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Distribution and thermal niche of the common skate species complex in the North-East Atlantic

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Running page header: Common skate distribution and thermal niche

ABSTRACT: Temperature is one of the most significant variables affecting the geographic distribution and physiology of elasmobranchs. Differing thermal gradients across a species' range can lead to adaptive divergence and differing developmental times, an important consideration for recruitment rates of exploited species. The critically endangered common skate (formerly *Dipturus batis*) has been divided into two species, the flapper skate (*D. intermedius*) and blue skate (*D. batis*), both of which have undergone dramatic population declines. Here we examine the environmental thermal and geographic distribution of these species, using observations from scientific trawling surveys and recreational angling around the British Isles. As similar sized specimens of the two species can be confused, we validated species identity using molecular genetic techniques. Both species had more extensive geographic ranges than previously reported and different spatial patterns of abundance. The distribution of the blue skate appears to reflect its partiality to thermally less variable and warmer waters, while flapper skate were found in more variable and notably colder areas. The thermal range and current geographic distribution of these species indicate future projected climate change could have a differential impact on distribution of flapper and blue skate in the North-East Atlantic.

Key words: Distribution · thermal niche · common skate species complex · *Dipturus* · flapper skate · blue skate · molecular markers

1. INTRODUCTION

Temperature is a fundamental environmental variable affecting the distribution and life-history of marine organisms (Wallman & Bennett 2006). It is a key determinant in the physiological performance of poikilotherms, and some species have thermoregulatory behaviors that drive habitat choice (Vaudo & Heithaus 2013). Temperature regulates feeding, growth, survival and development in fish (Pistevos et al. 2017), and is an important factor underlying the distribution and depth preferences of fish stocks (Perry et al. 2005, Dulvy et al. 2008, Rutterford et al. 2015). Temperature is known to affect the metabolism, development, growth, movement patterns and reproduction of elasmobranchs (Sinclair et al. 2016) and their overall life-history (Schlaff et al. 2014). Ambient temperature is particularly important to oviparous species because of the inability of developing embryos to utilize or avoid changes in the surrounding environment by engaging in thermotaxic behavior (Di Santo 2015). Embryos exposed to differing temperatures within the egg case have plastic growth rates that result in variable developmental durations (Pretorius & Griffiths 2013) across their distribution range.

Knowledge of the geographic range and habitat preferences of fish is fundamental for effective management, which can facilitate measures to limit the impact of anthropogenic threats, such as the establishment of marine protected areas (MPAs) (Tserpes et al. 2013). The spatial distribution and migration patterns of many elasmobranchs in the waters of the British Isles has only recently begun to be revealed with advances in electronic tagging (Hunter et al. 2005, Saunders et al. 2011, Neat et al. 2014, Doherty et al. 2017a,b, Biais, et al. 2017). Efforts to compile survey data have also been valuable for clarifying fish distributions (Heeson et al. 2015) in the Celtic Sea, North Sea, and Baltic Sea. Thermal ranges, however, remain difficult to assess and interpret because many elasmobranch populations are in decline due to overfishing, with some species already extirpated from areas within their former geographic range (Brander 1981, Ellis et al. 2005, Hunter et al. 2005). The situation is further exacerbated by the lack of species-specific landing data from commercial fisheries (Stevens et al. 2000), which can mask the extent of decline and collapse.

The common skate (formerly *Dipturus batis*) was once frequently encountered throughout European waters but has undergone extreme population declines and range contractions due to fishing practices over the last century (Walker & Hislop 1998). As a result of this decline the species was classified as critically endangered by the IUCN in 2006. Soon after this it became apparent that it was actually two species that could be differentiated on genetic and morphological characters (Griffiths et al. 2010, Iglesias et al. 2010). The most recent revision of their nomenclature (Last et al. 2016) defined the larger-bodied flapper skate as *Dipturus intermedius* (formerly *D. intermedia*) and the smaller-bodied blue skate as *Dipturus batis* (formerly *D. flossada*). The flapper skate reaches lengths over 2.5 m and attains sexual maturity at ~19 years of age, while the smaller blue skate reaches lengths of ~1.4 m and sexual maturity at ~11 years of age (Iglesias et al. 2010). The species complex is found off the Scottish west coast, the Celtic Sea, Rockall Bank, Iceland, and rarely encountered in the North Sea and Irish Sea (Dulvy et al. 2006), however, the spatial distribution and extent of overlap of the two species is not well resolved. Griffiths et al. (2010) showed some evidence of spatial segregation linked to thermal range, but their analysis was based on sea surface temperature, which does not reflect the true thermal regime experienced by benthic skates that spend most of their time living on or near the seabed. Both species can be found in a variety of habitats and range of depths from the surface and coast to the continental slope and depths up to 500 m (Wearmouth & Sims 2009, Griffiths et al. 2010, Neat et al. 2014, Bendall et al. 2017) and the full geographic range extends to Iceland and Norway in the north and into Bay of Biscay and the Mediterranean in the South.

Using data from trawl surveys, recreational angler catches and modelled bottom temperature, we test the null hypothesis that there is no difference in the spatial distribution and thermal ranges of the two species. We predicted that the spatial distribution of the common skate complex reflects differences in thermal preferences between the two species; with the larger flapper skate inhabiting colder more northerly waters and smaller blue skate warmer more southern and offshore areas (Griffiths et al. 2010). Molecular markers were used to verify specimens and we present data resolving the spatial distribution of flapper and blue skate populations around the British Isles and the offshore Rockall plateau.

2. METHODS

2.1. Sampling

Tissue samples from 915 specimens of 'common skate' were obtained between 2008-2013 from 8 different regions (Figure 1A) around the British Isles by Marine Scotland Science, the Centre for Environment Fisheries and Aquaculture Science (CEFAS), and from recreational anglers. Samples were obtained from: the Celtic Sea (CS; n=188), northern Scottish and Irish continental shelf (NSHLF; n=56), southern Scottish and Irish continental shelf (SSHLF; n=48), Rockall Bank (ROCK; n=129), western coast of Scotland (SWC; n=427; includes the Loch Sunart to Sound of Jura MPA), Ireland (IRE; n=7), far north of Scotland in Orkney and Shetland (FN; n=58) and a deep-sea area to the North of Shetland (DS; n=2; Table 1). Geographic coordinates, total length, and sex were recorded for all sampled skate, and depth was recorded during Marine Scotland scientific surveys. Length frequency distributions, and size comparisons between males and females of both species captured in each location were examined. Sex ratios, in each species, were examined using a 2-tailed binomial test in R (R Core Team 2020) to determine if the proportions of males and females were equal. The maturation status of each skate was assigned, using estimates of length at 50% maturity (L_{50}) from Iglesias et al. (2010), and numbers of mature and immature individuals were determined for both species.

2.2. Molecular Species Identification

Morphological characteristics (Iglesias et al. 2010), most notably size of mature specimens, eye colour and dorsal patterning, were used to differentiate blue and flapper skate. Molecular markers were required to validate the assignment of 406 individuals considered morphologically ambiguous by collectors from the CS (n=188), SWC (n=141), IRE (n=7), FN (n=58), NSHLF (10) and DS (n=2) surveys. A small tissue sample was removed from the tail or wing and immediately preserved in 95% ethanol or RNAlater® (Thermo Fisher Scientific) before returning fish to the water. Genomic DNA was extracted from ~20 mg of tissue using a modified phenol-chloroform protocol (Sambrook et al. 1989).

Five microsatellites (LERI 21, 33, 34, 44 and 50) from El Nagar et al. (2010), which previously showed clear species delineation (Griffiths et al. 2010, McCutchen 2012), were used to identify species. PCR primers were fluorescently-labelled with PET, NED, HEX and 6-FAM (Applied Biosystems) and fit into a multiplex with a LIZ500 internal size standard. PCRs were performed in an 11 µl reaction that contained 2 µl of 10ng/µl genomic DNA, 3 µl reaction buffer (Bioline), 1 µl forward primer, 1 µl reverse primer, 0.2 µl BIOTAQ DNA Polymerase (Bioline) and 3.8 µl H_2O on a T-Gradient Cycler (Biometra). Thermocycling conditions included: initial denaturation of 3 min at 94°C; 30 cycles of denaturation at 94°C for 30s;

annealing at 53°C for 30s; extension at 72°C for 30s; a final extension step of 72°C for 10 min. PCR products were separated on an Applied Biosystems 3730 DNA Analyzer at the Tayside Centre for Genomic Analysis (University of Dundee, Dundee, Scotland). Genotypes were called manually using GeneMarker Version 2.2.0.

Species membership was assigned using STRUCTURE v2.3.4 (Pritchard et al. 2000), which employs a Bayesian approach to identify the most probable number of clusters produced from the data (*K*). Ten replicates with 1,000,000 MCMC iterations and a 200,000 burn-in were used, and the number of clusters set between 1 and 6 to ensure other species were not included. STRUCTURE Harvester v0.6.93 (Earl & vonHoldt 2012) was used to examine the statistically best supported value of *K*, and the results summarized in CLUMPAK (Kopelman et al. 2015). Bayesian clustering indicated that the optimal value of K was 2 and assigned species membership for 406 ambiguously identified individuals (supplementary Figure S1), of which 179 were flapper skate and 227 blue skate.

2.3. Environmental data and species distribution

Data from the ICES hydrographic CTD database were used in a linear regression model (in combination with Kriging) to generate a surface of average monthly bottom temperature across the study area. Interpolation assigned a temperature (at a spatial resolution of 1 ICES rectangle of 0.5 degree X 0.5 degree) for each latitude and longitude position where a skate was sampled. For each sampled location values of minimum and maximum temperature were extracted for each month skate were sampled. Temperature and depth data were tested for normal distributions using a Shapiro-Wilk normality test, visualized in R (R Core Team 2020); however, the data were not normally distributed, and transformation failed to achieve normality. A non-parametric Mann-Whitney U test was used to determine if the observed differences between the means of minimum temperature, maximum temperature, temperature range and depth were statistically significant ($P<0.05$) when comparing the two species. To avoid issues of pseudo-replication, only a single skate, or one skate of each species, per haul or sampling event was included in statistical analyses, which consisted of 100 flapper skate and 73 blue skate in temperature analyses. Statistical tests were carried out in R (R Core Team 2020), and boxplots were produced in R (R Core Team 2020) using the package ggplot2 (Wickham 2016).The distribution of skates sampled in this study was mapped using the coordinates of 915 sampling locations. Scientific bottom trawls from Marine Scotland Science surveys were used to determine the numbers of each skate species caught per hour. The mid-point of each trawl was calculated and then summarised on a regular hexagonal grid with a cell width of 20 km by taking the mean value across those hauls contributing to each grid cell. This resulted in a mean catch per unit effort value for each grid cell. Derivation of catch rates was completed in R (R Core Team 2020), and the maps were produced using QGIS version 3.4.10 (2019).

3. RESULTS

3.1. Length, Maturity and Sex Composition

Flapper skate total lengths ranged from 21 to 230 cm, but 96% of sampled flapper skates were below L_{50} and only 4% were reproductively mature (>185.5 cm). The most abundant size group was the 41-60 cm length class, comprising 46% of flapper skate, followed by the 61-80 cm length class at 21%. The largest flapper skate were sampled in the Loch Sunart to Sound of Jura MPA (west coast of Scotland), Ireland and the Celtic Sea, while the remaining populations were mostly composed of small juveniles with a few larger individuals present (Figure S2A in supplementary information). The flapper skate sex ratio was not significantly different (P=0.415) with 234 females and 253 males sampled (Table S1).

Blue skate total lengths ranged from 21 to 148 cm, and over 40% were reproductively mature (>~115 cm). Nearly 45% of blue skates were in the 121-140 cm size class, which was followed by 14% in both the 81-100 cm and 101-120 cm length classes. The largest blue skate were sampled in the Celtic Sea (Figure S2B in supplementary information), with approximately 80% above L_{50}; however, only 15% of skate sampled in Rockall were at or above L_{50}. Only one blue skate from the far north of Scotland was at L_{50}, and no mature skate were sampled on the west coast of Scotland. The blue skate sex ratio was unequal (P=0.045) with a higher proportion of females (n=200) than males (n=161; Table S1).

3.2. Spatial Distribution

Sampling locations were mapped for 915 skate sampled in this study, of which 554 were flapper skate and 361 were blue skate. Both species had wider geographic distributions than previously reported (Griffith et al. 2010). Blue skate were found at latitudes ranging between 49.43°N and 60.58°N and longitudes of 2.32°W to 16.31°W and flapper skate were sampled between 49.48°N and 62.08°N latitude and -0.04°W to -9.53°W longitude (Figure 1B). Flapper skate were found from the Celtic Sea to north of Shetland; however, greatest concentrations of flapper skate were found along the western coast and continental shelf of Scotland (Figure 1B and C). Blue skate also had a wide range from the Celtic Sea to north of Orkney with an extensive representation around Rockall and the Celtic Sea (Figure 1B and D).

3.3. Bottom temperature and bathymetry

In this study, flapper skate occur in waters ranging from 4.96°C to 15.50°C, while blue skate were sampled in temperatures between 7.44°C and 13°C (Figure 2). Flapper skate were found in significantly colder minimum temperatures (W=5765; P<0.001; mean=8.41°C) than blue skate (mean=9.07°C; Figure 2A, Table S1) and significantly warmer maximum temperatures (W=1704; P<0.001; flapper skate mean=12.01°C; blue skate mean=11.09°C; Figure 2B, supplementary Table S1). Flapper skate were found in a significantly (W=1599; P<0.001) wider range of temperatures (0.424 to 7.830; mean=3.59) than blue skate (0.458 to 5.365; mean=2.01; Figure 3, Table S1).

Recorded depth ranges were similar for both species with flapper skate sampled from depths ranging between 51-500 m and blue skate sampled from depths of 56-550 m.

4. DISCUSSION

4.1 Spatial distribution

This study represents a comprehensive assessment of the geographic and thermal ranges of the common skate complex. Data collected from scientific trawling surveys and recreational angling indicate that flapper and blue skate have overlapping geographical distributions and are more widespread throughout the British Isles than previously reported (Griffiths et al. 2010). Blue and flapper skate appear to cohabit many of the same geographic areas and are often encountered in the same hauls, apart from the offshore Rockall Bank, where only blue skate were recorded. It is notable that the Rockall Bank is isolated from all other areas by water depths in excess of 1500 m and also has only a tiny proportion of its area that is shallower than 100 m. Strong spatial structuring of the two species was evident in this study, similar to that reported by Griffiths et al. (2010). Blue skate appear to predominate in offshore areas, whereas flapper skate are also found closer inshore. There was, however, no evidence of a strong latitudinal or allopatric separation as previously proposed (Griffiths et al. 2010). Blue skate, thought to be the "southern" species, were recorded as far north as Shetland and along the west coast of Scotland, whilst large sub-adult and reproductively mature adult flapper skate, the "northern" species, were recorded far to the south and in the offshore Celtic Sea. It is important to appreciate that populations of both species have been heavily depleted over the past century or more and that the current distribution may be highly patchy due to local extirpation and small areas of refuge.

Both species appeared to be absent between 50˚N and 54˚N of latitude in the Irish Sea and along the Irish continental shelf. This, however, reflects much less sampling of these areas. Historically, large common skate were an important component of fisheries in the Irish Sea, but catch rates began to decline drastically in the 1950s until they disappeared altogether in the 1970s (Brander 1981). Reported occurrences remain rare in the Irish Sea with individuals occasionally recorded in remote sites (Iglesias et al. 2010). No blue skate were sampled off the west coast of Ireland during this study, but several large adult and sub-adult flapper skate used in this study were sampled in Irish waters and records from recreational catch and release fisheries (Scottish Shark Tagging Program pers. comm.) suggest flapper skate are encountered in the seas off Northern Ireland.

4.2 Bottom temperature and bathymetry

There were significant differences between the mean minimum, maximum and range of temperatures the two species were found at. Although both species occurred in many of the same areas, the results of this study indicate differences in their thermal ranges, most notably with respect to the average minimum and maximum bottom temperatures experienced. In this study, flapper skate were found in cooler and warmer waters than blue skate. This may reflect their preference for thermally and bathymetrically variable inshore habitats that include both the deep, cold sea lochs along the west coast and islands of Scotland (Wearmouth & Sims 2009;

Neat et al. 2014) and close-by shallow coastal areas with highly variable seasonal temperatures. Blue skate, more closely associated with warmer temperatures, were more prevalent in the oceanic areas of Rockall and the Celtic Sea. Although present in the more northerly latitudes they were less abundant. Flapper skate were found in a wider range of temperatures, including the coldest and warmest temperatures recorded in this study, while blue skate appeared to predominate in areas where temperatures are moderated year-round by warm currents, such as the Rockall Bank and Celtic Sea. A major caveat of this type of analysis is that large elasmobranchs are likely to migrate throughout the year, and, therefore, the point of capture may not be representative of their annual thermal experience. However, Neat et al. (2014) showed that a significant proportion of flapper skate in the Loch Sunart to Sound of Jura MPA demonstrated site fidelity for most months of the year. This suggests that the temperatures in our dataset are likely representative of the integrated averages experienced by many individuals within these populations for a substantial fraction of the year.

Temperature can have a substantial effect on the development, survival and metabolic rate of embryonic oviparous elasmobranchs (Pretorius & Griffiths 2013, Di Santo 2015). The incubation period of catshark (*Poroderma pantherinum* and *Haploblepharus pictus*) embryos was shortened by up to 53% and embryos grew up to twice as fast when the temperature of developing eggs was raised by 3°C (Pretorius & Griffiths 2013). The metabolic stability of embryonic little skate (*Leucoraja erinacea*) from two geographic locations declined after reaching the thermal optimum, but the southern population was affected less by increased temperature, suggesting the narrower thermal tolerance of the northern population led to increased metabolic costs at higher temperatures (Di Santo 2015). Although little is known about the embryonic development of flapper or blue skate, fluctuations in temperatures cause an exponential change in the metabolic processes of embryonic elasmobranchs (Hoff 2008).

Development time of thorny skate (*Amblyraja radiata*), a species found at similar latitudes, could vary by as much as 1.5 years between populations differing in mean developmental temperatures (Berestovskii 1994). Developmental time is so sensitive to temperature in Alaska skate (*Bathyraja parmifera*) that an increase of 0.05°C in the mean environmental temperature can result in a 16% (~6 month) decrease in the developmental period (Hoff 2008). Although reduced developmental time in warmer conditions might improve survival probability to hatching, it can cause irregular coloration and patterning, skeletal abnormalities and increased metabolic rate and ventilation, which leads to a decline in overall fitness and significantly increases mortality rates of juvenile sharks (Rosa et al. 2014, Gervais et al. 2015). Early ontogenetic stages, incapable of thermotaxic behavior, will be most susceptible to climatic events (Pimentel et al. 2014).

Rising ocean temperatures associated with climate change are likely to have an effect on the recruitment and physiology of oviparous elasmobranchs and should be an important consideration for future conservation management plans in the North-East Atlantic. Elevated temperatures affecting the metabolic activity and foraging behavior of large marine predators, could have effects on ecosystem stability by altering the composition and distribution of important prey communities (Pistevos et al. 2016). According to the OSPAR commission (2009) and Morris et al. (2018), the North Sea surface temperature has warmed by 1-2°C over the last 25 years, during which time summer periods have become warmer and lasted longer, while winters have become shorter and milder. In the Irish Sea, temperatures are expected to increase by ~1.9°C over the 21st century, with shallow coastal water exhibiting the warmest temperatures, while deep channels remain cooler with less variability in temperature fluctuations and greater stratification between layers (Olbert et al. 2012). The rate of sea surface warming around the British Isles, excepting areas of stratification, has been reported to be up to six times faster than the global average (Dye et al. 2013), with the region recognized as one of 20 global hotspots of marine climate change based on ocean temperature trends (Hobday & Pecl 2014).

An aspect of particular relevance to restoration of endangered species is that when the pejus temperature (the limit of optimal haemolymph oxygenation) of a species is exceeded the associated increased metabolic costs compromise growth, fitness, and so population increase (Neuheimer et al. 2011). This could differentially affect blue skate, which appear to occupy a more restricted temperature range. However, large, mature flapper skates have an apparent preference for cold, deep trenches, which could put them at higher risk of rising temperatures if these important habitats become too warm. Further, although skates are largely associated with the benthic environment, flapper skate are known to actively hunt pelagic prey and utilize the entire depth profile available (Wearmouth & Sims 2009, Neat et al. 2014,), which suggests changes in sea temperatures could impact its foraging behavior.

The thermal scopes observed in this study have implications with respect to projected climate change scenarios. Recent work has identified increases in maximum annual temperatures as drivers of recent population extinctions, unless compensated by species niche (Roman-Palacios & Wiens, 2020). If temperatures increase in the North-East Atlantic the blue skate's association with warmer waters may predict a likely expansion northward and to greater depths. The flapper skate's apparent tolerance of a wider range of temperatures suggests it could pursue a more flexibile strategy requiring less range shift, provided critical components of its ecosystem, such as prey species and nursery areas, are not adversely affected. However, if the temperatures of their critical deep trench habitats increase with climate change, this could put the flapper skate at a greater disadvantage.

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Table 1. Summary of the number of skate from each sampling area for flapper and blue skate after genetic confirmation. Bottom temperatures were averaged over a 12 month period for each sampling location, and average depth was calculated for areas where depth was recorded. Numbers outside brackets are total numbers used in distribution mapping, while numbers in brackets are those with bottom temperature measures for sampling locations. * The Scottish west coast, including the Loch Sunart to Sound of Jura MPA. Data not available, na.

Sampling Area	Temp (C°)	Average Depth (m)	Dates	flapper skate	blue skate	Total
North Scotland (FN)	10.40	168.2	2011-2013	49	9	58
Deep NEA (DS)	5.11	na	2013	2 (1)	0	2 (1)
Ireland (IRE)	11.18	na	2013	7 (1)	0	7 (1)
West Coast* (SWC)	10.43	168.4	2011-2013	384 (324)	43	427 (367)
Rockall (ROCK)	10.65	200.5	2008, 2011-2013	0	129	129
Shelf North (NSHLF)	10.21	185.8	2012-2012	56	0	56
Shelf South (SSHLF)	10.63	151.3	2012-2013	47	1	48
Celtic Sea (CS)	10.48	na	2011	9	179	188
Total	-		2008-2013	554 (487)	361	915 (848)

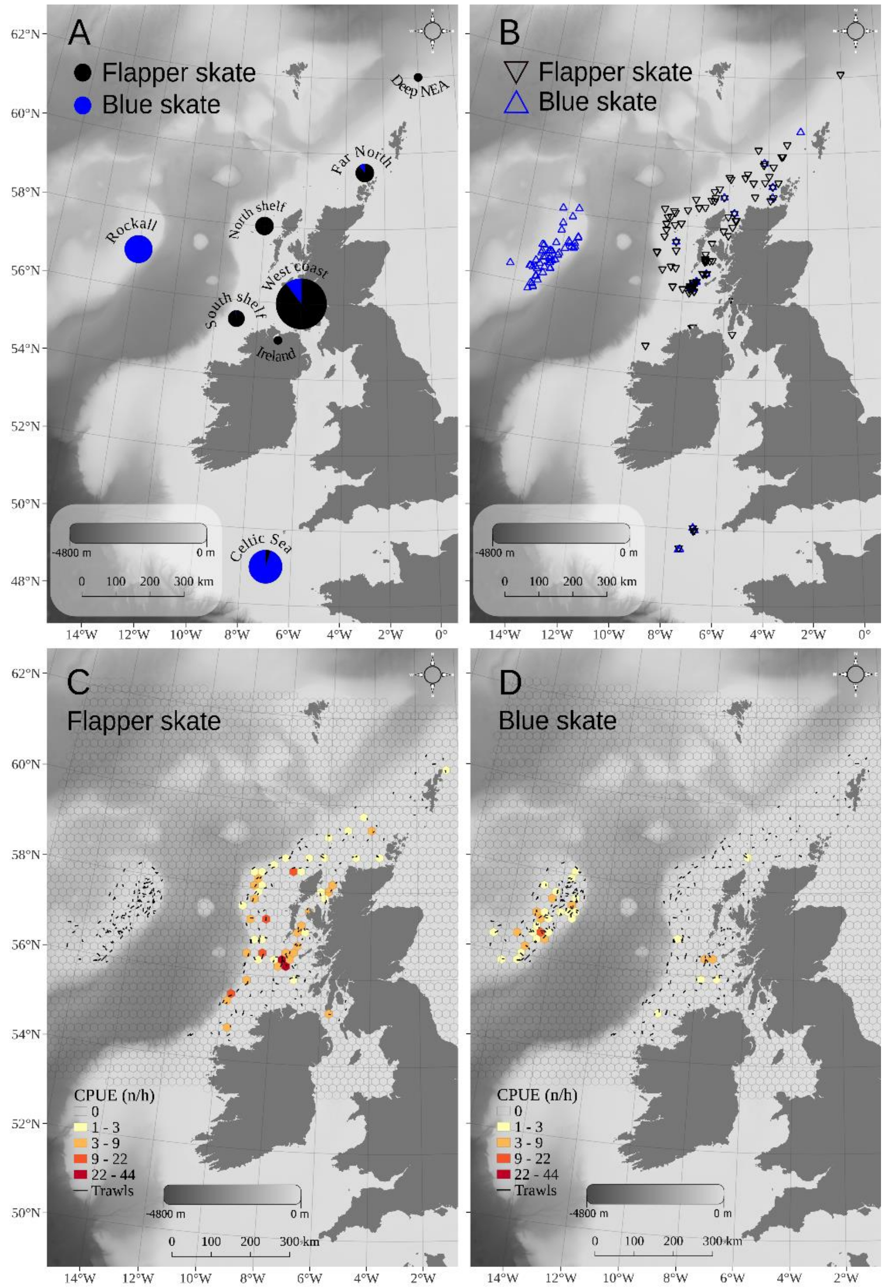


Fig. 1. (A) Map showing the relative proportions of flapper and blue skate sampled in this study. Sampling locations included: the Celtic Sea (n=188), the northern Scottish continental shelf (North Shelf; n=56), the southern Scottish and Irish continental shelf (South Shelf; n=48), the Rockall Bank (n=129), the western coast of Scotland (West Coast; n=427; includes the Loch Sunart to Sound of Jura MPA), Ireland (n=7), far north of Scotland in Orkney and Shetland (Far North; n=58) and a deep sea haul in the North-East Atlantic (Deep NEA; n=2). (B) Plot of capture locations of flapper and blue skate sampled in this study. (C) Map showing the catch per unit effort of flapper skate sampled in Marine Scotland Science surveys (D) Map showing the catch per unit effort of blue skate sampled in Marine Scotland Science surveys.

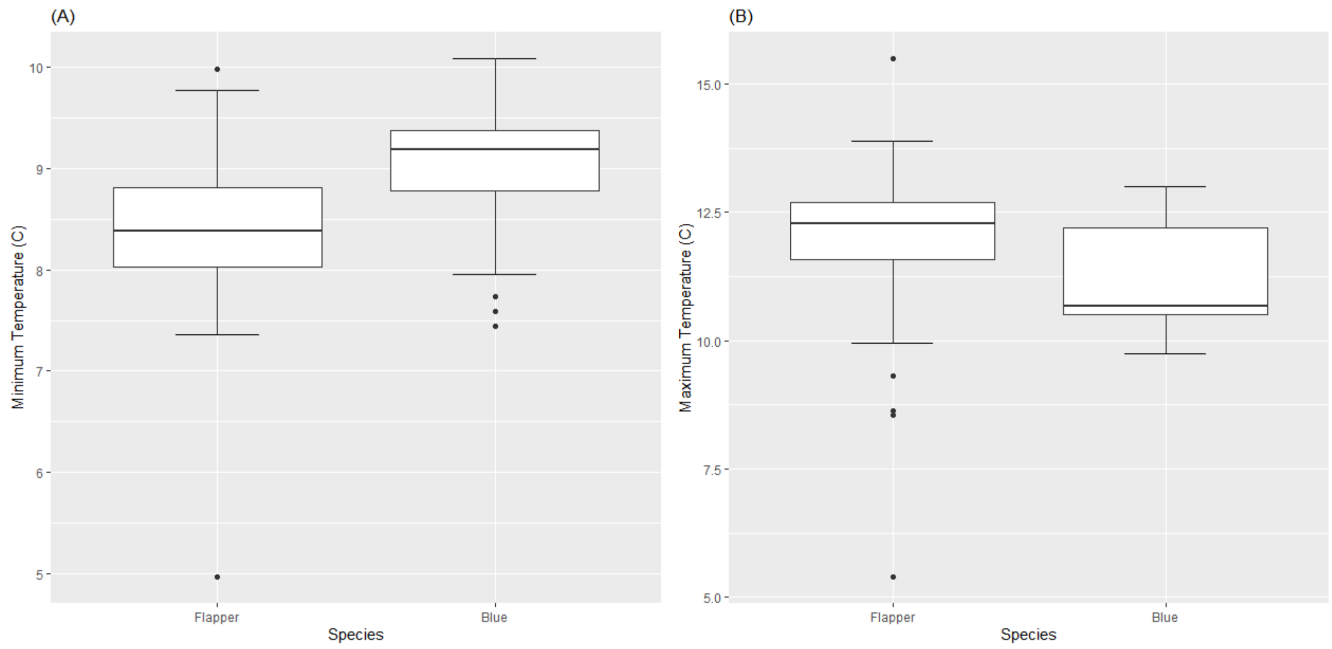


Fig. 2. Boxplots with error bars comparing the mean minimum (A) and maximum (B) temperatures (C°) characterizing areas where flapper skate and blue skate were found in this study. Box-plots include the median (solid line in box) and 25th and 75th percentiles; whiskers are the 10th and 90th percentiles with circles representing outliers.

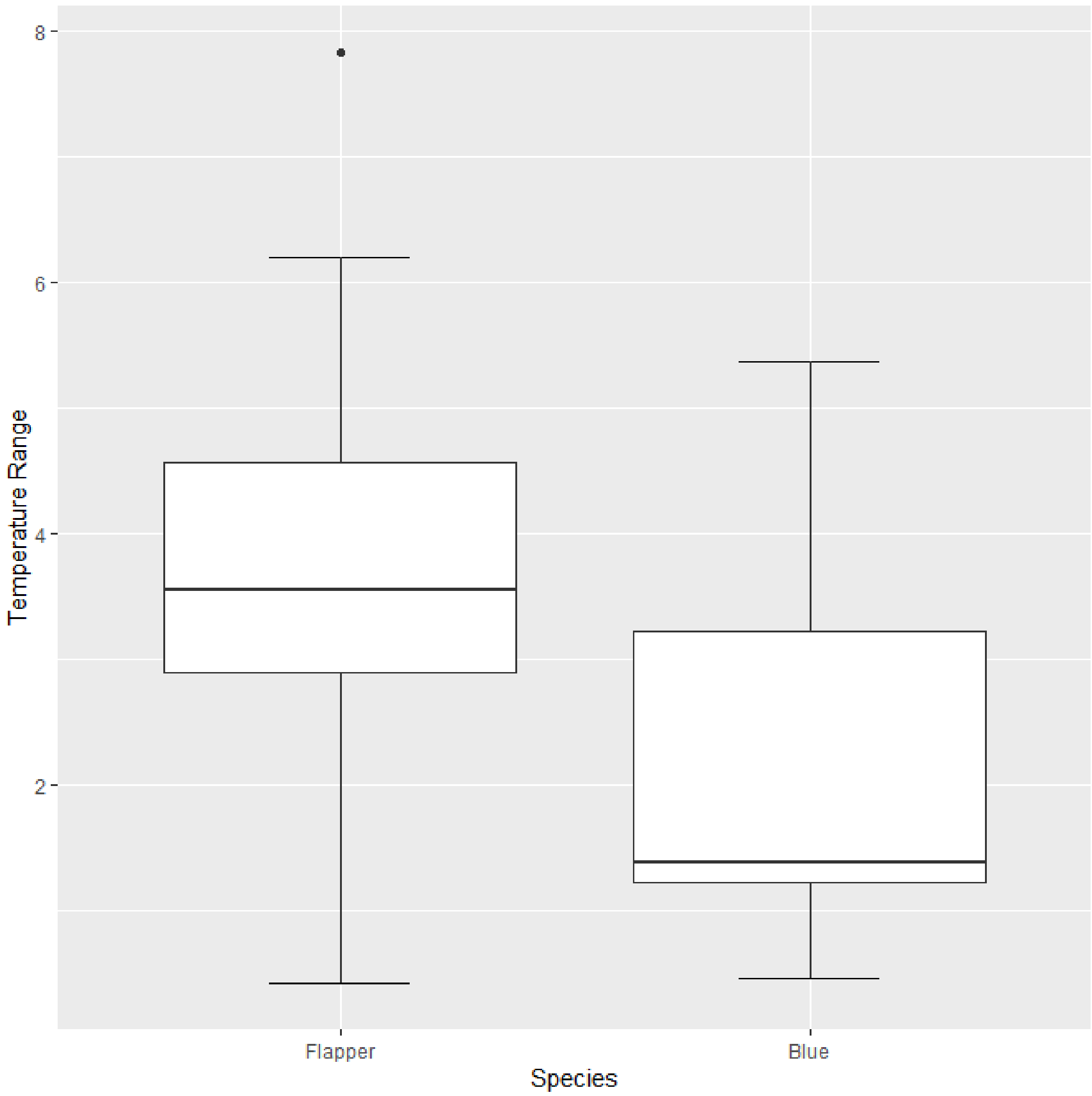
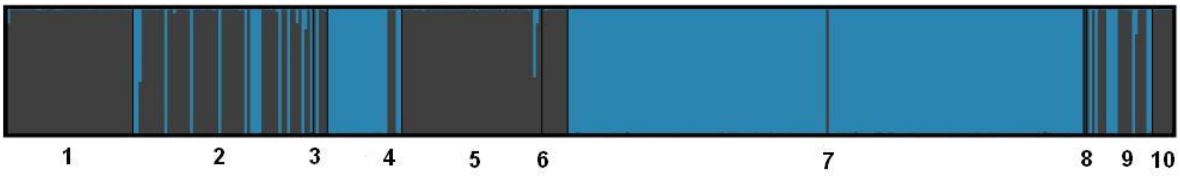
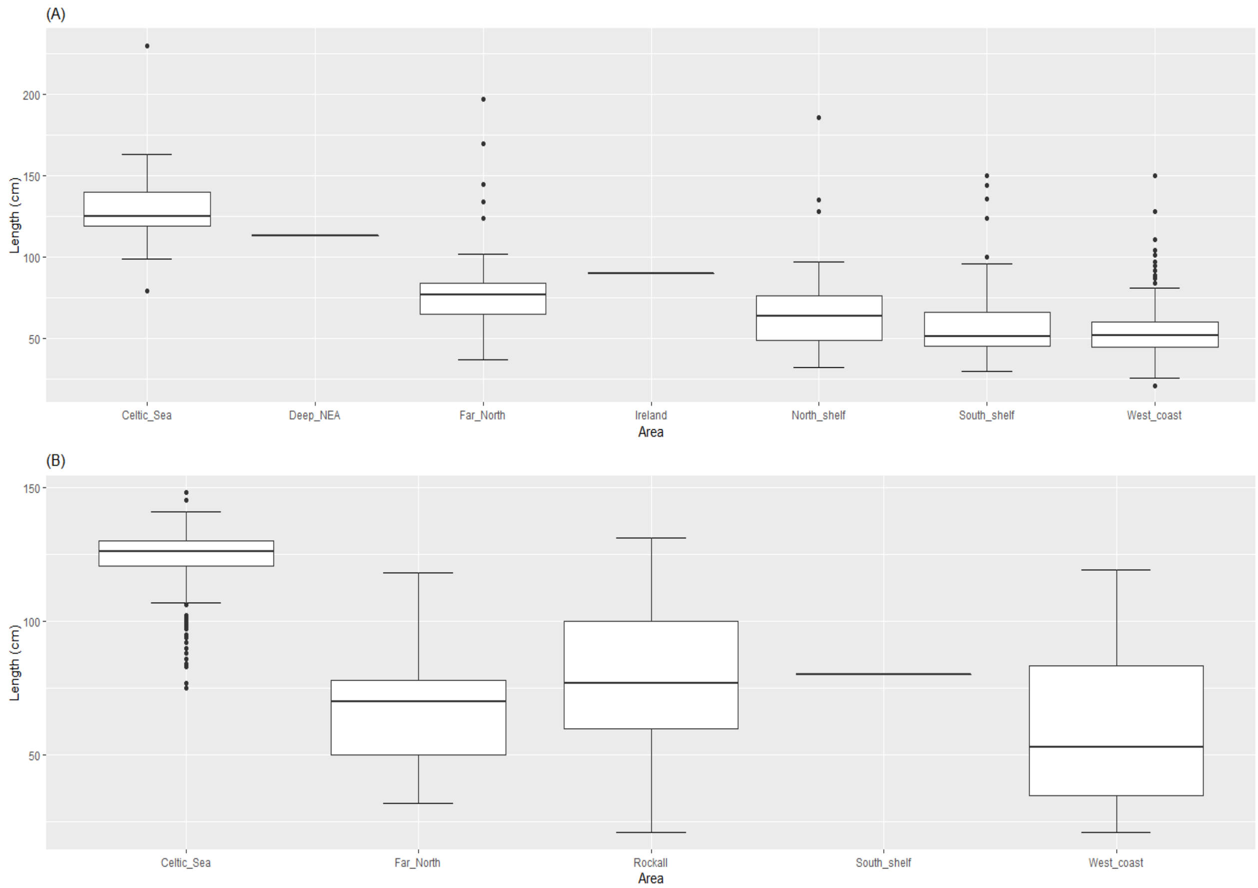


Fig. 3. Temperature ranges of areas where flapper skate and blue skate populations were found in this study. Boxplots with error bars show the mean range of temperatures for areas where each species was found. The box-plot includes the median (solid line in box) and 25th and 75th percentiles; whiskers are the 10th and 90th percentiles with circles representing outliers.

SUPPLEMENT



Supplementary Fig. S1. STRUCTURE outcome for *K*=2, indicating two clusters for species membership from 10 different surveys throughout the Northeast Atlantic. Each individual is represented by a vertical line; flapper skate are shown in gray and blue skate are blue. Numbers correspond to different research surveys in coastal waters of the British Isles. Research surveys included the following locations: north of Scotland (1, 3, 5, 8, 9), west coast or continental shelf of Scotland (2, 4, 5, 9) the Celtic Sea (6, 7) and Ireland (10). Two individuals, from survey 2 and 5, failed to amplify at all 5 microsatellites and were removed prior to any analyses (structure plot shows 404 samples).



Supplementary Fig. S2. Boxplots with error bars comparing the mean total length (in cm) of flapper skate (A) and blue skate (B) in sampling locations where each species was present. Locations include the Celtic Sea, Deep Northeast Atlantic (Deep_NEA), Orkney and Shetland (Far_north), Ireland, Rockall, Northern Scottish continental shelf (North_shelf), Southern Scottish and Irish continental shelf (S_shelf) and the West coast of Scotland (West_coast). Box-plots includes the median (solid line in box) and 25th and 75th percentiles; whiskers are the 10th and 90th percentiles with circles representing outliers.

Supplementary Table S1. Summary of Mann-Whitney U tests performed between species and binomial tests to determine if sex ratios were equal. **Test** gives the variable that was tested, **n** is the sample size, **Stat** is the test statistic used, and the **P-value, confidence intervals** and **mean** for each species (where applicable) is also presented. Mann-Whitney U tests were run on the minimum (Min), maximum (Max) and temperature range (Range), while a 2-tailed binomial test was used to examine sex ratios in flapper skates and blue skates. NA is no data available.

Test	n	Stat	P-value	Confidence interval	Mean (flapper skate)	Mean (blue skate)
Min	173	W=5765	**P<0.001**	(0.51, 0.86)	8.41	9.07
Max	173	W=1704	**P<0.001**	(-1.52, -0.89)	12.01	11.09
Range	173	W=1599	**P<0.001**	(-2.19, -1.42)	3.59	2.01
Flapper sex ratio	487	Exact binomial test	P=0.415	(0.44-0.53)	NA	NA
Blue sex ratio	361	Exact binomial test	P=0.045	(0.50-0.61)	NA	NA