Title: Improved management facilitates return of an iconic fish species

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Abstract:

Declines and losses of biota which persist for long periods often lead to a shifting baseline of where populations and species should live and neglect or abandonment of recovery actions aimed at ecological restoration. Such declines are frequently accompanied by contractions in distribution, negative ecological impacts and diminishing economic benefits. Here we show using citizen science information and data that after 50-60 years of near total absence from waters near Denmark, Norway and Sweden, the iconic top predator and highly migratory species bluefin tuna, *Thunnus thynnus*, returned by the hundreds if not thousands during August-October 2016. This remarkable return has been facilitated by improved fishery management for bluefin tuna and its prey. Its reappearance, despite a recent history of mismanagement and illegal fishing which led to population decline, offers hope that other marine ecological recoveries are possible under improved management of fisheries and ecosystems.

Short title: Return of an iconic fish species

One Sentence Summary: Improved management helps bring back an ocean icon to northern Europe.

Significance Statement:

Commercial fisheries are often perceived being in a state of decline and collapse, putting food and economic security at risk. Such declines are frequently accompanied by contractions in stock distribution, negative ecological impacts and diminishing economic benefits. Here we present an example based on one of the world's most valuable and controversial fish species, bluefin tuna, which demonstates that effective management of both bluefin tuna and its prey has been a key factor leading to a remarkable reoccupation of formerly lost habitat. This reappearance, following decades of absence, occurred despite the bluefin tuna stock having had a recent, long history of unsustainable and illegal exploitation. Marine ecological recovery actions can be successful, even in situations which may initially appear intractable.

Introduction:

Recovering the biomass and spatial range of depleted fish stocks is a challenge to fisheries managers and conservation ecologists (1–3). Once lost, former biomasses and ranges often disappear from human memory, thereby reducing motivation for and impairing recovery efforts (4–6). Biomass and range recovery often take longer than anticipated, even when fishing is reduced below sustainable levels, due to factors such as bycatch fishing mortality (i. e., captures as bycatch in other fisheries), and changes in stock productivity (1–3, 7, 8). Species that are highly migratory and whose migrations take them into the high seas and multiple fishing jurisdictions, such as tunas and billfishes, are potentially even more vulnerable to depletion and prolonged recovery times than stocks under single or few fishery jurisdictions (2, 9).

Here we report a recovery of the former range of distribution by a highly migratory, highly valuable, iconic top predator fish species (bluefin tuna, *Thunnus thynnus*). This species was the target of unsustainable exploitation for many years in the 1990s-2000s, and its biomass declined to record low levels in the late 2000s (10). As one of the world’s most valuable fish species, it has also been the subject of much scientific, public and conservation NGO scrutiny (11).

Bluefin tuna spawn in sub-tropical regions (e.g., Mediterranean Sea) and then migrate north long distances as adults to summer and autumn foraging areas (12, 13). In the northeast Atlantic, historical adult foraging areas are located in the Bay of Biscay, on the northwest European continental shelf off Ireland and the UK, and in the Norwegian Sea-North Sea-Skagerrak-Kattegat-Øresund (the latter are hereafter referred to as northern European waters; Supplementary Figure S1 showing ICES areas and sea names (12, 14)). Bluefin tuna occupy these waters in summer-early autumn before migrating southwards to overwintering areas. This long-distance migratory behaviour is a part of the species' life-history, having evolved through generations (13).

However, the migrations to northern European waters stopped almost completely in the early-mid-1960s and bluefin tuna have been extremely rare in the area since the 1970s (14, 15); the species has not supported commercial or recreational fisheries in the area since then (10) (Supplementary Figure S2). The reasons for both the disappearance and the long period before reappearance are unclear, but likely due to a combination of overexploitation of juveniles and adults of both the tuna and their prey, and changing oceanographic conditions (14, 16–18).

We describe the re-appearance using citizen science data (i. e., observations from non-scientists pursuing activities on or near the sea) and discuss possible reasons why it happened. Given the high level of illegal and unsustainable exploitation of this species in the recent past (mid-late 1990s until ca. 2008-2010; (10)), the recovery of the habitat and range of this species is extraordinary and could become a classic example of how recoveries can occur under a suitable combination of fishery management reguations and ecosystem conditions.

Results:

Bluefin tuna observations in 2015 and 2016:

We found and received many reports of bluefin tuna in the region. The observations are summarized in Figure 1 and Supplementary Table S2. The reports included observations of single individual tunas and of schools of various sizes from a few specimens (2-10) to hundreds. The species is relatively easy to identify and distinguish in this area, mainly because of their surface jumping behaviour, body shape, color and size. The sizes of tuna observed were usually large (ca. 1.5 – 3 m) and the jumping or surface-breaking behaviour is characteristic of this species. All observations we present are based on individuals which are partially or entirely out of the water due to jumping and surface swimming, which facilitated reliable identification; the observations are supported in many cases by photographs or videos available on public social media and angling or news media websites in Scandinavia. Some of these photographs are shown as part of Figure 2 and as Supplementary Figure S3, and some online videos of bluefin tuna jumping are listed in Supplementary Table S3.

The locations of most of the sightings we obtained were in the central part of the eastern Skagerrak, along the Swedish west coast in the Skagerrak, and in the Kattegat (Figure 1). For example, recreational fishing tour boats and individual recreational fishermen and the Swedish Coast Guard observed individual bluefin tuna swimming at the surface and jumping clear of the water near a Swedish national marine park (Kosterhavet). The estimated sizes of these bluefin tuna were 2-3 m. One bluefin tuna was caught by a Danish recreational angler north of Skagen, Denmark in the Skagerrak on Sept. 19 and released alive after capture. This fish was measured in the water to be 3.03 m and estimated to weigh app. 400-450 kg (19).

At nearly the same time (Sept. 17, 2016) and ca. 7 deg. latitude farther north, bluefin tuna were captured as part of a targeted commercial fishing operation in the Norwegian Sea, off Ona (62.8603°N 6.5543°E), Møre, Norway, approximately halfway between Bergen and Trondheim. The tuna caught (N = 190) each weighed ca. 170-300 kg (20–22). These tuna were captured by a Norwegian fishing vessel as part of the Norwegian bluefin tuna quota. Several Danish commercial fishermen, including one of the co-authors of this investigation (HSL), reported that they repeatedly saw schools in a localized area north of Skagen on several days during ca. two weeks in mid-late September, 2016; the total number of tunas observed on some days was in the hundreds. On Sept. 30, a school of 6-8 bluefin tuna were seen 200-250 m off the beach along the northern Danish Kattegat coast near Frederikshavn.

The first observation available to us in 2016 was made on August 12. A man in his sailboat, coming from the south through Øresund, observed a single tuna jumping out of the water four times, about 100 meters from his boat. The observation was made ca. 700-800 metres from the Danish coastline. The last observation reported to us was a sighting by a commercial fisherman in the Skagerrak on October 20. The cumulative amount of reports indicates that the species was present in large numbers for at least 2.5 months during late summer-autumn.

Ecosystem conditions:

The longest available time series of potential prey biomasses are from ICES stock assessments for herring and mackerel stocks in the North Sea, Norwegian Sea and northeast Atlantic. These show that the biomasses have been high since the late 1980s-early 1990s for the three stocks in the northeast Atlantic Ocean. The sum of the three biomasses has been at record-high levels since the early 2000s (Figure 3).

At the smaller spatial scale of the Skagerrak-Kattegat, demersal research surveys in late summer-autumn show that catch rates (considered to be a relative indicator of biomass) for four potential prey species (herring, sprat, mackerel, anchovy) were relatively low in 2016. The most abundant of these species is usually herring; however its abundance peaked in 2011 and has declined to low levels since then, including in 2015 and 2016. Other demersal and the pelagic surveys also show that prey abundance in 2015 and 2016 was approximately average or even below-average (Supplmentary Figure S4).

August-October surface temperatures have been well above long-term average since 1994 when a significant regime shift occurred (STARS test; $P < 0.0001$ (31)); this shift is evident in the larger northeast Atlantic region and the Skagerrak-Kattegat sub-region where our tuna sightings have been made. However temperatures in 2015 and 2016 were not unusually warm compared to other years during the most recent regime.

Discussion:

Bluefin tuna appear to have re-discovered former foraging habitat in northern European waters, which they vacated about 40-50 years ago. The observations are identical to those reported in historical fishery reports, newspapers and scientific literature from the 1920s-1960s (Figure 2), when bluefin tuna were common in these waters (e. g., (23, 24)); the jumping and surface-breaking swimming behaviour is typical for bluefin tuna foraging on prey species (23, 25). Our observations indicate that bluefin tuna were abundant throughout the combined Skagerrak-Kattegat and coastal Norwegian Sea region. Since neither Denmark nor Sweden has a fishing quota, and there are no surveys potentially monitoring the distribution and abundance of bluefin tuna, the public observations are essential for providing evidence of their return to these waters.

Cause of reappearance:

Given the long absence from the Skagerrak-Kattegat and neighboring waters, one must ask why bluefin tuna has finally returned now. The factor which has likely contributed most to the return is improved bluefin tuna fishery management since ca. the mid-late 2000s. Several changes were made during this period, including reductions in quotas, increases in minimum landing sizes from 6 to 10 kg and then to 30 kg so that a much larger share of juveniles can now survive long enough to reach maturity (assumed to be at an age of 4 years, or ca. 25 kg (10)), improved catch reporting requirements and documentation, and strengthened fishery surveillance and enforcement (10, 11).

Prior to implementation of these changes, the stock was overexploited both legally (because countries allocated themselves higher quota limits than those recommended by ICCAT (International Commission for the Conservation of Atlantic Tunas) scientists as being scientifically sustainable in the long term), and illegally (e. g., landings often exceeded the biologically sustainable limits agreed by the countries during many years in the late 1990s and early 2000s). Before the new regulations were implemented, historical exploitation of juveniles in southern parts of the stock range was high since the 1950s and has been considered to be a major factor leading to the disappearance and subsequent continued absence of bluefin tuna from northern parts of the range (18). In addition, the parent stock biomass in the early-mid-2000s was perceived to be declining (10) and at a rate that if continued could have met criteria for listing this stock as "critically endangered" according to IUCN (International Union for the Conservation of Nature) criteria (26).

Implementation of the new fishery management regulations appears to have had positive effects. Shortly after, several stock indicators of abundance started increasing, including the production rate of new young bluefin tuna "recruits" (10, 11). As the stock has increased, bluefin tuna appears to have expanded its migratory range, a pattern common among recovering fish stocks (3, 27), to explore new feeding habitats and to reduce density-dependent competition for prey, including into some northern areas beyond formerly documented distribution ranges such as Denmark Strait (east of Greenland (28)). This exploratory foraging behaviour may have led them to return to the northern European shelf waters, where they apparently have found sufficient prey for foraging.

A secondary reason for the return to these waters may be the relatively high biomasses of potential energy-rich prey species such as mackerel, herring, and sprat. Herring and mackerel dominate pelagic fish biomass in the region and their biomasses have recovered to or beyond historical estimates (29). Some of these species (herring and mackerel) were also overexploited in the 1950s-1970s leading to local collapses and fishery closures for these species. These declines may have been a factor inhibiting earlier return of bluefin tuna to this region. However following implementation of more sustainable fishing practices, the biomasses of these species have recovered, but the tunas did not reappear in large numbers until several years after the prey biomass recovered. This delay suggests that the main reason for the reappearance of bluefin tuna in the region was the increase in tuna biomass itself, and the time required to re-learn former migration pathways and foraging habitats (17, 30).

Moreover, as a large, fast-swimming schooling species with high daily energy intake, bluefin tuna have high potential for quickly learning where prey concentrations are located. For example, bluefin tuna have learned to follow or locate mackerel migrations to Iceland and east

Greenland waters in the early 2010s and have been caught as bycatch in Greenlandic mackerel fishing operations (28). It is likely therefore that if bluefin tuna had been more abundant in the 1990s and 2000s, they would have already appeared in high abundance in the Norwegian-North Sea-Skagerrak-Kattegat area several years earlier than now.

Ocean temperature conditions are also known to affect tuna distributions and migrations (16, 31, 32), and have been generally warmer since 1994. However temperatures in 2015 or 2016 were not exceptionally warm and were in fact colder than in some earlier years in the recent warm regime (post-1994). Notably, bluefin tuna have been present in the Skagerrak-Kattegat during many earlier years (e. g., 1920s-60s) when temperatures were lower than during the post-1994 regime (compare Figure 3 and Supplementary Figure S2), and have occupied colder areas farther north in the past (e. g., in the Norwegian Sea and along the west Norwegian coast; see Ref.(24) for temperature data). We conclude that temperatures in the Skagerrak-Kattegat or northeast Atlantic region appear to have had little direct role on the re-appearance of bluefin tuna, although they may have had indirect effects via changes in local food abundance, migration behaviour or distribution. However the exact mechanisms by which temperature may have acted, if at all, are unclear and remain speculative.

Appearances of bluefin tuna in other northern regions also suggest that the species range has expanded, possibly due to its increased abundances. Bluefin tuna have appeared for the first time known to science in waters north of its usual summer feeding range and entered the Denmark Strait-Irminger Sea in 2012 (28). The entry of bluefin tuna in this region is likely due to the higher tuna abundance, warmer temperatures in a habitat which formerly was close to or colder than the lower tolerance limit for bluefin tuna, and large biomass of a key prey (mackerel) (28), whose summer distribution has also been extending into these waters since the 2010s (33).

In summary, both food and temperature conditions have been higher than average for many years before the tuna returned to the Skagerrak-Kattegat and probably also the wider North Sea-Norwegian Sea-Skagerrak-Kattegat region. We consider it unlikely that either of these factors in 2015-2016 were the main direct drivers for the recent appearance of bluefin tuna in the Skagerrak-Kattegat region, although adequate prey and temperature conditions likely induced exploratory foraging bluefin tuna to remain in this region, once it was re-discovered.

Contribution of citizen science to bluefin tuna ecology:

For reasons explained above, our investigation relies on input from the public to document the species presence in this region. As with all citizen science reports, there is a possibility for some false, biased and otherwise incorrect reporting. We believe that such records are not likely present in our compilation because of the nearly simultaneous nature of the records over a wide area (e. g., the many sightings reported in the eastern Skagerrak-Kattegat on nearly the same day as the large commercial catch in central Norwegian coastal waters), the similarity of the reported behaviour to historical sightings of tuna in the region (e. g .,(23); see Figure 2 of main manuscript and Supplementary Figure S3) and the distinguishable features of bluefin tuna behaviour and size that reduce the likelihood of misidentification with other species.

Moreover, some of the reports were made by highly reputable observers, including on-duty officers of national coast guard services or by off-duty members of our research vessels while participating in recreational sea-based activities. Their observations and reports were identical to those made by other members of the public and by commercial and recreational fishermen targeting other species. For example, some fishermen observed tuna while trawling for pelagic fish (e. g., herring and mackerel) that are prey for bluefin tuna in this region. Lastly, several of the reports and our interviews via email or telephone include statements by the observers that they had never seen such behaviour before despite years and even decades of activity on the sea and that they had knowledge of the species' former presence in the area from older generations. We are confident therefore that our observations represent a valid and reliable source of documentary evidence of the presence of the species in these waters.

We are aware however that the reports based on citizen reporting reflect the spatial distribution of where the reporting observers were located. That is, they do not necessarily represent the full spatial distribution of where the tuna were located because (1) some tuna may have been observed in other areas, but not reported to us, (2) some tuna may have been present in other areas (and of course depths), but not seen by any human observers; and (3) observers were surely present over a much wider area than indicated by our few reports, but it is not possible to know which of those observers saw or did not see bluefin tuna. The spatial distribution of tuna based on our observations must therefore be interpreted cautiously, and we cannot exclude the possibility that bluefin tuna were present over a much wider area than is indicated by our data. We have tried to minimize such observer bias by making broad contact to the public and especially commercial fishermen (e. g., via their associations). Nevetheless, to obtain a more representative distribution in the area, alternative methods would need to be employed such as aerial surveying via airplanes (25, 34) or with drones (35) or tagging with electronic tags (36, 37) and subsequent modelling (30, 38). In addition, increased public awareness of the species in the area and the need for its documentation could also increase public reporting of bluefin tuna observations and the reliability of distributional maps. Such combined survey- citizen science methods could also potentially be used to derive estimates of relative abundance in the region, which is not possible with our dataset.

Future perspectives:

The return of bluefin tuna to northern European waters opens many new possibilities for both scientific understanding of species biology/dynamics and for socio-economy. Regarding science, a priority should be to investigate the migration behaviour and population origin of the bluefin tunas which have appeared in these waters using a combination of modern tagging, genetics, otolith and modelling methods. Bluefin tuna in the Atlantic are managed as two stocks (western and eastern stocks, the latter including the Mediterranean) with separate quotas and other regulations (10). Historically, bluefin tuna caught in the northern European region had migrated both from the northeast and northwest Atlantic (12), and any future commercial or recreational catches should be assigned to the correct stock. Such assignment would need for example genetic or otolith-based evidence (39, 40).

New sustainable commercial and recreational fisheries would support and diversify local fishery economies in primarily rural areas of the region. Furthermore, given the recent interest in the general public for the return of this species to northern European waters (41, 42) (e. g., 5 video clips made by citizen scientists have been viewed on social media > 270,000 times: Supplementary Table S3), and the possibility that jumping bluefin tuna can be seen from relatively small boats operating within minutes to a few hours of shore, there is potential that the species could create and contribute to the eco-tourism industry.

A pre-requisite for realizing these scientific and socio-economic opportunities is that the recent fishery management regulations for both bluefin tuna and their prey, and their compliance, continues in future. In general, it presently appears as if efforts towards sustainable fishery management both for the bluefin tuna and its prey species are having positive benefits for these stocks. Should this be true, bluefin tuna may become a regular summer component of local fish communities and food webs, and contribute to small but lucrative commercial and recreational fisheries and eco-tourism economies.

The re-establishment of summer migration to this region, together with the recent increase in overall stock biomass, indicates that, as with some other recovering large iconic fish stocks (3), improved management, enforcement and compliance can yield positive benefits when ecosystem conditions for stock production are suitable (3, 7). These observations apply even for species such as bluefin tuna which has historically suffered from much illegal and over-fishing and whose highly migratory behaviour takes them into multiple fishing jurisdictions including international waters. The reappearance of bluefin tuna in the Skagerrak-Kattegat and neighboring seas serves as an example of the benefits of implementing effective recovery actions, despite a decades-long absence from the region and a highly unsustainable fisheries exploitation situation. In this case, implementation has not been too late to promote recovery. Similar efforts with other populations and species could also yield positive outcomes. These findings offer some optimism for the long-term recovery and sustainability of commercially-exploited fish stocks, the ecosystems in which they live, and the economic sectors which they (could) support.

Materials and Methods:

General:

As there are presently no commercial, recreational or scientific fisheries (surveys) for bluefin tuna in the Skagerrak-Kattegat, the only source of information available for documenting presence were reports from the public, including commercial and recreational fisher observations. We consider all these records to be "citizen science" and compiled observations from reports in newspapers, social media and via direct contact of the public with us. Details for the data compilation are available below. The observations were then organized chronologically, assigned a record number and visualized to display their spatial-temporal distribution. To place our work in the historical context of past fisheries for bluefin tuna in the region, we compiled and plotted officially reported landings data from ICES and other historical sources (summarized in (24)) for the years 1903-2014, which was the last year for which landings data are available from ICES. We use officially reported data from ICES instead of from ICCAT because the former are available at higher spatial resolution for our region of interest.

Ecosystem conditions (e. g., local food concentrations, temperatures) are known to affect distributions of bluefin tuna (16, 28). We derived estimates of the inter-annual variability in abundance of major prey species and sea surface temperatures (i. e. those most likely experienced by bluefin tuna during summer foraging on the continental shelf) for the Northeast Atlantic to evaluate whether food and/or temperature conditions were unusually favorable in 2015 and 2016 compared to earlier years. Further details of the data sources and compilation are presented below.

Bluefin tuna observations:

We compiled observations of bluefin tuna from primarily public sources such as social media (i. e., Facebook, YouTube) and websites representing both commercial fishermen and anglers in

Denmark and Sweden. We also obtained and used information sent to us by the public following announcements on the DTU Aqua website and sent to Danish commercial and sportsfishermens' organizations and contact by SLU Aqua with Swedish sportsfishermen that we were interested in receiving sighting observations. We supplemented these citizen science observations with reports of commercial catches and bycatches in the Norwegian Sea, North Sea, Skagerrak, Kattegat and Øresund. The time period covered was August-October 2016. However during the course of this data collection, we also received or found reports of observations in 2015 which we used to support our overall results and conclusions. In many cases, the sightings were supported by photographs or video recordings of bluefin tuna. The information provided by members of the public included date and location of the observation, how many bluefin tuna were observed (e. g., single individual, school, approximate number of schools and number of fish per school), behaviour (jumping over water surface, breaking water surface), and prey escape behaviours observed at the surface. The observations were entered into a database and visualized geographically to illustrate their spatial distribution in relation to distance from land, bottom topography and sea surface temperature.

Estimates of abundance of potential prey for bluefin tuna:

We estimated abundances of potential prey for bluefin tuna in the region from regional stock assessments for main prey species and from fishery research vessel surveys. We used the North Sea herring, Norwegian spring-spawning herring and Northeast Atlantic mackerel total stock biomass estimates from the ICES assessments as indicators of potential prey for bluefin tuna in the region of our study. These stocks occupy large areas (see ICES stock management area map, Supplementary Figure S1), which overlap with the historical distribution of bluefin tuna in the region (12, 14, 15, 24); moreover tuna which enter the Skagerrak and Kattegat historically passed through the northern North Sea and Norwegian Sea on their way to this region (12, 15) and would potentially encounter these prey during the migration and while foraging for prey. These biomass estimates are based on stock assessments of the various stocks (29).

We also used scientific research vessel surveys to estimate prey abundances more locally in the Skagerrak-Kattegat and where bluefin tuna were observed in 2015 and 2016. Hydro-acoustic and bottom trawl surveys are conducted annually in the region as part of population status monitoring in the region for fisheries management purposes (43–46). The surveys are conducted in February-March (demersal survey in Kattegat-Belt Sea), late June-early July (hydro-acoustic pelagic survey in Skagerrak-Kattegat), and August-September (demersal survey in Skagerrak-Kattegat). The three surveys when considered in aggregate provide information about the relative abundance of potential prey (herring, sprat, mackerel) among years. The demersal survey in August-September is conducted when bluefin tuna were present in our area and we present its results in the main article; survey estimates at other times of year are presented as Supplementary Information.

The main characteristics of the surveys (depth sampled, geographic location, year and seasonal coverage) are summarized in Supplementary Table S1. The notable feature for all the surveys is that sampling methods and gear within each survey are the same throughout the time periods shown here (43–46). As seen in the Table, only the acoustic survey is directly designed to estimate abundance and biomass of pelagic fish species (e. g., herring, sprat); this survey is used as input to ICES stock assessments for herring in the western Baltic Sea and in the North Sea (43). The other two surveys are designed to capture demersal fish species as part of the International Bottom Trawl Survey (IBTS) (47) and Baltic International Trawl Survey (BITS) (44). However these surveys regularly capture pelagic fish species, including herring and sprat, and these data can indicate relative trends and fluctuations in biomass, even though they may not necessarily represent true abundances due to lower catchability for pelagic fishes which are distributed higher in the water column than the demersal sampling gear. For the acoustic survey, we use the total abundances of all size groups estimated on the survey in specific strata of the survey (i. e., Kattegat, and waters along the Swedish west coast in the northeastern part of the Skagerrak (45)). For the demersal surveys, we calculated annual geometric means of catch-per-unit-effort (CPUE) using biomass/trawl hour as a relative biomass metric. Full details of the survey methods and sampling gear are available in literature (43–46, 48).

Estimation of sea surface temperature:

Bluefin tuna occupy mainly surface waters (i. e., above the seasonal thermocline) when feeding on continental shelves in summer as in the region of our study. This habitat is also the depth layer predominantly occupied by their main prey (e. g., herring, sprat, and mackerel) in the region. We assumed that sea surface temperature (SST) as estimated by satellite imagery is an approximate indicator of the temperatures available for and experienced by bluefin tuna while foraging in the region.

We calculated the average SST for the region for the months of August, September and October for the time period 1870-2016 using a large international database of in situ and satellite-derived observations(49) available online (http://wps-web1.ceda.ac.uk/ui/home) at 1 degree monthly resolution. This time series allowed us to evaluate whether 2015 and 2016 were exceptionally warm summers relative to historical variability and trends. We calculated mean temperatures for both the Skagerrak-Kattegat (8^o – 13^o E; 55^o – 59^o N) and a larger area of the northeast Atlantic Ocean (20^o W – 13^o E; 50^o – 66^o N) through which bluefin tuna migrate when entering the

Norwegian-North Sea-Skagerrak-Kattegat. We evaluated whether regime shifts in temperature occurred using the STARS algorithm (50); settings used for testing were Huber parameter = 1 and series length = 10. Higher resolution (0.05 degree daily) satellite-based estimates of SST (51) in the Skagerrak and Kattegat region were averaged temporally over the main period where tuna were observed (7th – 21st September 2016) and used to characterize the thermal environment in which the fish were observed.

Acknowledgments: We thank Jeppe Olesen for GIS and mapping expertise and members of the public without whom this investigation could not have been possible. The work was partly supported by the Nordic Council of Ministers (project no. 141-2016-Tuna; NordTun) and has been conducted using MyOcean Products.

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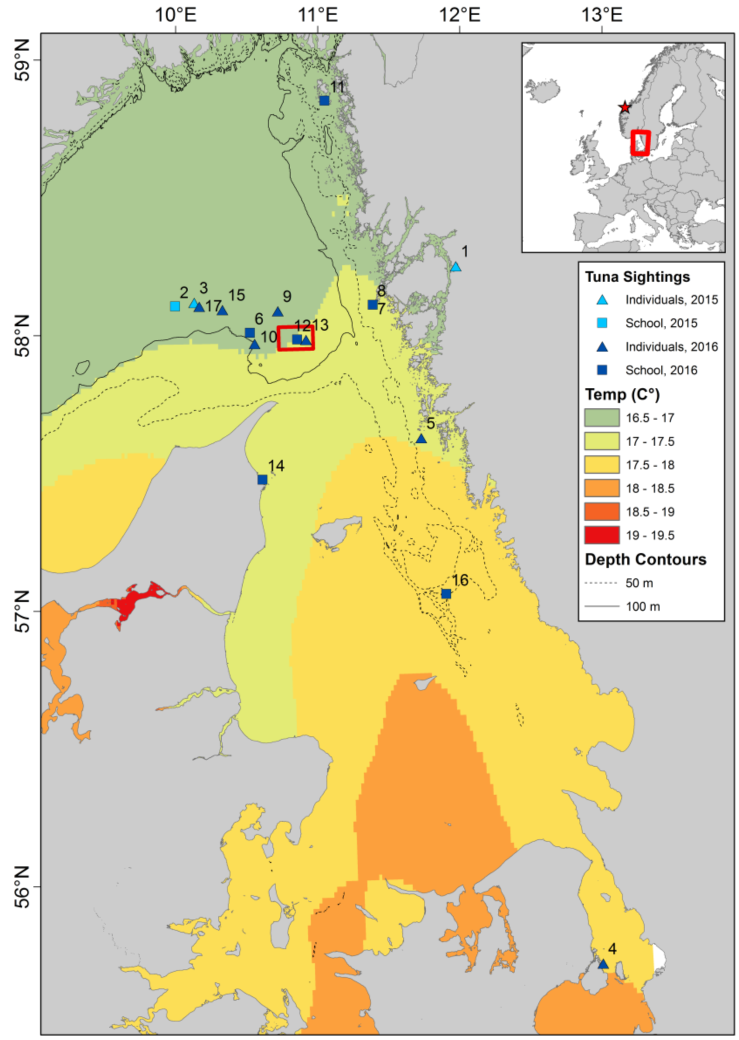
Figure legends (figures are located after legends):

Figure 1. Locations where individual or schools of bluefin tuna were observed in Skagerrak-Kattegat-Øresund in 2015 and 2016. Numbers beside observations correspond to records in Table S1. Colour contours: averaged sea surface temperature as derived from satellite imagery (51) during Sept. 7-21, 2016. Black contour lines: bottom topography. Red box on main map shows where one of the authors (HSL) saw hundreds of bluefin tuna in schools during several days centred on Sept. 22, 2016. Red star on inset map: location where 190 bluefin tuna were captured on Sept. 17, 2016 in one haul by a Norwegian commercial fishing boat (21).

Figure 2. Photographic documentation of presence and jumping behaviour of bluefin tuna in the Skagerrak and Kattegat in a historical period (1947 (23)) and in 2016 (four lower photographs). The photographs 3-6 correspond to observation numbers 8, 11, 6 and 11 respectively in Table S2. The historical photographs illustrate the similarity of historical bluefin tuna size, shape and behaviour with that observed in 2016. Additional photographs and links to web-based video

clips on social media are available in Supplementary Figure S3 and Table S3. All images are reproduced with permission from photographers.

Figure 3. Indicators of potential prey biomass and temperature conditions in the Skagerrak-Kattegat and neighboring regions. A: interannual variability in total stock biomass of key prey species (and their sum) for bluefin tuna in northern European continental shelf regions. The stocks are autumn-spawning herring in the North Sea, spring-spawning herring in the Norwegian-Barents Sea, and mackerel in the northeast Atlantic (52). B: mean ln CPUE (ln kg/hour + 0.001; $\pm$ 2 x standard error) for herring, sprat, mackerel and anchovy in the Skagerrak-Kattegat during August-September research vessel surveys. C: inter-annual variability in late summer-autumn (mean of August, September and October) sea surface temperature in the Skagerrak-Kattegat and a larger area of the northeast Atlantic (20^{o} W – 13^{o} E; 50^{o} – 66^{o} N) for 1870-2016 (black solid line with dots and black dashed line with squares) and regime-specific mean temperatures (red: Skagerrak-Kattegat; blue: northeast Atlantic) for different statistically significant regimes (50). Data source: Hadley Climate Research Unit, UK (49)).



564

565 Figure 1.

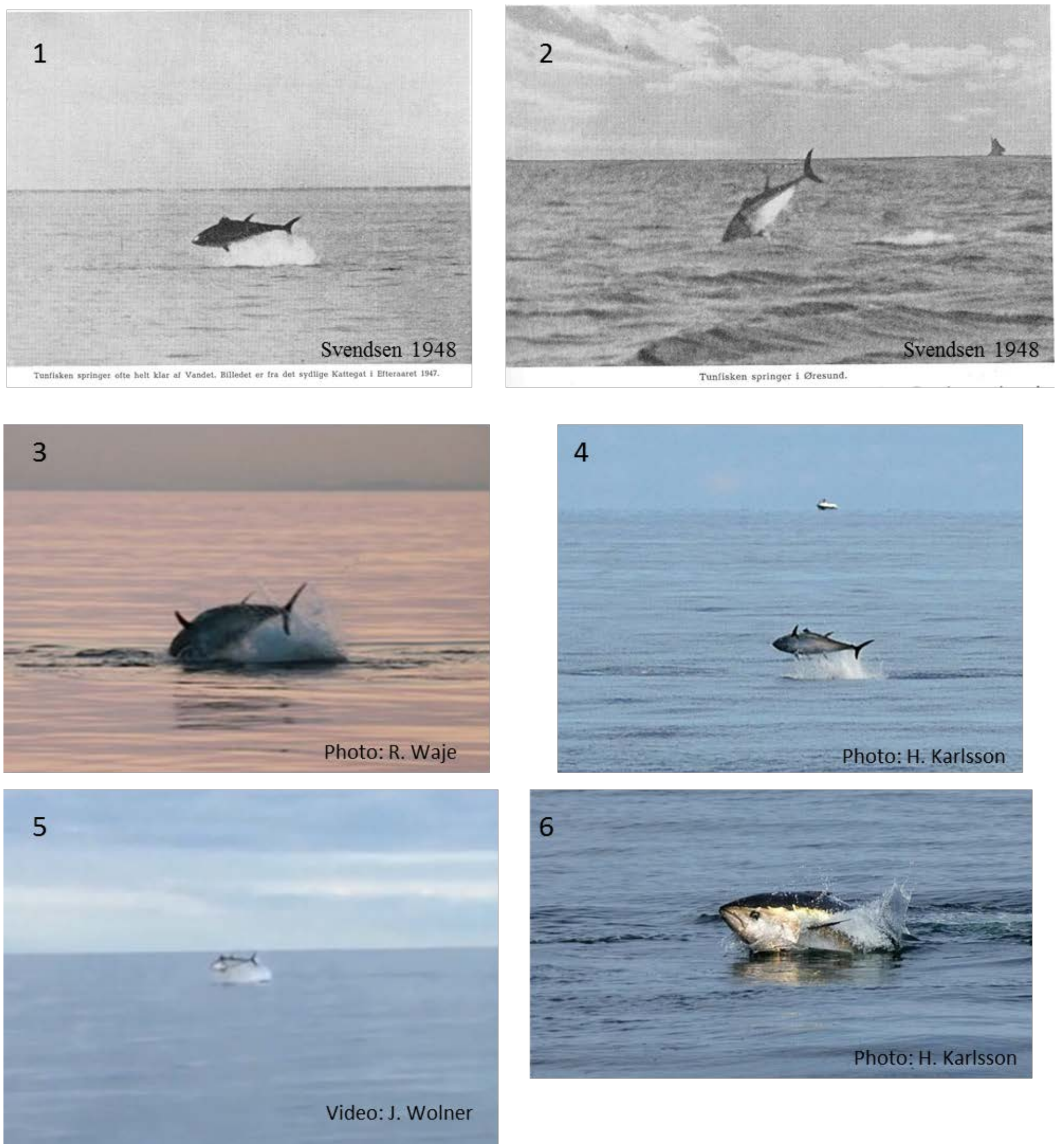

1
Svendsen 1948
Tunfisken springer ofte helt klar af Vandet. Billedet er fra det sydlige Kattegat i Efteraaret 1947.
2
Svendsen 1948
Tunfisken springer i Øresund.
3
Photo: R. Waje
4
Photo: H. Karlsson
5
Video: J. Wolner
6
Photo: H. Karlsson

Figure 2.

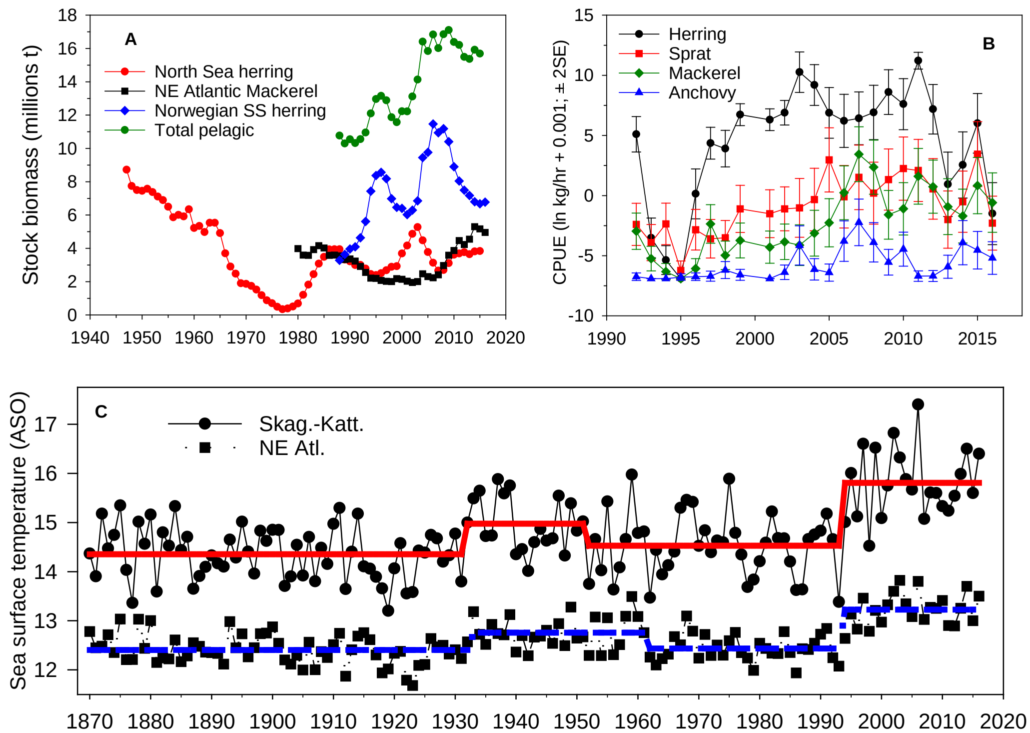

A
Stock biomass (millions t)
North Sea herring
NE Atlantic Mackerel
Norwegian SS herring
Total pelagic
B
CPUE (ln kg/hr + 0.001; ± 2SE)
Herring
Sprat
Mackerel
Anchovy
C
Sea surface temperature (ASO)
Skag.-Katt.
NE Atl.

Figure 3.

Supplementary Materials:

Supplementary Figures:

Figure S1. ICES fishery stock management areas.

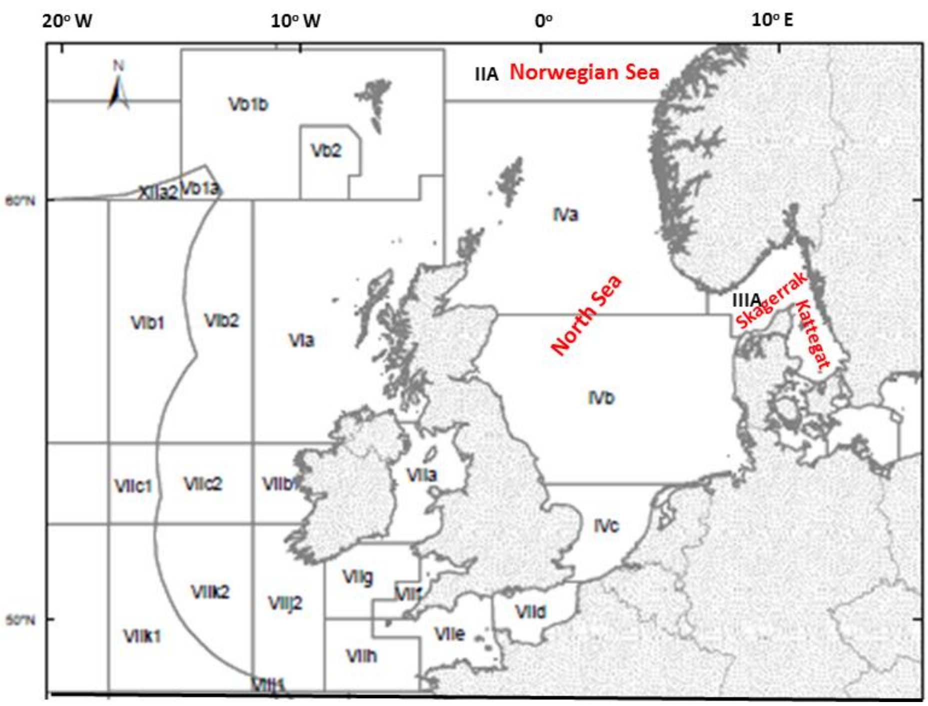


Figure S2. Reported catches of bluefin tuna in ICES areas II, III and IV corresponding approximately to respectively the Norwegian Sea, North Sea, and Skagerrak-Kattegat-Øresund (see Figure S1 for map of ICES stock management areas). Catch data officially reported to ICES from 1903-2014 are from ICES databases available online (www.ices.dk). Additional catch data from before 1927 were compiled from historical fishery reports, catch records, museum records and other documents as summarized in (24).

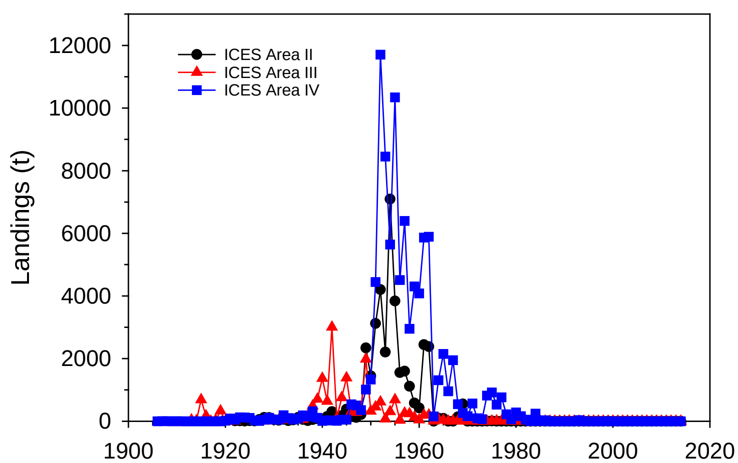
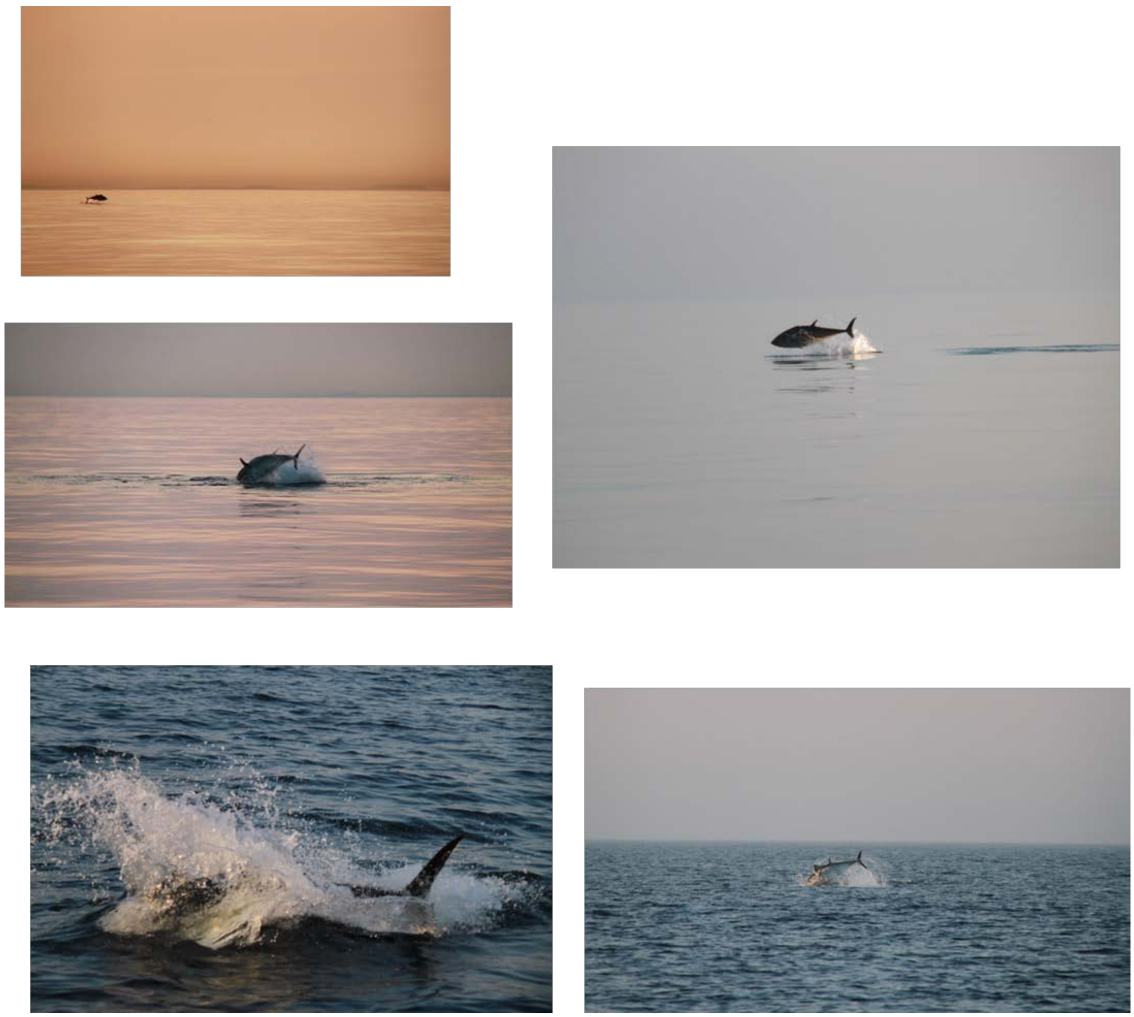


Figure S3. Photographs showing bluefin tuna in the Skagerrak-Kattegat during September 2016. Photos provided with permission by members of the public. Collage 1: R. Waje, collage 2: H. Karlsson, collage 3: J. Wolner.

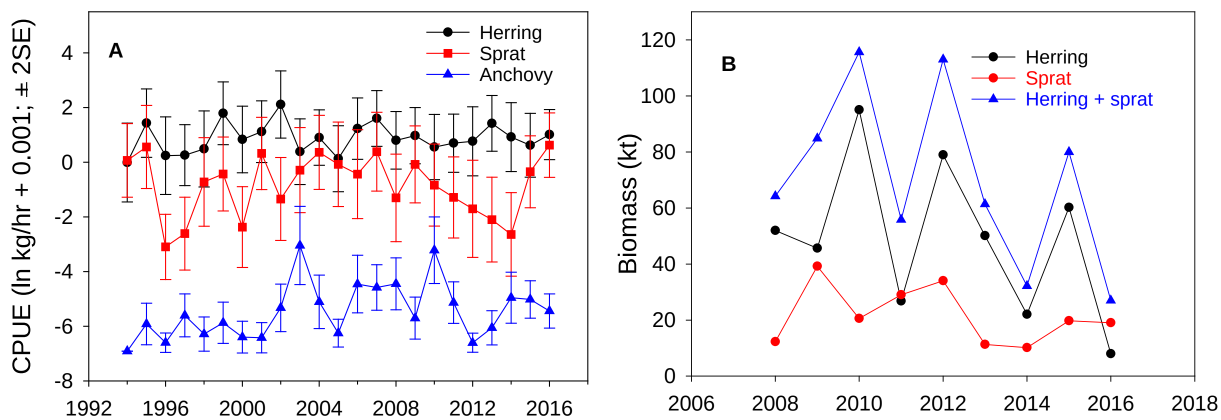


Collage 1 – R. Waje.

Collage 2: H. Karlsson

Collage 3: J. Wolner

Figure S4. A: mean ln CPUE (ln kg/hour + 0.001; ± 2 x standard error) for herring, sprat and anchovy in autumn (late October-early November) research trawl surveys in Kattegat-Øresund-Belt Sea (north of 55 N.) during 1994-2016. B: estimates of prey biomass as derived from research vessel hydro-acoustic surveys in the Skagerrak-Kattegat-Øresund during 2008-2016 (see Table S1 for survey details).



Supplementary Tables:

Table S1. Overview of research vessel surveys which provided estimates of biomass of potential prey for bluefin tuna in the Skagerrak-Kattegat-Øresund. The surveys are part of international bottom-trawl and acoustic surveys in the region designed and coordinated internationally by ICES.

Characcteristic	Survey vessel		
	RV Havfisken (Denmark)	RV Dana (Denmark)	RV Argos (Sweden)
Sampling gear	Demersal trawl	Hydro-acoustics with pelagic and demersal calibration trawls	Demersal trawl
Year coverage	1994-2016 (October-November)	2008-2016	1992-2016 (August-September)
Location	Kattegat, Øresund, Belt Sea north of 55 N.	Skagerrak, Kattegat	Skagerrak, Kattegat
Target species	Demersal fish community	Herring and sprat	Demersal fish community

Table S2. Observational data for sightings of bluefin tuna individuals and schools in the Skagerrak, Kattegat and Øresund during 2015 and 2016. The data were recorded by members of the public ("citizen scientists"). The observation record numbers correspond to the sightings displayed visually in the map in Figure 1 of the main manuscript. Observers' identities are known to the authors.

Obs. ID no.	Date	Latitude	Longitude	Approx. Number of individuals	School or Individuals?
1	Aug. 7, 2015	58.21947	11.90087	1	Individuals
2	Sept. 10, 2015	58.103	9.967	several schools, with individuals jumping. Probably ca. 1000 tuna in total.	School
3	Sept. 21, 2015	58.0994	10.1363	2	Individuals
4	Aug. 12, 2016	55.66719	12.65734	1	Individuals
5	Aug. 21, 2016	57.60167	11.61889	1	Individuals
6	Sept. 13, 2016	5800264	1047578	> 100	School
7	Sept. 15, 2016	58.09183	11.32073	"enormous school"	School
8	Sept. 16, 2016	58.09183	11.32073	ca. 100	School
9	Sept. 19, 2016	58.078	10.67	1	Individuals
10	Sept. 21, 2016	57.96167	10.50667	1	Individuals
11	Sept. 21, 2016	58.83729	11.03239	a whole school	School
12	Sept. 22, 2016	57.97375	10.79687	Some fishermen saw 100s in	School

				schools of different sizes. Other fisherman "saw several jumping tuna, lots of large splashes and individual tunas under boat seen on sonar" (Danish: "Så adskillige springende tun, rigtig mange store plask og enkelte fisk under båden på loddet."). Others seen in previous 14 days.	
13	Sept. 24, 2016	57.97167	10.85833	1	Individuals
14	Sept. 30, 2016	57.469	10.539	Small school (6-8 individual fish)	School
15	Oct. 13, 2016	58.087	10.29167	1	Individuals
16	Oct. 17, 2016	57.033	11.7447	ca. 5-10	School
17	Oct. 20, 2016	58.1	10.13333	1	Individuals

Table S3. Examples of videos on social media of bluefin tuna *Thunnus thynnus* swimming and jumping at surface in the Skagerrak-Kattegat and off Norway during 2015 and 2016. Also indicated is the number of views of each videoclip. The total number of views was 270,291 as of July 12, 2017.

Link	Location	Date recorded or uploaded	Filmmaker	Comments and notes	Views as of July 12, 2017
https://www.youtube.com/watch?v=IKOF843Ew74	Skagerrak	Sept. 10, 2015 (recorded) Sept. 11, 2015 (uploaded)	Thomas Kolmorgen; Fiskeavisen.dk		23,346
https://www.youtube.com/watch?v=Rd9mRhHTpt0	Swedish west coast, near Måskeår	Sept. 15 (recorded), 2016	Micael Karlsson		40,961
https://www.youtube.com/watch?v=eXGZ4nUhk6w	Ona, Møre, Norway	Sept. 16-17, 2016 (recorded) Oct. 11, 2016 (uploaded)	Magnus Tangen	Short documentary (7:22) of commercial fishing on Norwegian	85,995

				vessel Hillersøy, which captured 190 tunas in one haul.	
https://youtu.be/ESL0vS_NZRk	Skagerrak	Sept. 18, 2016 (recorded) Sept. 21, 2016 (uploaded)	Uffe Nielsen	Exact location not specified. Can see tuna in distance.	115,520
https://youtu.be/GSmDHQyDud8	West coast of Sweden	Uploaded Sept. 17, 2016	Bo Svensson	Very clear and sharp video; calm water, easy to see tuna	4,469

Author Contributions: BRM designed research, compiled data and wrote the manuscript; all authors contributed to the design of the study and edited drafts of the manuscript. KA, MCh assisted with data collection in Denmark and MCa assisted with data collection in Sweden. CS and HSL assisted with data collection from recreational and commercial fishers. MRP produced satellite imagery temperature products.