT were sampled near Atlantic herring spawning grounds during spawning, stomach content analyses may indicate a concomitant increase in the relative importance of Atlantic herring in ABFT diet during that period. Stomach content samples used in the Varela et al. (2020) study were collected in fall from ABFT landed in Port Hood, and although capture location was not directly identified in the study (but see Fig. 1 in Turcotte et al. 2023), it is likely that the fish were captured on or around Fisherman's Bank, an important spawning ground for fall spawning herring in the sGSL (Messieh 1987, Turcotte et al. 2022). Therefore, it is highly plausible that the change in prey consumption from predominantly Atlantic mackerel in 2015 to predominantly Atlantic herring in 2016 and 2017 identified by Varela et al. (2020) was the result of stomachs being analyzed after feeding on spawning aggregations of herring and thus would not necessarily be indicative of general feeding trends in Canadian waters in those years. By contrast, the samples used in Turcotte et al. (2023) were largely collected off the north-east coast of Prince Edward Island and indicate feeding predominantly on Atlantic mackerel. Furthermore, our study included individuals captured in September and October; therefore, our isotope values are likely reflective of feeding from late May or early June until the time of capture and thus are likely less sensitive to capture locations.

Atlantic mackerel spawn in the sGSL in June and July, feed there throughout the summer and fall in schools and shoals and then migrate south in mid to late October (Van Beveren et al. 2023, DFO 2023). Atlantic mackerel would therefore be available for consumption by ABFT foraging in the sGSL during the summer and fall and easily detectable in ABFT tissue samples, given the expected tissue turnover rates. Atlantic mackerel have been estimated to be at or below the limit reference point (LRP) defined for the stock since approximately 2010 (DFO 2023). Despite being

Table 5. Mean, median and 95% credible interval of estimated directional overlap of isotopic niche among Atlantic bluefin tuna adults captured in each year (2014–2018) and juveniles in the southern Gulf of St. Lawrence (sGSL) and Scotian Shelf. Values are given as probabilities (%) that the isotopic niche of group A overlaps the isotopic niche of group B

Capture location	Group B	Group A	Stable isotope overlap probability			
			Mean	Median	95% credible interval	
sGSL	ABFT2014	ABFT2015	87	87	75–96	
		ABFT2016	87	88	74–97	
		ABFT2017	85	85	74–95	
		ABFT2018	81	81	63–95	
	ABFT2015	Juvenile	65	65	30–93	
		ABFT2014	96	97	88–100	
		ABFT2016	95	96	89–99	
		ABFT2017	94	94	88–98	
	ABFT2016	ABFT2018	91	92	81–98	
		Juvenile	88	90	68–99	
		ABFT2014	90	91	78–97	
		ABFT2015	88	88	78–95	
	ABFT2017	ABFT2017	90	90	82–96	
		ABFT2018	89	90	76–97	
		Juvenile	89	91	70–99	
		ABFT2014	95	95	87–99	
	ABFT2018	ABFT2015	92	93	86–97	
		ABFT2016	95	95	90–98	
		ABFT2018	92	93	82–98	
		Juvenile	92	94	77–99	
	Juvenile	ABFT2014	90	91	73–99	
		ABFT2015	88	89	76–97	
		ABFT2016	94	94	84–99	
		ABFT2017	91	92	81–97	
		Juvenile	92	94	73–100	
		ABFT2014	35	33	13–68	
		ABFT2015	43	42	22–68	
		ABFT2016	58	57	35–83	
	ABFT2017	52	50	32–76		
	ABFT2018	58	58	34–83		
	Scotian Shelf	ABFT2014	ABFT2015	52	51	25–85
			ABFT2016	41	38	17–77
			ABFT2017	56	54	31–88
			ABFT2018	52	50	26–84
		ABFT2015	Juvenile	25	21	6–62
			ABFT2014	91	94	64–100
			ABFT2016	81	82	66–94
			ABFT2017	95	95	87–99
		ABFT2016	ABFT2018	85	85	70–96
			Juvenile	72	73	51–89
			ABFT2014	85	87	54–99
			ABFT2015	80	81	65–92
		ABFT2017	ABFT2017	88	89	78–96
			ABFT2018	82	83	68–94
			Juvenile	84	84	70–94
			ABFT2014	90	93	63–100
		ABFT2018	ABFT2015	90	90	79–97
			ABFT2016	82	83	70–92
ABFT2018			83	83	70–94	
Juvenile			73	73	58–85	
Juvenile		ABFT2014	90	93	64–100	
		ABFT2015	87	88	73–97	
		ABFT2016	84	84	69–95	
		ABFT2017	92	94	81–98	
		Juvenile	71	72	53–89	
		ABFT2014	66	68	26–97	
		ABFT2015	82	83	64–95	
		ABFT2016	92	93	82–98	
ABFT2017		88	89	74–97		
ABFT2018		83	84	67–95		

at historically low biomass levels in recent years, Atlantic mackerel appears to be frequently and consistently preyed upon by ABFT when both species co-occur in the sGSL. Results, therefore, provide support for the notion that predation by ABFT is likely an important contributor to the mortality of Atlantic mackerel. Spring-spawning Atlantic herring in the sGSL have also been estimated to be at low spawning stock biomass and below the LRP for the stock since 2002, and fall spawners have been experiencing declining biomass since approximately 2011, with rapid declines in the 2014–2018 period (DFO 2022, Rolland et al. 2022). The occurrence of spawning aggregations, which concentrate herring both spatially and temporally, may nonetheless make Atlantic herring readily available for consumption by ABFT during periods in late August through early October. For instance, the elevated proportion of gravid herring identified in stomach contents in some sampling events undertaken by Pleizier et al. (2012) and the strong presence of ABFT on herring spawning grounds (Turcotte et al. 2021a) is consistent with the targeting of herring aggregations by ABFT. However, unlike what we observed for Atlantic mackerel, the temporally integrated isotope mixing models suggest lower relative reliance on Atlantic herring as prey during the 2014–2018 period in the sGSL and is consistent with their declining biomass and potential availability.

Our stable-isotope-based estimate of diet that integrates the history of consumption over a period of months suggests that Atlantic mackerel constitute the majority of ABFT diet in the sGSL, with among-year similarities in isotope values (Table 2) and high isotope niche overlap (Table 5) indicating relative constancy in the trophic ecology from 2014 to 2018 within the sGSL. As previously noted, discrepancies between our results and those reported by Varela et al. (2020) are likely related to the disproportionate sampling of ABFT

during or after their feeding on Atlantic herring spawning aggregations in that study. Pleizier et al. (2012), who collected samples of ABFT stomachs near Port Hood, Nova Scotia from 27 September to 5 October 2010 when fall spawning Atlantic herring was at its peak spawning stock biomass (Turcotte et al. 2021b, Rolland et al. 2022), found that Atlantic herring constituted approximately 40% of diet by weight and was in approximately 65% of stomachs. The results suggest a high overlap between availability and use, although Pleizier et al. (2012) also identified a notable amount of unidentifiable fish (26% by weight) which may have been Atlantic herring or other species such as sandlance.

The present study indicated higher relative proportions of sandlance than other diet studies in the sGSL. However, our study also included a larger number of smaller individuals, which were at sizes that appear to consume more sandlance (Fig. 3) (Logan et al. 2011). Sandlance, being a small-bodied fish, may be subject to more rapid digestion and, therefore, may be underestimated when using stomach content analyses. Furthermore, sandlance in the sGSL appear to occur in geographically restricted areas (e.g. Benoît et al. 2003), and sampling biases in stomach content analyses like those described above for herring are likely. Nevertheless, previous studies of ABFT diets in the Mid-Atlantic Bight, Southern New England, Gulf of Maine and Georges Bank regions have indicated substantial consumption of sandlance, particularly by smaller individuals (Logan et al. 2011, 2015), and have estimated that sandlance comprise up to 69% of ABFT stomachs by weight (Chase 2002, Staudinger et al. 2020). Collectively, these studies highlight that ABFT frequently consume substantial amounts of sandlance and concur with our results that suggest similar consumption patterns within the sGSL.

Bayesian isotope mixing models indicate that the diet of ABFT captured in the Scotian Shelf ecosystem was dominated by a combination of Atlantic herring and sandlance (Table 3). Relative proportions of Atlantic herring consumption in this study matched well with previous observations of stomach contents in the Scotian Shelf near Canso, Nova Scotia, which identified 40% stomach content by weight in 31 individual ABFT (Pleizier et al. 2012). The relative proportion of sandlance was substantially higher than observed by Pleizier et al. (2012), although their study contained a high proportion of unidentified fish (44%) that could have included substantial proportions of sandlance. Furthermore, as previously mentioned, several other studies along the eastern coast of the USA have identified significant consumption of

sandlance by ABFT (summarized in Staudinger et al. 2020). For instance, Chase (2002) found that sandlance constituted 63% of ABFT tuna stomach contents by weight along the Stellwagan Bank from 1988 to 1992 and a total of 23% by weight across 5 study areas along the eastern USA. Logan et al. (2011) also observed that sandlance were the most predominant prey item for young ABFT along the Mid-Atlantic Bight, comprising 29% of stomach contents by weight. Our temporally integrated stable-isotope-inferred diet estimates from 2014 to 2018 from the Scotian Shelf suggest that sandlance may be a more important prey, particularly for smaller ABFT (Fig. 4), than has been previously estimated based on stomach content analyses in the region and are more consistent with observations from the eastern coast of the USA. It is important to note that the ABFT used in this study were captured from a range of locations on the Scotian Shelf. Although we analyzed a substantial number of individuals and our method is relatively insensitive to capture location, additional studies are required to better characterize the trophic ecology of the species along the Scotian Shelf.

The isotopic niche of juveniles in the sGSL was substantially lower than for adults and for both juveniles and adults on the Scotian Shelf. The result suggests more constrained foraging behavior both spatially and temporally by juveniles in the sGSL. The Layman metrics of CR and NR (Layman & Post 2007, Jackson et al. 2011) are narrowest for juveniles in the sGSL and suggest constrained trophic and basal resource use, respectively, compared to juveniles and adults along the Scotian Shelf. However, CR and NR suggest the highest diversity of trophic and basal resource use by sGSL adults, despite the higher diversity of prey exploited by Scotian Shelf adults. The difference was most prominent in 2017 and may be linked to combinations of the isotopic niche size of prey, particularly Atlantic mackerel and the spatial extent of foraging. However, differences in isotopic niche size were minimal between adults in both foraging areas in 2016 and 2018. Further research is required to better understand what is driving differences in isotopic niche size; in particular, telemetry studies paired with isotope analyses could provide valuable insight into foraging behavior (Monk et al. 2023). Overall, within each foraging ground, the isotopic niche overlap of adults among years was high, indicating consistency in terms of diet and trophic ecology over the 5 yr study. The isotopic overlap of adults with the isotopic niche of juveniles was relatively low (~50%) in the sGSL but not in the Scotian Shelf and is likely linked to more pronounced and less uncertain ontogenetic shifts in

diet in the sGSL. Additional research into the trophic ecology and general feeding habits in each region would help further understand these differences.

This study provides a valuable application of stable isotopes for improving our understanding of the trophic ecology of ABFT but is contingent on several assumptions. First, the isotopic values of prey are assumed to have remained relatively consistent among years. Given the consistency in ABFT isotope values over years and high isotopic niche overlap of adults among years, this appears to be a reasonable assumption. Additionally, the isotope mixing models can only provide relative proportions of prey consumed for the prey that are included as sources in the model; therefore, we included prey sources that ABFT are known to consume, although we cannot rule out that prey sources that were not included could contribute to the diet of ABFT. Furthermore, we assume isotopic values of ABFT are representative of foraging within the respective regions and not representative of foraging during migration. To ensure conformance with the assumption as far as possible, we used fish captured in September and October and examined isotope values of red muscle tissue, which represents isotope turnover rates on the order of several months (MacAvoy et al. 2001, Varela et al. 2020). As such, our values were likely representative of foraging that occurred from as early as late May through to the time of capture, when ABFT are typically resident in the areas of capture. For example, tagging studies suggest that ABFT reside in the sGSL from approximately June through late November before migrating back to their spawning grounds (Block et al. 2019).

This study, to our knowledge, represents the first comprehensive application of stable isotopes to understand the trophic ecology of ABFT during their summer and fall foraging along the Atlantic Coast of Canada. Our results provide valuable temporally integrated insight into the diet and trophic niche of ABFT, confirming some previous diet observations via stomach content analysis (Pleizier et al. 2012, Turcotte et al. 2023) whilst also providing some novel insights. We identified greater interannual consistency in prey consumption than previously thought (e.g. Varela et al. 2020), suggesting that if ABFT are consuming what is available within the environment, then prey availability has not changed substantially over the 5 yr study or that sufficient prey exist for ABFT to selectively feed on a preferred diet. The results also speak to the potential of integrated diet studies as a tool for helping detect ecosystem shifts that can impact predator population dynamics. Finally, we point to notable ontogenetic shifts in prey consumption that are im-

portant for understanding the effective implementation of ecosystem-based approaches to fisheries management for both forage fish and ABFT. The temporal and spatial insights provided into the trophic ecology of ABFT along the Atlantic Coast of Canada have the potential to be integrated into investigations of predator impacts on forage fish. Notably, we found that the relative contribution of Atlantic mackerel to ABFT diets in the sGSL (median value: 50–70% depending on length) was in the upper range of values assumed in recent estimates of consumption by all predators (assumed uniform distribution between 10 and 75%; Van Beveren et al. 2024). This, combined with more recent estimates of the prevalence of ABFT in the sGSL (Hanke 2021, Turcotte et al. 2021a), suggests that forage fish losses from ABFT predation may be greater than has been estimated. By contrast, previous estimates of Atlantic herring consumption by ABFT in the sGSL assumed that they constituted 50% of the diet (Benoît & Rail 2016). In light of our results, this is likely an overestimate of consumption, at least for the 2014–2018 period.

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