Global Change Biology
August 2014, Volume 20 (8), Pages 2484-2491
http://dx.doi.org/10.1111/gcb.12597

A cascade of warming impacts brings bluefin tuna to Greenland waters

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Abstract:

Rising ocean temperatures are causing marine fish species to shift spatial distributions and ranges, and are altering predator-prey dynamics in food webs. Most documented cases of species shifts so far involve relatively small species at lower trophic levels, and consider individual species in ecological isolation from others. Here, we show that a large highly migratory top predator fish species has entered a high latitude subpolar area beyond its usual range. Bluefin tuna, *Thunnus thynnus* Linnaeus 1758, were captured in waters east of Greenland (65°N) in August 2012 during exploratory fishing for Atlantic mackerel, *Scomber scombrus* Linnaeus 1758. The bluefin tuna were captured in a single net-haul in 9–11 °C water together with 6 tonnes of mackerel, which is a preferred prey species and itself a new immigrant to the area. Regional temperatures in August 2012 were historically high and contributed to a warming trend since 1985, when temperatures began to rise. The presence of bluefin tuna in this region is likely due to a combination of warm temperatures that are physiologically more tolerable and immigration of an important prey species to the region. We conclude that a cascade of climate change impacts is restructuring the food web in east Greenland waters.

Keywords: bluefin tuna ; Climate ; food web ; Greenland ; Mackerel ; predator-prey ; temperature ; trophic cascade

1. Introduction

Temperatures in the Atlantic Ocean and in many regional areas of the north Atlantic have been rising in recent decades (Levitus *et al*., 2012; Valdimarsson *et al*., 2012; ICES, 2013) and in some areas temperatures in the early 2000s exceeded those observed during the previous 120 years (MacKenzie & Schiedek 2007). These changes are having major impacts on the spatial distributions and migrations of marine biota, including fish (Astthorsson et al. 2012; Cheung et al. 2013; Hazen et al. 2013; Hollowed et al. 2013; ICES 2013). Species richness of local fish communities has been increasing as warm – adapted species enter regions formerly dominated by colder-tolerant species, some migratory species have been moving to more northerly waters (e. g., mackerel to waters south of Iceland (Astthorsson et al. 2012; ICES 2013)), and other, formerly local temperature-restricted populations, are expanding (e. g., anchovy, *Engraulus encrasicolus* Linnaeus 1758, in the North Sea (Petitgas et al. 2012)). Collectively, these changes, if they continue, will lead to transient mixing between, and geographic shifts, in entire biogeographical provinces (Longhurst 2007; Reygondeau et al. 2013) and will alter local food webs in the coming years and decades.

Bluefin tuna is a highly-migratory commercially important top predator in the Atlantic Ocean and seasonally migrates from spawning areas located in sub-temperate areas to temperate-boreal areas for foraging (Mather et al. 1995). Appearance in northern areas (e. g., Norwegian Sea, North Sea, Scotian Shelf, north coast of Newfoundland) is partly temperature-dependent, and the probability of occurrence of the species in the Atlantic declines sharply as sea surface temperature (SST) falls below 7-10^o C (Fromentin et al. 2013). For example, bluefin tuna historically migrated into the Norwegian Sea when surface temperatures exceeded ca. 11-13^o C and remained there as temperatures rose during summer and until temperatures declined again in autumn (Mather et al. 1995; MacKenzie & Myers 2007). Similar seasonal migratory behaviour is evident in the northwest Atlantic (Mather et al. 1995). During its seasonal residency in northern waters, bluefin tuna forages on prey species such as mackerel and herring *Clupea harengus* Linnaeus 1758 (Tiews 1978; Cury et al. 1998; Overholtz 2005).

The northern range limit of the species is therefore determined partly by the timing and magnitude of seasonal warming, and by the potential energetic benefit obtained from migrating to and feeding in such areas (Lawson et al. 2010; Chapman et al. 2011), which in turn is related to temperatures and food conditions (quantity and quality of prey). Changes in temperature due either to long-term changes in heat input associated with global and regional warming (Levitus et al. 2012), or due to changes in circulation patterns (e. g., strength and location of the North Atlantic sub-polar gyre; Hatun et al. 2009), can therefore potentially have major impacts on the large-scale spatial distribution and migration behaviour of bluefin tuna. Such changes could, for example, provide access for bluefin tuna to food resources in otherwise thermally-stressful habitats.

Here we investigate how ocean temperatures have been changing in the East Greenland-Denmark Strait region using both long-term historical *in situ* measurements and satellite imagery, and how the changes are affecting the northern range limit of bluefin tuna and some of its key prey species. We hypothesize that the recently reported high abundance of prey species such as mackerel near, but south of, our study region (i. e., on the south Icelandic continental shelf) combined with warmer temperatures has created new suitable habitat for bluefin tuna.

Materials and methods:

Fish data: During summer-fall 2012, a scientifically-monitored exploratory fishery for mackerel, a well-documented prey species for bluefin tuna (Tiews 1978; Fromentin & Powers 2005), was conducted in waters east of Greenland in the Denmark Strait-Irminger Sea region. The objective of this fishery was to identify and document recent changes in the spatial distribution, range and abundance of mackerel whose distribution has expanded north from the northwest European continental shelf and slope towards the Faroe Islands and south Icelandic shelf (Astthorsson et al. 2012).

Fishing was conducted by five chartered fishing vessels with biological observers onboard and employed commercial fishing practices and gear. Catch information was retrieved from the observer reports and the mandatory logbook information provided for each haul operation. A full description of the results (e. g., distributions and abundances of different species by month, etc.) will be presented elsewhere. Although the fishery was targeting mackerel, other species were caught as bycatch; the bycatch data are the focus of the analysis presented and discussed below.

Temperature data: Bluefin tuna are primarily located in the upper mixed layer of the water column; hence sea surface temperature (SST) is a representative indicator of the dominant thermal conditions experienced by this species (Fromentin et al. 2013). We used two main sources of SST data derived using different but complementary methods: satellite-based measurements, and direct *in situ* measurements from research vessels, ships-of-opportunity, and drifting and moored instruments.

Satellite-based direct observations of SST in the trawl area were not available for the day in question due to cloud cover, which is a frequent phenomenon in this region (see below and Supplementary Figure S1). This pattern of cloud cover in the area is a persistent feature for this region, as seen by the spatial variability in number of months of coverage during July, August and September by the NASA Pathfinder SST satellite reanalysis during 1982-2009 (Supplementary Figure S2). In particular, the area with the lowest satellite coverage in the entire northern hemisphere north of 60^o N (and excluding the main ice-covered part of the Arctic Ocean) corresponds closely with the position where bluefin tuna were captured in the Denmark Strait region. The low data return is a combination of cloud cover and a strong horizontal gradient in SST (i. e., a frontal zone), which can be misinterpreted by the Pathfinder data processing scheme as a cloud edge.

Instead, we employed the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA; Donlon et al. 2012) to identify the temperature of the haul in which the bluefin tuna were caught. This product combines remote sensing data from several satellites with *in situ* measurements from ships and drifting and moored buoys to produce a gap-free product on a 0.05 degree daily grid. We checked the veracity of the OSTIA product in this region by examining non-gap filled satellite images of the area (ODYSSEA L3 SST product; MyOcean 2013) for the week preceding and following the haul to confirm the position of the haul relative to a nearby front (see details below in Results). On the day in question, August 22, 2012, the haul position was covered by cloud. However, as is evident from a time series of uninterpolated images (Supplementary Figure S2), the frontal location was relatively stable during most of this period, and consistently north of the location of the haul where bluefin tuna were captured. This indicates that the bluefin tuna were captured in either warm or frontal water.

Time series of temperatures for August were subsequently derived from the OSTIA by concatenating reanalysis (1985-2007) and near-real time (2008 onwards) products and averaging over the region 58-65^o N and 45-20^o W and across all days in the month of August. Although changes in the composition of the input-data stream to this product may cause minor discontinuities in the time series, it is not expected that they will have a significant impact at the large spatial and temporal scales over which we are averaging.

A second time series based on *in situ* data for the time period 1870-1981 and combined *in situ* data and satellite imagery for the post 1982 period was generated from the Hadley Centre Sea Ice and Sea Surface Temperature data set (HadISST1) (Rayner et al. 2003) for the investigated region. This dataset, particularly since 1985 (when OSTIA become available), should not be considered fully independent of the time series based on OSTIA, because the latter also incorporates both satellite and *in situ* data. We employ HADISST1 primarily to provide a longer perspective to temperature conditions in this region.

We also used the satellite imagery (OSTIA product) to examine how the spatial patterns of variability in SST changed among years. We produced maps of SST for August of each year to visualize this variability. To illustrate how the warming has progressed in time and space, we plotted the spatial distribution of the proportion of years in the first decade of the OSTIA time series (1985-1994 inclusive) and the last pentad (2007-2011 inclusive) where the mean August temperature per pixel exceeded 11^o C, and compared this with the position of the 11^oC isotherm on the day of capture (August 22, 2012). We also calculated the approximate area of water in this region (i.e. the boundaries of Figure 2, 50^o – 10^o W, 54^o N-70^o N) where the mean August temperature exceeded 11^o C for both the OSTIA and HadISST1 products.

Although we use 11^o C as an approximate indicator of the lower threshold temperature for bluefin tuna habitat in the region, we are aware that the species does occasionally experience much colder temperatures (0-5^o C; Boyce et al. 2008; Fromentin et al. 2013) and can therefore tolerate such cold tempratures for at least short periods of time (e. g., minutes-hours) due to an efficient thermo-regulatory capability (Lawson et al. 2010; Galuardi & Lutcavage 2012). However it is unlikely that the species can withstand these cold temperatures for the longer periods of time that characterise occupation of a feeding habitat. Surface temperatures in the most frequently occupied summer feeding habitats for this species are > 10-11^o and usually several degrees (5-10^o) warmer than this (Lawson et al. 2010; Galuardi et al. 2010; Vanderlaan et al. 2014). Bluefin tuna typically occupy such habitats for several weeks-months, usually while temperatures rise to summer maxima, and then decline (Mather et al. 1995; MacKenzie & Myers 2007; Galuardi et al. 2010; Lawson et al. 2010; Vanderlaan et al. 2014). We assume therefore that, given migration behaviour and ocean conditions in summer habitat, the species cannot tolerate temperatures < 10-11^o C for such long periods of time without incurring substantial metabolic and bioenergetic costs.

To visualize long-term variability and trends in time series, we fitted a smoothing spline (a General Additive Model – see MacKenzie & Schiedek 2007 for details) to the Hadley Centre time series, or a linear regression to the OSTIA time series. Rate of temperature increase was estimated from the GAM and linear regression fits for the period of satellite coverage (1985-2012).

Results:

The 2012 exploratory fishery in east Greenland waters for mackerel incidentally captured other species as bycatch, including bluefin tuna. Three individuals were captured on August 22, 2012 in one haul. These individuals each weighed ca. 100 kg and were therefore most likely adults (Figure 1), given size-at-maturity information (ICCAT 2012).

The haul that captured the bluefin tuna also captured 6 tonnes of mackerel (official fisheries statistics database of the Greenland Fisheries License Control). Other bycatch species captured during exploratory fishing in summer-fall 2012 included additional prey species of bluefin tuna such as blue whiting, *Micromesistius poutassou* Risso 1826 (19), and herring, *C. harengus*; however mackerel was the most abundant of the three species captured in exploratory fishing in 2012 (5219, 406 and 293 t of mackerel, blue whiting and herring respectively were captured; Greenland Fisheries License Control).

SST was ca. 9-11^o C where these bluefin tuna were caught on the day of capture (Figure 2). The capture site was located in a frontal zone separating cold and warmer water masses (ca. 5^o C change over 100 km; Figure 2). Time series of regionally-averaged temperatures from satellite imagery and *in situ* instruments shows that temperatures in the Denmark Strait-Irminger Sea have been increasing (Figure 3; Supplementary Figure S3). August temperatures in 2012 and 2010 were warmer than any time since 1870. The size of newly created habitat with temperatures suitable for bluefin tuna is large: for example, between the periods 1985-1994 and 2007-2012, the area of water with temperatures $\geq$ 11^o C in the Denmark Strait-Irminger Sea region has increased by 720,000 km^2, i. e., an amount larger than that of Texas (Figure 3).

Discussion:

Our study demonstrates that bluefin tuna were present in the Denmark Strait, which is one of the northernmost, and historically coldest, regions ever recorded to have been occupied with certainty by this species. The presence of bluefin tuna in waters near Greenland is a very rare event (Møller et al. 2010; Fromentin et al. 2013). The species was recorded at unspecified locations near Greenland and Spitzbergen in 1671 (Di Natale 2012), and a stranding occurred in 1900 in Qaqortoq, SW Greenland (Møller et al. 2010) (formerly Julianehåb; 60°43′20″N 46°02′25″W). Occasional strandings or bycatches have occurred on the south coast of Iceland in the intervening centuries (Sæmundsson 1926).

The recent catches in 2012 therefore are the first scientifically confirmed presence of the species in east Greenland waters (Denmark Strait-northern Irminger Sea) in 342 years, and demonstrate that a large highly mobile fish species is changing its range and spatial distribution towards northern regions. The early sighting of bluefin tuna from 1671 is based on an explorer's report to the Greenland-Spitzbergen region (Di Natale 2012). However the exact locations of the sightings were not stated and therefore are unknown.

There is one other unconfirmed report of bluefin tuna near Greenland. A pop-up tag from a bluefin tuna tagged near Gibraltar as part of a tagging program during 1998-2000 was detected in the Greenland Sea at 75.123^o N – 1.095^o E (DeMetrio et al. 2002). However the responsible scientists at the time believed that the tag became detached from the fish and was transported to this location by currents, or that the fish may have been eaten by a killer whale migrating to this area (DeMetrio et al. 2002; Di Natale 2012). Consequently the capture of three individuals in 2012 may be the first ever record of this species in the Denmark Strait area, though we cannot exclude the possibility that occasional catches, strandings or sightings have occurred previously.

Given the available data, it is impossible to estimate how many additional bluefin tuna may have been present in the area in 2012. However, the capture of three individuals in the same haul suggests that a school (typically containing 10-100 individuals; Lutcavage et al. 1997; Schick & Lutcavage 2009)) was likely present. Schooling behaviour during foraging is common in bluefin tuna (Lutcavage et al. 1997; Schick & Lutcavage 2009).

A major factor affecting the presence of bluefin tuna in this region is the increase in local temperatures. Our datasets document that temperatures in waters east of Greenland have been increasing significantly in the last several years and are now within ranges of temperatures experienced by bluefin tuna when they occupied other northerly areas (e. g., Iceland Basin, Newfoundland shelf) farther south in the past. A commercial fishery for bluefin tuna in the shelf-break and Iceland Basin areas south of Iceland started in the late 1990s but was discontinued in the 2000s when abundances became too low to support a fishery (ICCAT 2012). Catches south of Iceland at that time would have been in waters strongly influenced by the northward flowing Gulf Stream and sub-polar Gyre and were warmer than those in the Denmark Strait-northern Irminger Sea region (Valdimarsson et al. 2012; Astthorsson et al. 2012). The temperature increases in the Denmark Strait-Irminger Sea region are part of overall warming trends in northern boreal-polar regions (Valdimarsson et al. 2012; ICES 2013). Given the increase in temperature and a biogeographic link between probability of occurrence and temperature for bluefin tuna in the Atlantic Ocean (Fromentin et al. 2013), we conclude that, from a temperature perspective, this area has recently become suitable summer habitat for bluefin tuna.

While physiologically tolerable temperature conditions are a major factor controlling the distribution of a species, biotic factors including prey abundance are also important. The catch of both mackerel and bluefin tuna in the same haul demonstrates that not only were temperature conditions suitable for bluefin tuna, but that a key prey item was available, and in close (foraging) range of one of its predators. Mackerel has been expanding its spatial distribution farther north and west of its previously – documented (Astthorsson et al. 2012) range and thereby into Icelandic and Greenlandic waters (ICES 2013).

A second biotic factor which may have led to the occurrence of bluefin tuna in east Greenland waters is the overall abundance of bluefin tuna itself. The biomass of this species in the eastern Atlantic and Mediterranean Sea has been increasing during the last 3-5 years following implementation and compliance with several fishery management regulations intended to conserve and recover biomass (ICCAT 2012). It is possible that as abundances have increased, the range of the species has spread to reduce density-dependent competition (e. g., for prey). Consequently the presence of large new habitats with suitable thermal and forage conditions could potentially become occupied by a species such as bluefin tuna which is increasing, highly mobile and therefore possesses high dispersal potential.

Frontal zones in the oceans can be areas of higher productivity and abundance of biota (Longhurst 2007). The capture of bluefin tuna near such a region is consistent with such observations, although the distribution and abundance of potential prey near this frontal zone in August 2012 is unknown. In general, the biological characteristics of this frontal zone (i. e., abundance and biodiversity of biota at different taxonomic and trophic levels) are also unknown. However, mackerel presence and capture near this frontal zone may have been due to their avoidance of colder (4-6^{o} C) water on the north side of the front, which may have functioned as a thermal barrier to further northward distribution. For example, mackerel usually avoid temperatures < 8^{o} C (although they do occasionally enter colder water (Utne et al. 2012)). The front may have been a local aggregation mechanism at which predators such as bluefin tuna could forage.

Notably, temperatures in the water masses both north and south of the front have been increasing over time, but the location of the front has not changed substantially during the warming period (Supplementary Figure S3). As we document here, this warming is leading to changes in local species distributions of both a predator and its prey. Such changes, mediated by rising temperatures, are a first step towards establishment of new trophic interactions for this region and changes in the species assemblages of local biogeographical provinces.

If summer temperatures in the Denmark Strait-Irminger Sea region continue to rise or remain at levels seen in August 2012, then it is likely that bluefin tuna could become a seasonally more frequent component of the regional fish fauna, assuming that it and its prey are exploited throughout their ranges at sustainable levels or lower. The migration of bluefin tuna to the area may therefore be associated with the immigration of important forage species such as mackerel, herring and blue whiting, and given associations between foraging bluefin tuna and prey in other waters (Schick & Lutcavage 2009; Golet et al. 2013), it is indeed likely that schools of bluefin tuna followed the seasonal mackerel migration as it progressed into these waters. The migration and range expansion of the forage species, all of which are primarily zooplanktivores (Utne et al. 2012; ICES 2013), itself may be a response to previously documented climate-induced northward range expansions of zooplankton in the north Atlantic (Beaugrand et al. 2009; Reygondeau & Beaugrand 2011). New knowledge of the ecology and temperature tolerances of not only bluefin tuna but also its major prey species is needed to increase understanding of the mechanisms that are leading to changes in both species distributions and food web interactions.

The expansion of bluefin tuna distribution to the Denmark Strait, and its probable link to increasing temperatures (having effects directly on bluefin tuna via availability of physiologically suitable habitat, and indirectly via distribution of prey species) is consistent with some other reports of temperature impacts on changes in spatial distribution and migration phenology of bluefin tuna. The migration of juvenile and adult bluefin tuna into the Bay of Biscay is earlier in warmer years (Dufour et al. 2007). Moreover the recent allocation of fishing quotas for bluefin tuna to Iceland and Norway for 2014 (31 t each; http://www.noraregiontrends.org/marineresources/marinenews/article/iceland-and-norway-get-bluefin-tuna-trial-quotas/87/) indicates that the species is occupying northern habitat, which previously had been vacated (ICCAT 2012).

The appearance of bluefin tuna east of Greenland raises many ecological questions about the migration and distribution of this species and how it interacts with its prey. Two immediate questions are: where did these individuals migrate from, and where were they born? Bluefin tuna spawn in the Mediterranean Sea and Gulf of Mexico (Mather et al. 1995). Conventional tagging in the 1950s-1960s and advanced data storage tagging in the last 10-15 years demonstrate that bluefin tuna undergo trans-Atlantic, as well as north-south, migrations (Mather et al. 1995; Block et al. 2005). The tuna captured near east Greenland could have migrated from the Mediterranean, or alternatively from the west Atlantic: bluefin tuna migrate north from the Gulf of Mexico to eastern Canada and the Grand Banks area and possibly could continue northeastwards (with an ultimate destination in European waters) if oceanographic conditions were suitable. Such migration from eastern North America to Europe occurred in the 1950s-1960s (Mather et al. 1995).

However, multi-annual time series of satellite imagery showing the spread of warm water from the southeast towards east Greenland (Figure 4) suggests that recent warming and climate change may have opened a migration pathway from the European shelf towards Greenland for migratory species such as bluefin tuna and their prey. If so, then rising temperatures may be facilitating dispersal from, and connectivity between, formerly isolated habitats, communities and foodwebs, and altering the boundaries of biogeographical provinces in the North Atlantic Ocean. Alternatively the bluefin tuna may have arrived from the northwest Atlantic: this area experienced record warm SST during summer 2012 (Mills et al. 2013). The population origin of new immigrant species such as bluefin tuna and mackerel is presently unclear and can probably be identified using modern genetic approaches (Nielsen et al. 2012).

However, and despite the present lack of knowledge of the population origins of the immigrating species, our results show that rising temperatures have been progressively leading a high-trophic level trophic cascade into east Greenland waters via improved thermal conditions for migratory prey (e. g., mackerel, blue whiting, herring) and predator (e. g., bluefin tuna) species. The sequence of events documented here provides initial evidence based on field observations of how the ranges of ecologically – interacting species in the ocean are changing at large biogeographic scales. These recent dynamics in the East Greenland marine ecosystem highlight the need for knowledge on how climate variability and change affects migratory behaviour, spatial distribution of predators relative to prey and not least the population origin of new immigrant species. Such new knowledge will be core information when new flexible resource management plans will be developed to take account of the warming impacts.

Acknowledgments: The research leading to these results has received funding from the European Union 7th Framework Programme (FP7 2007-2013) under grant agreement nos. 308299 (NACLIM project) and 264933 (Euro-Basin project), and the Danish Agency for Science, Technology and Innovation. We thank the Danish National Research Foundation for support to the Center for Macroecology, Evolution and Climate. The study is a part of the Greenland Climate Research Centre and has been conducted using MyOcean Products. We are grateful to the Greenland Fisheries License Control for providing logbooks and additional data and information from the exploratory mackerel fishery.

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Figure legends and figures:

Figure 1. Photograph showing two of the three bluefin tuna captured as bycatch during an exploratory scientifically-monitored mackerel fishery in the Denmark Strait area, east Greenland on August 22, 2012. Capture location is indicated on Figure 2. Photo credit: Greenland Institute for Natural Resources.

Figure 2. Sea surface temperature (SST) based on the OSTIA product (Donlon et al. 2012) for August 22, 2012 in the east Greenland-Iceland area of the north Atlantic Ocean. A white star marks the location of the haul (65 deg. 42 min. N, 30 deg. 50 min. W) which captured three bluefin tuna (*Thunnus thynnus*) using pelagic fishing gear during exploratory scientifically-monitored fishing for mackerel (*Scomber scombrus*). Depth contours are drawn at 200 m (thin line) and 1000 m (thick line). Dotted line indicates sea region used for calculating time series of annual August SST from the HadISST1 and OSTIA satellite imagery datasets (see also Figure 3). See Supporting Information Figure S3 for maps of annual August SST for this region for all years during 1985-2012.

Figure 3. Inter-annual variability in SST (a) and in the area of water warmer than 11 ^{o}C (b) during August in the Denmark Strait – Irminger Sea area east of Greenland for 1870-2012 from the HADISST1 database (Rayner et al. 2003) and from the OSTIA product (Donlon et al. 2012) for 1985-2012. The HADISST1 data were extracted for an area corresponding to the box in Figure 2. The area of water > 11^{o} C was estimated within the region 55-70^{o} N and 50 – 10^{o} W (i. e., the entire region represented in Figure 2). General Additive Model fits to HADISST1 data for the whole time period were statistically significant (pseudo-R^2 = 0.39 and 0.38 respectively for the SST and area time series; $P < 0.001$ for both). Linear regression fits to OSTIA data (1985-2012) for SST (SST = 0.08·year – 157.1; $R^2_{adj.} = 0.65$; $P < 10^{-7}$) and area (area = 33466·year – 6.55 x 10^{-7}; $R^2_{adj.} = 0.64$; $P < 10^{-7}$) were both statistically significant. The thin solid line with gray dots are the observed data, and the thick solid black line is a GAM fit to the data with 95% prediction intervals (dashed lines); satellite image derived measurements (OSTIA data product) are shown in red for years 1985-2012.

Figure 4. Proportion of years where SST > 11^{o} C for a) 1985-1994 (first decade of time series) and b) 2007-2011 (five years prior to capture). The contour line shows location of the 11^{o} C isotherm for 2012. Data source for SST is satellite imagery (OSTIA product; Donlon et al. 2012). The position of the haul that caught three bluefin tuna on August 22, 2012 is shown as a white star near 65^{o} N, 30^{o} W.

Figure 1

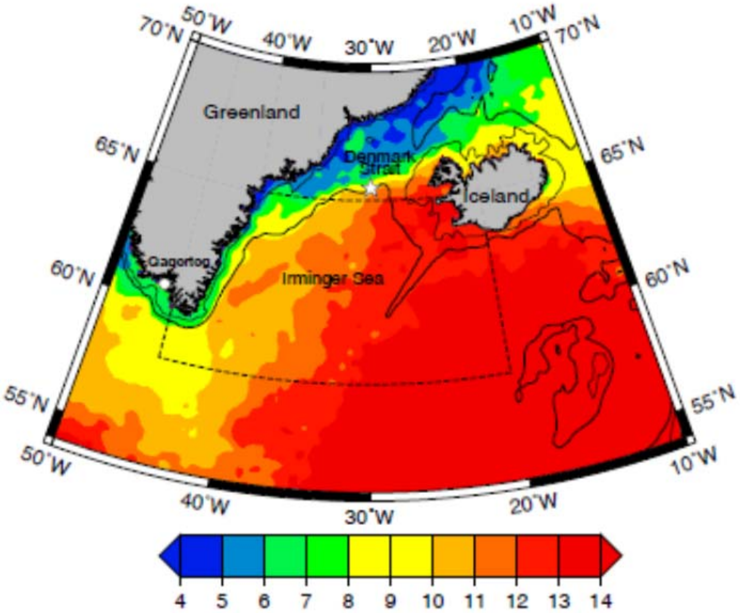

70°N
50°W
40°W
30°W
20°W
10°W
70°N
Greenland
65°N
Denmark Strait
Iceland
65°N
60°N
Qaqortoq
Irminger Sea
60°N
55°N
55°N
50°W
40°W
30°W
20°W
10°W
4
5
6
7
8
9
10
11
12
13
14

Figure 2.

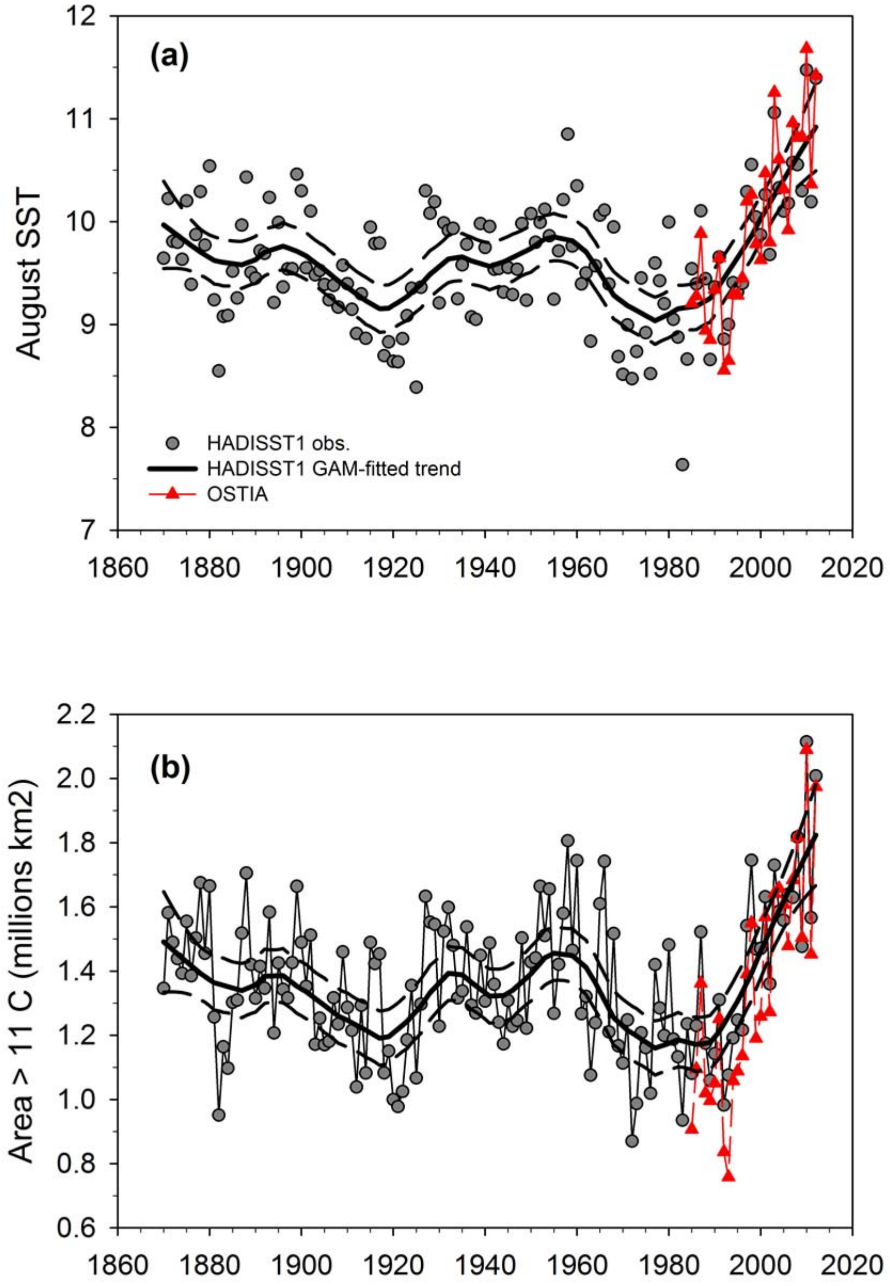

(a)
August SST
12
11
10
9
8
7
1860
1880
1900
1920
1940
1960
1980
2000
2020
HADISST1 obs.
HADISST1 GAM-fitted trend
OSTIA
(b)
Area > 11 C (millions km2)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
1860
1880
1900
1920
1940
1960
1980
2000
2020

Figure 3.

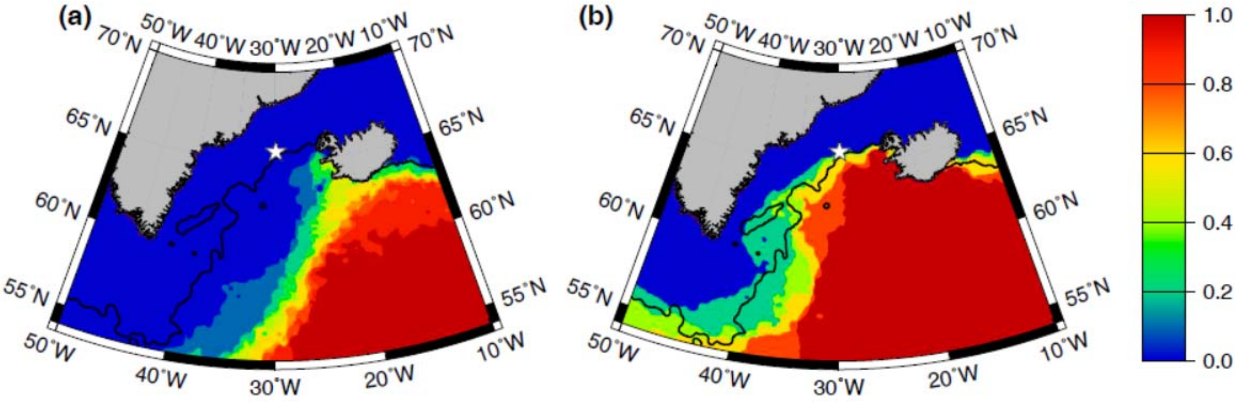


Figure 4.

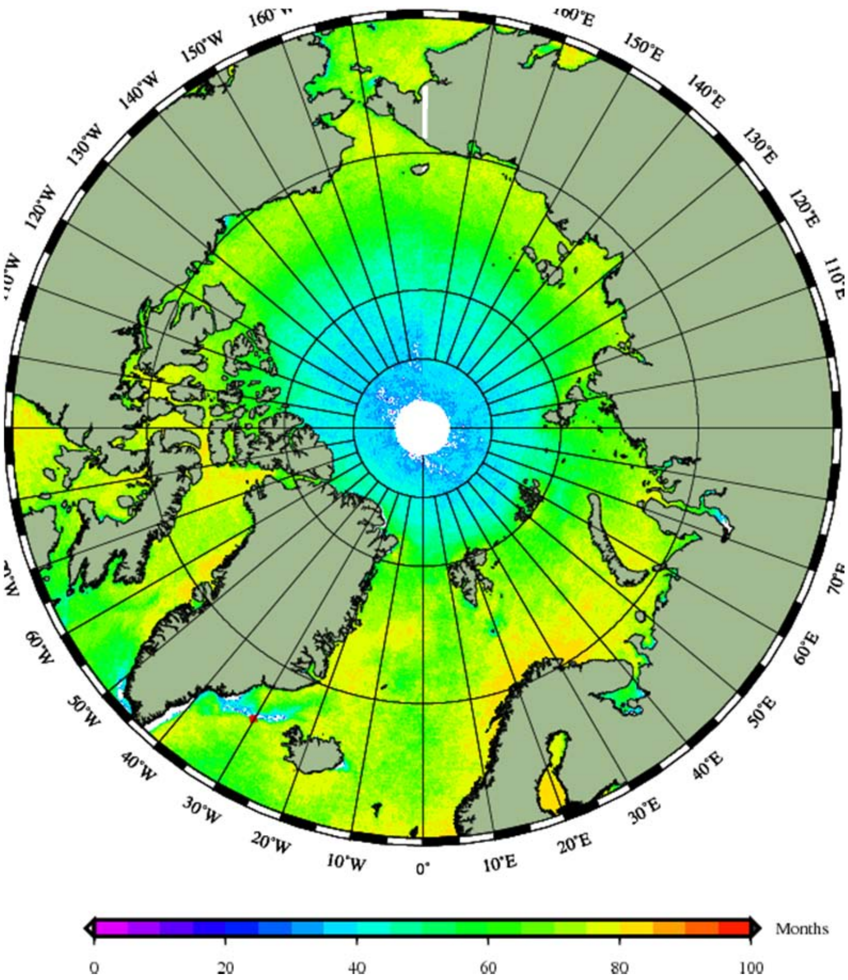
Supporting Information:

Supporting information consists of four supplementary figures. Captions are listed below.

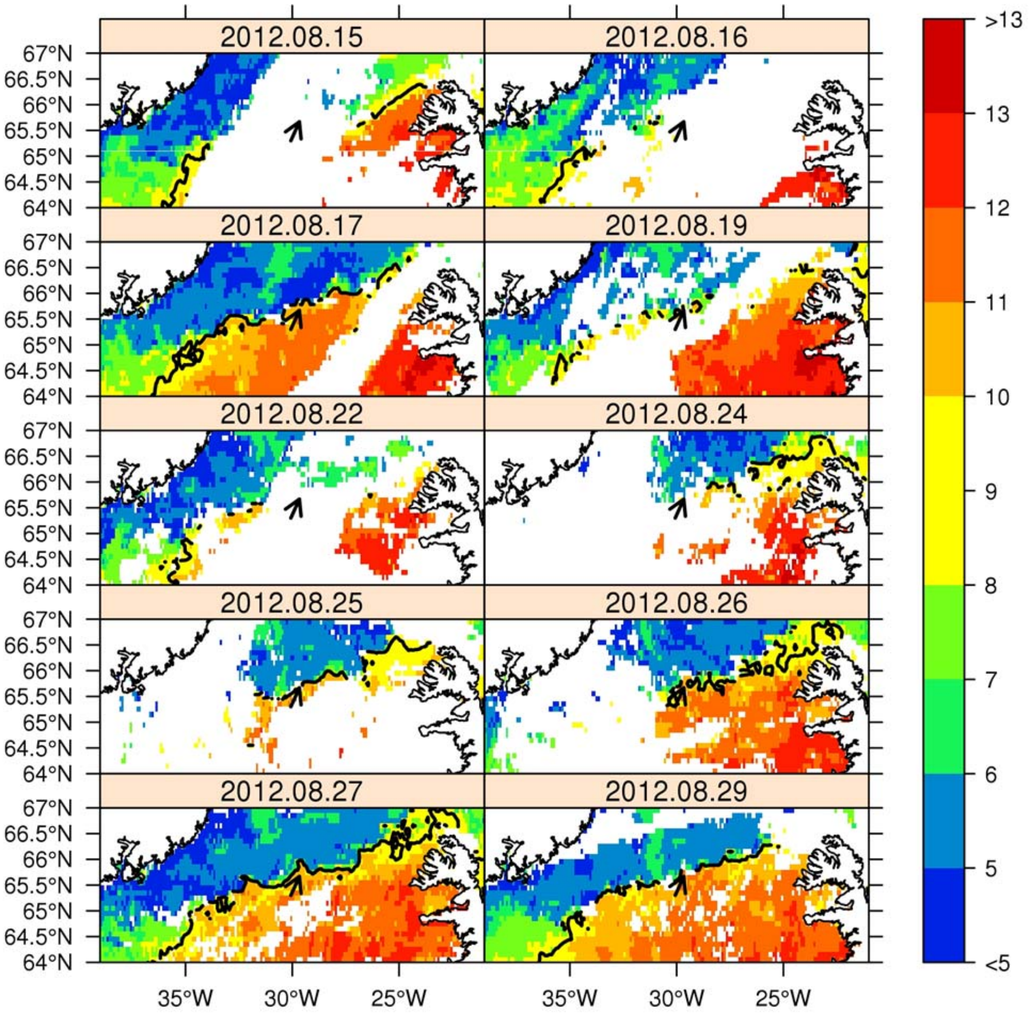
Supplementary Figure S1. The number of months in June-July-August 1982-2009, where satellite imagery observations of SST are available. The data set used for this image is the Pathfinder 4 km SST version 5.0 and 5.1. Pathfinder quality flags larger than 3 is used when producing the monthly averages. The low number of data in the East Greenland Current is probably due to a combination of persistent cloudiness and large SST gradients, which have been classified as clouds in the processing. The red dot shows the location of the net-haul which captured three bluefin tuna and 6 t of mackerel on August 22, 2012.

Supplementary Figure S2. ODYSSEA Level 3 Sea-surface temperature observations from satellite. These images are based only on remotely-sensed temperature data from satellites and exclude any gap-filling and *in situ* data. The arrow marks the length and direction of the haul in which the tuna individuals were caught. White areas are those where no data is available due to cloud cover. The date of the image is marked at the top of each panel, in the year-month-day format: the haul in question was performed on August 22, 2012. Only days where there is a relatively clear view of the region are shown here. The approximate position of the front between cold Polar waters and warmer Atlantic warmers is denoted here by a thin (interrupted) black line, corresponding to the 9^{o} isotherm (approximately half-way between the $4\text{-}7^{o}$ Polar waters and the $11\text{-}14^{o}$ Atlantic waters). Although the image on the day of capture is obscured by cloud, the position of the front appears relatively stable on the time-scales considered here and the haul is always on the warm side of the front.

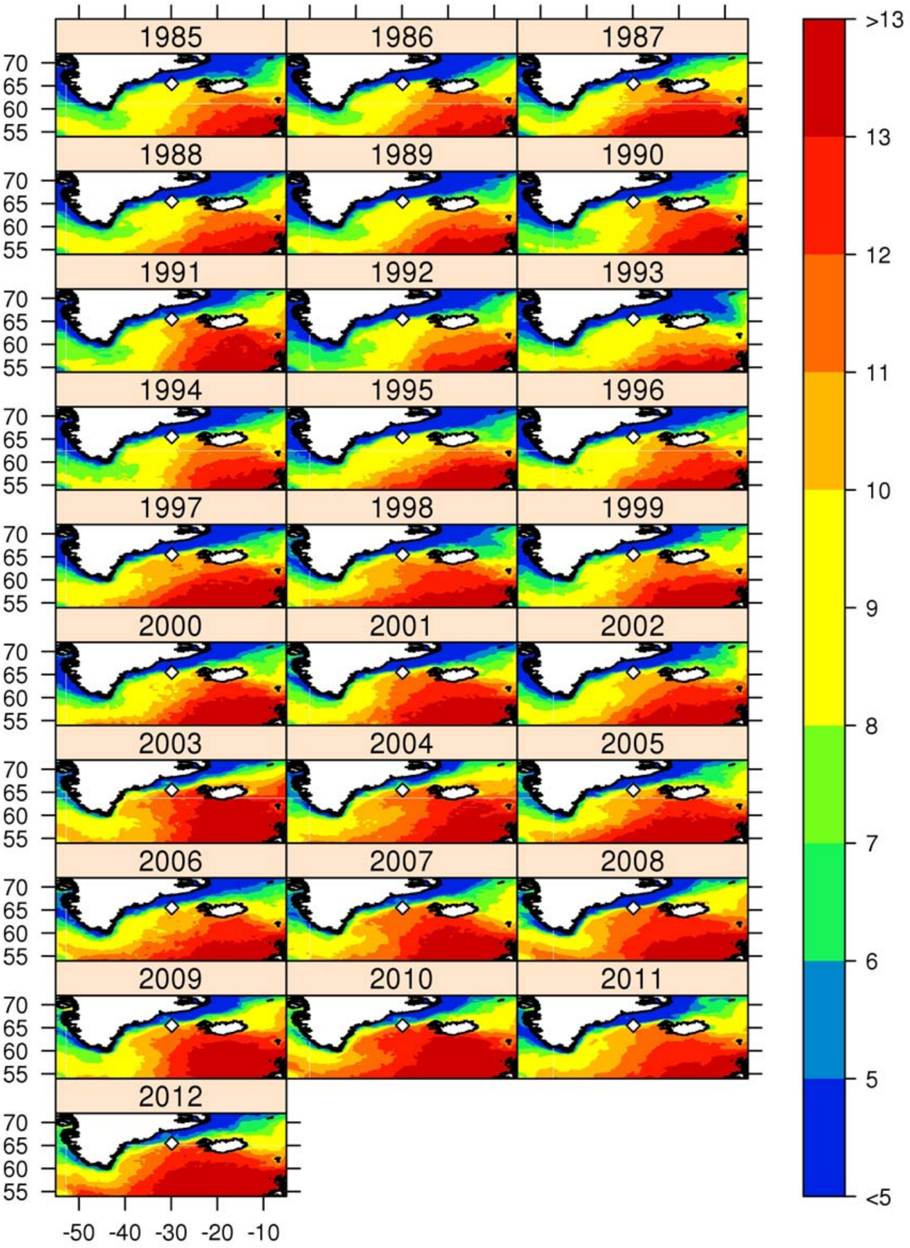
Supplementary Figure S3. Annual SST in the Denmark Strait-Irminger Sea area for August during 1985-2012 from the OSTIA data product (Donlon et al. 2012). The location of the haul which caught three bluefin tuna on August 22, 2012 is shown for reference as a black spot. Note that in all years the position of the frontal zone between cold, Polar water and warmer, Atlantic water is relatively stable.



Supplementary Figure S1.



Supplementary Figure S2.



Supplementary Figure S3.