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# Atlantic bluefin tuna (*Thunnus thynnus*) in Greenland – mixed-stock origin, diet, hydrographic conditions and repeated catches in this new fringe area

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20 21 22	Keywords: bluefin tuna, Greenland, Irminger Sea, mackerel, Scomber scombrus, temperature, prey, genetics

# 24 Abstract

Based on collaboration with the Greenlandic fishing fleet, we document the presence of Atlantic 25 bluefin tuna (Thunnus thynnus) in most years from 2012 to 2018 in the waters east of Greenland 26 (northern Irminger Sea). In total, 84 individuals have been registered as bycatch in the commercial 27 fisheries in Greenland waters, which indicates that the first catch of 3 individuals in 2012 was not a 28 single extreme observation, but that East Greenland waters have become a new outer limit of an 29 expanded tuna habitat. Genetic analyses indicate that specimens from this region are mostly of 30 Mediterranean origin with a small proportion originating from the Gulf of Mexico stock. Stomach 31 32 content analysis suggests that the main prey is Atlantic mackerel (Scomber scombrus). The tunas ranged in size from 140 - 270 cm corresponding to an estimated age range of 5-16 years; most were 33 probably mature. The wide size-age range suggests that many year-classes are participating in the 34 migration to this region. Sea temperatures during summer have been above the long-term average in 35 recent years of interest. Summer residence of bluefin tuna in the region could be due to a 36 combination of increasing temperatures and higher overall abundances of both bluefin tuna and a key 37 38 prey species (Atlantic mackerel).

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# 44 Introduction

Distributions and migratory behaviour of species depend on a range of abiotic and biotic 46 47 factors. These include properties of the environment that directly affect bioenergetics and physiology of the species, as well as density-dependent abundance-distribution effects, and the 48 presence of interacting species such as prey, predators and competitors (MacCall, 1990; 49 Heithaus et al., 2008; Olafsdottir et al., 2019). During the past decades, there have been 50 numerous reports of changes in spatial distributions, and phenologies of a variety of species at 51 different trophic levels and functional groups (plankton, benthos, fish; zooplanktivores; 52 53 piscivores) from the tropics to polar seas (IPCC, 2019). The primary factor associated with many of these documented changes is rising temperatures associated with global climate 54 change (IPCC, 2019). 55

Changes have occurred in waters east of Greenland in the Irminger Sea-Denmark Strait region. 57 Three Atlantic bluefin tuna (Thunnus thynnus), were reported in the area in 2012 (MacKenzie 58 et al., 2014), which is several hundreds of km beyond their nearest previously documented 59 northern summer feeding range (Iceland Basin: Fromentin et al. 2013; Olafsdottir et al. 2016; 60 northern Newfoundland: Mather et al. 1995). This species, caught as bycatch in the mackerel 61 fishery in the Irminger Sea, is a large highly migratory top predator which migrates northwards 62 in summer for feeding after spawning in more temperate regions (Mediterranean Sea, Gulf of 63 Mexico and the recently discovered Slope Sea (Richardson et al., 2016)). In the northern 64 regions (e.g., North Sea, Norwegian Sea and Iceland Basin), it preys on pelagic and 65 mesopelagic prey, including herring, mackerel, squids and barracudinas (Tiews, 1978; 66 Olafsdottir et al., 2016). The appearance of Atlantic bluefin tuna in Greenland waters in 2012 67 coincided with unusually warm temperatures over a large area of the east Greenland region 68 (MacKenzie et al., 2014). These warmer temperatures may have been due to changes in ocean 69 circulation and atmospheric warming in the region. The region is characterized by influx of 70 relatively warm water via the Irminger Current and north Atlantic Drift from the south and 71 72 delimited by the southward flow of cold Arctic water associated with the East Greenland Current (Astthorsson et al., 2012; Olafsdottir et al., 2019). Alternatively, or perhaps 73 74 synergistically, the changes may have been associated with general warming of the oceans. 75

Warm temperatures in the same region have led to a major expansion of habitat for another 76 pelagic migratory species, Atlantic mackerel (Scomber scombrus) (Jansen et al., 2016). This 77 species has spread from the European northwest continental shelf-slope waters north and 78 westwards towards the Faroe Islands, Iceland and East Greenland during the 2000s-2010s 79 (Astthorsson et al., 2012; Jansen et al., 2016; Nøttestad et al., 2016). This range expansion is 80 believed to be due to a complex interaction between temperatures, mackerel population 81 dynamics, and the availability of zooplankton (Trenkel et al., 2014; Jansen et al., 2016; 82 Olafsdottir et al., 2019)). One potential prey species (mackerel) has therefore become more 83 abundant in waters east of Greenland. Both the Atlantic bluefin tuna and mackerel have been 84 absent or very rare in this region until recently. In the 1990s, mackerel has sporadically been 85 caught in low numbers around Iceland (Astthorsson et al., 2012) whereas few Atlantic bluefin 86 tuna has been caught in a Japanese long line fishery near the Greenlandic EEZ (ICCAT, 2018). 87 The overall biomasses of both species have been rising during the past 10-15 years according 88 to stock assessments (ICCAT 2018; ICES 2019). As Atlantic bluefin tuna is relatively new to 89 the region, its presence is demonstrating new migration behaviour and habitat use which 90 deserve documentation and description to help understand factors affecting its distribution and 91 ecological role, stock mixing, as well as the general dynamics of the marine ecosystem in this 92 region. Given that there are two assessed stocks having different biomasses, demographics and 93 fishing regulations, it is important for fisheries managers to know and understand the extent of 94 stock distributions and potential mixing throughout the species range (Rooker et al., 2007; 95 ICCAT, 2017a). The population origin of the tuna which appears in East Greenland is 96 presently unknown. 97

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In this study, we document the presence of Atlantic bluefin tuna in waters off East Greenland 99 (Irminger Sea) in the years 2012 - 2018. We present biological sampling of size distributions, 100 stomach contents and genetic analyses in the area. Stomach samples provide insight to the 101 trophic relationships in the northern foraging areas for which no data are available since 1999 102 (Olafsdottir et al., 2016). The genetic analysis provide information about Mediterranean or 103 Western Atlantic origin. Our study therefore contributes with new ecological knowledge of 104 Atlantic bluefin tuna in a new region and extends current understanding of migration 105 behaviour, habitat use, trophic role and stock mixing. 106

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# 108 Materials and methods

# 110 Tuna observations and stomach content

111 Vessels longer than 9.4 meters fishing in Greenlandic waters are required by law to report catches (including bycatches) in a logbook and send it to the Greenland Fisheries License Control Authority 112 (GFLK) (GFLK, 2014). Discarding is illegal. The logbooks contain the dates and positions of the catches. 113 114 These data were obtained from the GFLK database "Luli" on the 6<sup>th</sup> of August 2019. In 2019 and 2020, the pelagic fishery for mackerel ended exceptionally early because of a reduction in the mackerel 115 116 migration into Greenlandic EEZ. To encourage reporting and sampling of the bycatches, we have met with vessel owners and skippers before and after the mackerel fishing season (main pelagic fishery in 117 Greenland) since 2014. During these meetings, we urged the skippers to measure the length and 118 119 weight of each tuna, to sample stomachs for diet analysis, and muscle tissue for genetic analysis. Lengths were measured as total lengths (TL) from tip of snout to end of tail, and often rounded up or 120 121 down to the nearest 10 cm. The weight was sometimes measured and sometimes estimated, but we 122 have no valid information on which weights were measured and which were estimated, except for three individuals captured in 2012 whose weights were estimated to be ca. 100 kg (MacKenzie et al. 123 124 2014). Because of these uncertainties, weight data, except for the 2012 captures for which length information is missing, were not used in our analyses. For the individual tunas, whose length was 125 126 measured, we estimated weight from the available length measurements. However, available length -127 weight relationships for bluefin tuna in adjacent regions, including the one used by the ICCAT bluefin 128 tuna assessment group (ICCAT, 2017a), are based on straight fork length (SFL). Similarly, the currently used age-length relationship by the ICCAT bluefin tuna assessment working group is also based on 129 fork length. In order to achieve comparable length and weight measurements with other regions and 130 attain information on age we converted the data. Total lengths were converted to straight fork length 131 using the relationship: 132

133 SFL = 6.47 + 0.9554\*TL

[Eq.1]

based on 1699 individual tunas spanning a length range of ca. 120-260 cm caught in Spanish trap
fisheries during 1956-61 (Rodríguez-Roda, 1964).

Given the estimated SFL, we calculated whole weights (W) using a previously-derived straight fork
length – whole weight relationship for bluefin tuna in the northeast Atlantic and Mediterranean Sea
(Rodriguez-Marin *et al.*, 2015):

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W (kg) = 0.0000350801\*SFL<sup>2.878501</sup> [Eq.2]

(SFL in cm). This relationship is based on sampling during all months of the year (Rodriguez-Marin *et al.*, 2015).

Ages were estimated by re-arranging the age-length relationship (Cort, 1991) used in the 2017 stock assessment (ICCAT, 2017a):

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$$L = 319^{*}(1 - e^{(-0.93(t + 0.97))})$$
 [Eq.3]

These calculations allowed us to estimate weights and ages of the bluefin tuna captured in east Greenland waters. Similarly, for the three tunas whose weights had been estimated in 2012, we derived straight fork lengths and ages. The total number of tunas for which size and estimated age information was available was 49.

Bluefin tuna spawning stock biomass (SSB) was estimated by ICCAT (ICCAT, 2017a). Bluefin tuna abundance index in East Greenland was, for discussion purposes, proxied by the catch in numbers per year in relation to the mackerel catch per year. The mackerel catch was chosen as the measure of effort instead of e.g. trawl-hours because the pelagic mackerel fishing fleet developed over the years as experience was gained with pelagic trawling in Greenland, and with variable participation of experienced foreign skippers.

Whole stomachs from 18 individual tunas in 2014 (10), 2015 (1) and 2017 (7) (table 1) were frozen 156 onboard and shipped to the Greenland Institute of Natural Resources (GINR) for analysis. The 157 sampling was done by the fishermen and, despite guidance on sampling procedures by scientists 158 before the fishing season, can best be described as opportunistic and random in the sense that it was 159 done where practically possible by the most compliant fishermen. In the laboratory, stomachs were 160 thawed until they could be opened, and the prey items could be sorted into taxonomical groups, 161 162 counted and weighed. Digestion stage were evaluated according to two criteria: 1. Light or no visible digestion, 2. Digesting i.e. skin from prey fish is absent and, in some cases, only a backbone was 163 present. Backbones with or without remains of tissue were, in all cases, assigned to species because 164 165 prey with similar sizes and appearances in less digested states were present in various degrees of 166 digestion. It was the impression of the authors (TJ and SP) that sufficient comparable material were present to assign the remains to species. However, genetic identifications of the most digested prey 167 168 were not performed, so these assignments could not be verified.

#### 169 Genetic analysis

DNA was extracted from muscle samples of 34 bluefin tuna caught in 2014 (21), 2015 (7) and 2017 (6) 170 (table 1) using the E.Z.N.A.TM kit (Omega Biotek, Norcross, Georgia, USA). Sampling was opportunistic 171 172 and random as described for the stomachs. SNP genotyping was conducted using the BiomarkTM HD platform (Fluidigm) and 96.96 Dynamic Array IFCs. We used a newly developed, genetic stock 173 identification panel (Rodríguez-Ezpeleta et al. 2019) consisting of 96 highly discriminatory Single 174 Nucleotide Polymorphisms (SNPs) for assigning fish back to the genetic populations from the two 175 well-known spawning grounds - Gulf of Mexico (GOM) and Mediterranean Sea (MED). Individuals 176 177 sampled in Greenlandic waters were assigned back to either spawning area based on genetic baseline samples (from Rodríguez-Ezpeleta et al. 2019) consisting of larvae, young of the year and spawning 178 179 adults from GOM and MED. Assignment was conducted with the GeneClass2 software (Piry et al. 180 2004) using a minimum assignment score criterion of 80% for positively inferring population of origin. Individuals with lower assignment scores were classified as "unassigned". 181

#### 182 *Hydrographic data*

A dataset of historic Sea Surface Temperatures (SST) from 1870 - 2019 was created by the Hadley 183 Centre using the interpolation procedure described by Rayner et al. 2003. The so-called HadISST1 184 185 temperatures are based on in situ measurements and contain global monthly estimates of SST at 1° longitude x 1° latitude resolution (Rayner et al., 2003). We obtained this dataset from the Hadley 186 Centre (www.metoffice.gov.uk/hadobs/hadisst) on June 17, 2019. We used August SST as a general 187 indicator of thermal conditions in the region, as this is the month when temperatures are warmest, 188 the mackerel fishing is concentrated and bluefin tuna have been caught in the region. We averaged 189 190 the August SST in each grid cell for the years 2012-2019 and produced a map using these averages to 191 visualize the spatial variability of SST in the area and in relation to the positions where bluefin tunas 192 were caught during this time period.

We derived two indicators of long-term variability of thermal conditions to put the recent
temperatures into historical context. One indicator is the time series of mean August SST by year for
an area within the Irminger Current. This polygon (63°N 35°W, 63°N 25°W, 65.5°N 25°W, 64.8°N
30°W) was selected so that it did not include the area near the Arctic front (the front between the
warm Irminger Current and the cold East Greenland Current). This was done to ensure that the time
series reflects the SST in the Irminger Current, and not the relative position of the Arctic front.

A second indicator is an area estimate of thermal habitat covering a wider geographic region, thereby 199 potentially including sea areas through which bluefin tuna may have migrated to reach the locations 200 where they were captured. This area is bounded by 58 - 70 °N and 20 - 45 °W, and was defined as the 201 202 sea surface areas whose temperature exceeded 11 and 8 °C. We use two temperatures because the lower temperature preference of bluefin tuna has not yet been determined with certainty. For 203 example bluefin tuna commonly experience colder temperatures (e.g., 2-5 °C) for shorter periods (e. 204 g. during dives), but have access to warmer water for recovery (Block et al. 2001; Teo et al. 2007). 205 Temperatures in the 8-11 °C range are however close to those at the surface in northern feeding areas 206 (e.g., Norwegian Sea, southern Gulf of St. Lawrence; Canada) when bluefin tuna begins emigrating in 207 208 the autumn to warmer regions (vander Laan et al. 2014; MacKenzie and Myers 2007), and are therefore probably similar to those which the species can tolerate for long periods of time (weeks-209 months) without severe physiological stress. This range is also similar to the lower temperature 210 tolerance derived from probability of occurrence maps (Fromentin et al., 2013) and other thermal 211 212 habitat information (Boyce et al., 2008). Running means of the time series were calculated and 213 spanned 5 years, except for the second to first and second to last that were calculated over 3 years.

Welch Two Sample t-test was used to test if the mean temperature after 1996 differed from the mean
of from 1870 - 1996.

#### 216 Mackerel data

217 Mackerel has been surveyed annually in East Greenland waters since 2013 as part of the International Ecosystem Summer Survey of the Nordic Seas (IESSNS) (Nøttestad et al., 2013, 2019). The survey uses 218 stratified random sampling with a "Mulitpelt 832" pelagic trawl. At each station, a surface trawl was 219 towed for approximately 30 min at a speed between 4 and 5 knots. Vertical opening of the trawl was 220 typically 30-40 m. The trawl catch was identified to species and weighted. Specimens representing the 221 whole catch fraction where length and weight measured, and otoliths were extracted for age 222 223 determination. In total, 182 surface trawl stations have been taken in Greenland EEZ from 2014-2020. Results from the survey (swept area estimate, area, and total estimate in tonnes) are reported 224 225 annually by Exclusive Economic Zone (EEZ) in annexes or working documents in the ICES WGIPS 226 reports (see ICES, 2019 for the latest report). Since 2014 this has included the Greenland EEZ.

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# 228 **Results**

84 Atlantic bluefin tunas were registered as bycatch in the mackerel trawl fishery in East Greenland in 229 five different years from 2012 to 2018 (Table 1). All were caught in the Irminger Sea in East Greenland 230 during late summer, between August 11<sup>th</sup> and September 16<sup>th</sup> (Figure 1). No tuna were caught prior to 231 2012, or in the last two years (2019 and 2020). The sizes (estimated straight fork lengths) of the tunas 232 ranged from 1.4 m to 2.6 m (Figure 2a). Only 7 of the 49 length estimated specimens were shorter 233 than 2 m; the rest were between 2.0 and 2.7 m. This corresponded to ages from ca. 5-18 years (mean 234 = 12; SE = 0.4). In weight, the tunas were estimated to range from 53 to 329 kg, with 7 specimens 235 below 130 kg, and the remaining 42 between 142 and 329 kg (Figure 2b). 236

## 238 Stomach content

Stomach content analysis of 18 tunas indicated that Atlantic mackerel was the primary prey as 8 of the tuna stomachs contained solely Atlantic mackerel. One tuna stomach contained a mixture of Atlantic mackerel and myctophids (family *Myctophidae*), and two stomachs solely myctophids. 8 of the stomachs were empty. In summary, 98 % of the prey weight were mackerel, while 2 % were myctophids. 67 of the 72 mackerel found in the stomachs were only slightly digested. These mackerel had an average weight of 0.44 kg, corresponding to large mature mackerel of 6 - 9 years and 36 – 38 cm pinched tail length (Hansen *et al.*, 2018; ICES, 2018). All myctophids were partly digested.

#### 246 *Genetic analysis*

DNA was successfully extracted, amplified and genotyped from muscle tissue for 34 of 36 samples. Of
the 34 individuals, 25 were genotyped at all 96, 8 at 95 and one at 94 SNP markers. 30 individuals
were assigned back to population of origin with an assignment score of above 80%, while four
specimens were unassigned. Three individuals were assigned to GOM, two from 2014 (both with
100% probability) and one from 2017 (probability score of 83%), while the remaining 27 were
assigned to MED (probability scores ranging between 83% and 99%).

#### 253 Hydrographic conditions

The tunas were caught in the northwestern extreme of the Irminger Current (Figure 1) close to the Arctic front. The in situ temperature at the exact times and places were not known. SST in the region where bluefin tunas were caught were ca. 8-10 °C (Figure 1). The SST in the warmest month (August) increased substantially in the late 1990s (Figure 3a). SST was significantly higher in 1997-2019 (t-test,

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p<0.001) compared to 1870-1996. However, two of the last four years (2016 and 2018) were colder</li>
than the long term average.
Estimates of the size of the area of thermally suitable habitat in east Greenland (defined as SST> 8 or

261 11 °C) followed a similar historic development as the SST (Figure 3b). For example, the area was only

262 below average in one year since 2003 (threshold SST = 8 °C). The sizes of the areas with

temperatures > 8 and > 11 °C were significantly correlated ( $r^2 = 0.68$ ; p < 0.001; Pearson's productmoment correlation).

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# 266 **Discussion**

We have documented that Atlantic bluefin tuna have become a near-annual seasonal guest in east 267 268 Greenlandic waters since 2012. This observation indicates that the single catch of 3 specimens in 2012 269 was not a unique phenomenon but likely part of a wider and multi-annual population- or species-level change in migration behaviour and habitat use. The reasons for such a change could include both 270 abundance changes of the tuna and their prey as well as oceanographic condition. This is discussed 271 272 further below. The recent pattern of annual seasonal occurrence is evident despite the unintentional 273 nature of the data source and collection method: that is, the presence is documented only from monitored bycatches in commercial fisheries and does not originate from targeted bluefin tuna 274 surveys or fisheries. On this basis, we cannot estimate the total abundance in the area, extent of the 275 276 season (the season of the mackerel fishery starts in mid June and ends in mid September (Jansen et al., 2016)), or the total spatial distribution of the Atlantic bluefin tunas in this region because the 277 fishing vessels involved were targeting other species in a limited time and area. The capture of bluefin 278 tunas in mackerel fishery hauls is consistent with the known diets of bluefin tunas in northern feeding 279 areas: mackerel are an important prey species in many of these areas (Tiews, 1978; Chase, 2002; 280 281 Pleizier et al., 2012), and it is likely that Atlantic bluefin tuna in east Greenland waters were captured while foraging directly on mackerel schools (as also supported by our limited stomach sampling data), 282 or were within close proximity to such schools. The presence of mackerel as far south as Cape 283 Farewell (Jansen et al., 2016) suggests that tunas could have been present further south than where 284 we have documented them from the mackerel fishery. 285

Stomach content and trophic interactions

Our stomach analysis shows that the sampled bluefin tuna were feeding on mackerel and rarely on other species (mesopelagic fishes: 2 % of the diets by weight). The analysed stomachs were limited to a very small number and may not be representative of the whole population in the region. Some mackerel found in the stomachs could have been from net-feeding during capture, which is a general problem with analysis of stomach content of predatory fish. However, we suspect that this phenomenon was limited or not present because mackerel were observed in all stages of digestion.

The extreme rarity of prey species other than mackerel in the diets represents a major dietary and 296 trophic difference from bluefin tunas (N = 421) captured in the Iceland Basin in 1998-1999. The latter 297 298 tunas consumed a diet dominated by European squid and a variety of barracudina species along with 299 other mesopelagic fish and squid species. Mackerel on the other hand were absent (Olafsdottir et al., 2016), as could perhaps be expected because the mackerel was still rare in the region at that time 300 (Astthorsson et al., 2012; Olafsdottir et al., 2019). An additional difference in the foraging behaviour 301 302 between these two regions is the proportion of individuals with and without prey in the stomachs. In 303 our samples from the northern Irminger Sea, 55 % contained prey, whereas 86 % of the tunas captured in the Iceland Basin had prey in their stomachs (Olafsdottir et al., 2016). In general, the 304 share of bluefin tuna individuals having prey in stomachs ranges from 39-91 % in different feeding 305 306 studies (summarized in (Olafsdottir et al., 2016)), so the feeding incidence of the bluefin tuna 307 investigated in this study, although based on a lower sample size compared to that for the Iceland 308 Basin, is within the range observed previously in other areas.

We have not found strong evidence of deep dives for mesopelagic foraging in east Greenlandic 310 311 waters. Mesopelagic foraging may have been limited because an alternative abundant, lipid-rich prey such as mackerel was available. Mackerel are distributed at shallower depths (down to 30-40 m; 312 (Olafsdottir et al., 2019)) and in warmer waters than mesopelagic species (several 100s m, although 313 they do rise to the top 50 m during the night; (Jansen et al., 2019)) in this region and may be less 314 costly energetically to pursue, capture and consume due to shallower diving required. The energetic 315 benefits and costs of feeding on different prey types needs further investigation. Furthermore, 316 additional stomach samples from bluefin tuna are needed to derive more comprehensive and 317 representative dietary information. New investigations (e.g. tagging studies to resolve vertical 318 migration behaviour; stomach sampling including isotope and DNA-based approaches; process-based 319 foraging models) will help clarify the trophic role and feeding behaviour of tunas in this region. 320 321

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There is currently much scientific and public interest in the level of ingestion of plastic by marine consumers (ref.). However, we detected no large (i. e. > 1 cm<sup>2</sup>) pieces of plastic in these stomachs.

#### 325 Size and age distributions

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The range of sizes and estimated ages of the Atlantic bluefin tunas caught near Greenland suggests 326 that they were most likely mature, given the ICCAT stock assessment and the likely geographic origin 327 328 of most of these specimens (i. e. east Atlantic-Mediterranean). The ages were estimated to be ca. 5-329 18 years (mean = 12; SE = 0.4), indicating individuals born in 1998-2013. Resolving this into specific 330 year classes is uncertain because no direct aging was done. The results suggested that the dominant yearclasses were 2001 and 2002 (10 individuals each), followed by the 2004 (N = 6) and 2003 and 331 1999 yearclasses (5 individuals each). The dominance of yearclasses in the early 2000s may reflect the 332 overall strength of several of these yearclasses as seen in other bluefn tuna catch time series, and in 333 stock assessments for both the eastern and western stocks (ICCAT 2017). In general, however, the 334 range of sizes and ages indicates that many cohorts have discovered the foraging area east of 335 Greenland. This discovery or learning process by which new migration behaviours develop is poorly 336 337 documented and probably complicated, possibly including social interactions within and among cohorts (De Luca et al., 2014; Petitgas et al., 2010). 338

The size range of bluefin tunas captured near East Greenland is broader than that seen in some other 340 northern feeding areas. For example, the size range in the Skagerrak-Kattegat juncture (Denmark-341 342 Sweden) in 2017-2019 during tagging operations was 185-266 cm curved fork length (N = 159) and 343 dominated by yearclasses from ca. 2005 (Birnie-Gauvin et al., 2018, 2019; MacKenzie et al., 2018). The tuna sample from near Greenland includes therefore smaller individuals than caught, tagged and 344 345 released so far in the Skagerrak-Kattegat. However, smaller individuals similar in size to some of those captured in East Greenland have also been common in the past in waters near Denmark, Germany, 346 347 Norway and Sweden (Hamre, 1958; Hamre et al., 1966; Mather et al., 1995; MacKenzie and Myers, 348 2007). New studies of the size distribution of bluefin tunas in the newly occupied summer foraging 349 areas such as East Greenland, Norwegian Sea and Skagerrak-Kattegat are needed to understand 350 potential size-based differences in spatial habitat use and migration behaviour.

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#### 352 Mixed stock composition

Our genetic results revealed that individuals from both the eastern and western Atlantic populations
 are present in the region, although most individuals were assigned to the eastern population. This

could indicate that the foraging area east of Greenland constitutes a mixed-stock feeding area, similar 355 to most fished areas in the North Atlantic and with the estimated proportions comparable to other 356 recent genetically based estimates of mixing in the Central and Eastern North Atlantic (Puncher et al., 357 358 2018; Rodríguez-Ezpeleta et al., 2019; Rooker et al., 2019). Individuals from the western population 359 were found in both 2014 and 2017, with the estimated total proportion among samples of approximately 10 %. This could be explained, to some extent, by the documented mis-assignment rate 360 between populations using the specific SNP panel (see Rodríguez-Ezpeleta et al., 2019). However, mis-361 assignment rates between populations is not symmetrical, i.e. only 2 % of individuals of known 362 eastern origin were assigned to the western population whereas 10 % from the western population 363 364 were assigned to east (Rodríguez-Ezpeleta et al., 2019). Thus, a hypothesis of purely eastern Atlantic origin of bluefin tuna east of Greenland is highly unlikely, also considering that two of the three 365 individuals were assigned with 100 % probability to the western population. Still, given the low, but 366 potential, misassignment and the limited number of samples, it is not possible to document how 367 368 representative the western proportion is and how much it varies among years, thus further baseline 369 improvements and sampling is needed to draw firm conclusions. Additionally, alternative explanations 370 for the origin of the misassigned and unassigned individuals have been recently suggested (Brophy et al. 2020). 371

373 Tagging studies in the 1950s-1960s in eastern USA waters and more recent satellite tracking data 374 (Block et al., 2001, 2005; Walli et al., 2009; Galuardi et al., 2010) show that bluefin tunas migrate between the North American east coast and the Northeast Atlantic. Unfortunately, the genetic origin 375 376 of most of these tagged trans-Atlantic migrating individuals is not known, which could be due to the presence of a third spawning component or other causes (Brophy et al. 2020). However, based on the 377 genetic evidence of mixed stocks (Puncher et al., 2018; Rodríguez-Ezpeleta et al., 2019), it appears 378 that extensive mixing of the two populations is common across the species distribution and 379 380 particularly in central Atlantic areas, suggesting that extensive feeding and spawning migrations are common for both populations. Given that bluefin tunas historically (Mather et al., 1995) and recently 381 (since 2017) have been present in waters of northern Newfoundland and even Labrador 382 383 (CentralVoice, 2017; CBC, 2018; DFO, 2019), and temperatures in the Irminger Sea region have been 384 relatively warm since the 2010s (MacKenzie et al., 2014; Jansen et al., 2016), it is conceivable that some western tunas could have migrated further north and east to the Denmark Strait-Irminger Sea 385 with relatively low thermal stress. These western tunas along with eastern individuals emigrating from 386

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the Mediterranean Sea and Bay of Biscay presumably all migrated to the region potentially by
 following and/or searching for prey such as mackerel (MacKenzie *et al.*, 2014).

#### 390 Hydrographic conditions

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Surface temperatures during late summer - early autumn in the Irminger Current in Southeast 391 392 Greenland have increased to an unprecedented level in the last decades (Figure a; (MacKenzie et al., 2014; Jansen et al., 2016)). Temperatures increased most in the mid/late 1990s. Temperatures since 393 394 the late 1990s have become less thermally stressful for bluefin tuna than they were previously. 395 Similarly the area of suitable thermal habitat in summer assuming two different criteria as lower temperature suitability (MacKenzie et al., 2014) has increased since the late 1990s. For example, since 396 397 1870, the 8 years with largest area of SST > 8 °C have occurred after 1997. These developments have therefore opened potential (at least in terms of thermal suitability) new foraging habitat for bluefin 398 399 tuna in east Greenland waters. New tagging investigations, which include temperature data storage, 400 in northern areas would help identify the lower thermal tolerance limit of bluefin tunas and therefore facilitate quantifying the sizes and locations of thermally suitable habitats for this species, and how 401 402 future climate change might affect distributions. Erauskin-Extramiana et al. (2019), based on SST and other variables, predict a northern expansion of Atlantic bluefin tuna habitat under future climate 403 change, but additional knowledge on environmental preferences would allow to improve projections 404 405 of future distributions.

The first Atlantic bluefin tuna captured in East Greenland were caught in waters close to the front 407 between the southward flowing East Greenland Current and the Irminger Current (MacKenzie et al., 408 2014). The catches in subsequent years were also located in or close to this same hydrographic 409 feature. This represents a thermal boundary to the cold tolerance of the mackerel distribution (since 410 the fishery was targeting mackerel) and possibly an area of mackerel aggregation; mackerel are 411 usually associated with temperatures > 8-9 °C (Olafsdottir et al., 2019). If so, the frontal zone, where 412 temperature changes substantially over a short distance, and waters to its immediate south, could be 413 414 a stimulus for bluefin tuna aggregation and foraging.

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# Local abundance and factors affecting presence in the Greenlandic part of the Irminger Sea

The time series of bluefin tuna catches in East Greenland is too short for rigorous quantitative analysis
of the factors affecting bluefin tuna presence in this region. However, in general, there are at least

three variables which have changed in the last 5-10 years which would have increased the likelihood 420 that bluefin tuna would become seasonal guests in the waters of East Greenland (figure 3). One of 421 these is the increase in temperatures to levels which are more physiologically suitable for this species 422 423 than they were in the past (see previous section and figure 4a). The causes of such a rise in 424 temperature are unclear but could be at least partly associated with the overall global warming trend of recent decades. Observation that temperatures have risen intermittently and plateaued with large 425 inter-annual fluctuations indicates that other factors may be involved. These could include changes in 426 the relative strengths of warm and cold currents entering the region, and larger – scale oceanographic 427 phenomena, such as the intensity and strength of the North Atlantic Subpolar Gyre which affects 428 429 water masses and other biota in the region and in areas through which bluefin tuna must pass when migrating to East Greenland (Hátún et al., 2009, 2017; Post et al. 2020). Our study region is within the 430 area represented in the Atlantic Multi-decadal Oscillation (AMO) of north Atlantic temperature, which 431 has recently been proposed to reflect thermal habitat and affect distributions of bluefin tuna in the 432 433 Atlantic Ocean (Faillettaz et al., 2019).

Furthermore, changes in prey availability, in this case particularly mackerel distribution and migration 435 may also have had an effect on the distribution of bluefin tuna (figure 3b). This species has spread 436 437 westward into Greenland waters simultaneously with the tuna and could have provided a foraging 438 trail and stimulus for bluefin tuna to enter east Greenland waters. The range expansion of mackerel is 439 believed to be due to a complex interaction between rising temperatures, mackerel population dynamics, and the abundances of zooplankton (Trenkel et al., 2014; Jansen, 2016; Jansen et al., 2016; 440 Olafsdottir et al., 2019). This may therefore be regarded as a cascading spatial bottom-up effect from 441 442 physics and plankton, via mackerel to tuna.

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Third, the overall abundance of Atlantic bluefin tuna has increased substantially in the eastern Atlantic-Mediterranean Sea (figure 4c) since a recovery plan was implemented in 2007-2008 (ICCAT, 2017a). It is possible that population increase has stimulated bluefin tuna to forage more widely to reduce density – dependent competition in more southerly areas. Larger sized fish also tend to migrate further (Nøttestad et al. 1999). This factors, combined with the increase in mackerel biomass and an increasingly warmer habitat in a northern region would promote migration to new habitats.

This combination of factors may have contributed to the presence of bluefin tuna in the region. In this
 context, the most recent years, 2019 and 2020, have somewhat unusual sets of circumstances for the

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region: relatively warm temperatures (Figure 3a), relatively abundant bluefin tuna stock in the 453 454 northeast Atlantic-Mediterranean (Figure 3b), but low biomass of a key prey (mackerel) (Figure 3b). The limited availability of mackerel as a prey may or may not have affected the tuna migration. 455 456 Unfortunately, this effect is confounded with the likelihood of detecting tunas. The mackerel fishery closed early in 2019 and 2020 due to low mackerel availability – earlier than when the bluefin tuna 457 have usually been caught in previous years. Therefore, it is possible that tuna might have migrated to 458 the region and foraged on other (e.g. mesopelagic) species, as bluefin tunas used to do in the 459 neighbouring Iceland Basin before the mackerel expansion to that region (Olafsdottir et al., 2016). 460 461

462 The expansion of Atlantic bluefin tuna distribution into Greenland waters is not a geographically isolated event. Tunas has increased in abundance in other northern summer foraging areas, including 463 those formerly occupied but vacant for ca. 50 years. These include the Norwegian Sea (Nøttestad et 464 al. 2020), North Sea and the Skagerrak-Kattegat, where the species has been reported since the early-465 466 mid-2010s, MacKenzie et al. 2018) As a result of these changes in distribution and abundance, Iceland 467 and Norway now have received commercial fishing quotas (ICCAT, 2017b). In fact, as bluefin tuna continues to move north (Erauskin-Extramiana et al., 2019), the management arena might need to 468 469 adapt and countries, which now host tunas, should consider ICCAT membership.

470 471

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the project GENPES.

## 480 Figures

481 482

Figure 1. Locations of Atlantic bluefin tuna catches in Greenland waters (known positions indicated by
large blue points), and catches of mackerel (small dark grey points). Contours indicate the mean sea
surface temperature in August in the years with bycatches of Bluefin tuna (2012, 2014, 2015, 2017,
2018). The map was created in R using the package 'lattice' v.0.20-41 (Deepayan, 2008) and 'maps'
v.3.3.0 (Brownrigg et al., 2018).

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489 Figure 2. Size distribution of Atlantic bluefin tunas caught in Greenland waters in a) length

490 (measured), b) weight (some measured, some estimated), and c) estimated ages.

Figure 3. Time series of a) mean SST in August in the polygon indicated in **Error! Reference source not** found., and b) area of suitable habitat within 58 - 70 °N and 20 – 45 °W defined as SST > 8 °C (blue) and SST > 11 °C (red). Blue and red lines indicates running means (see material and methods) and the black lines indicates the mean over all years.

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Figure 4. Time series of normalized values of bluefin tuna CPUE (= numbers caught \* mackerel catch<sup>-1</sup>)
together with a) bluefin tuna SSB from ICCAT stock assessment (ICCAT, 2017a), b) mean SST in august
and c) mackerel abundance in East Greenlandic (from pelagic trawl survey IESSNS with assumed 0
before the first mackerel observation in 2011).

# 502 Tables

Year	No. caught	Date of first tuna capture	Date of last tuna capture	No of stomachs	No. of genetic samples	Mackerel catch (t)	Mackerel biomass index in East Greenland
2012	3	22 Aug.	22 Aug.	0	0	5 458	*
2013	0	-	-	0	0	54 150	*
2014	55	24 Aug.	16 Sept.	10	21	78 580	1 164
2015	10	13 Aug.	20 Aug.	1	7	30 429	321
2016	0	-	-	0	0	36 190	1 026
2017	12	15 Aug.	19 Aug.	7	6	36 753	530
2018	4	11 Aug.	Early Sept.	0	0	53 132	293

2019	0	-	_	0	0	6 624	15
2020	0	-	-	0	0	0.014	0
Total	84	-	-	18	34	-	-

# 503

Table 1. Observations and samples of Atlantic bluefin tuna in East Greenland (ICES area 14b) in 2012-

2020. \*Pelagic trawl survey of mackerel biomass started in 2014.

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