

Supplementary Information for

Three decades of increasing fish biodiversity across the north-east Atlantic and the Arctic Ocean

Cesc Gordó-Vilaseca*, Fabrice Stephenson, Marta Coll, Charles Lavin & Mark John Costello

*Cesc Gordó-Vilaseca is the corresponding author

Email: francesc.g.vilaseca@nord.no

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Supplementary Information Text

Results

SBT model. A linear regression with time, longitude and latitude as the explanatory variables for the changes in SBT from 1993 to 2019 in the main study area explained 20% of the deviance and suggested a rate of warming of 0.03 °C/yr.

Methods

Boosted Regression Trees Environmental variables correlated higher than pearson = 0.9 were eliminated to deal with extreme collinearity (BRT are highly robust to collinearity), which was not met between any variables. Additionally, variables that did not improve the model were also eliminated to keep the model as simple as possible without compromising model quality (**Table S3**) (meaning not improving total explained deviance and individually accounting for < 4 % of deviance explained) To improve the model calibration and reduce computational requirements, we conducted a bootstrapping process: we fitted a model to 75% of the trawls, and predicted each year's species richness distribution with it. Then, we repeated this process 50 times and reported the average of the 50 models per year. Each time, the data used for calibration was a random selection with replacement, of the size of the whole calibration dataset (75% of trawls). Each model was limited to 20,000 trees, and tree complexity was set to 3 to allow for interactions between the explanatory variables. The learning rate was adjusted to 0.01, bag fraction to 0.3, and other parameters were set to their defaults. Model validation was conducted through Pearson correlation with the remaining 25% of the dataset that was not used for model calibration.

Richness was projected annually for each of the 50 models from bootstrap, using each year's environmental layers. We additionally created a "swept_area" raster file using the unique value of 28 km² across the whole area, which maximized the species richness in the BRT partial dependence plots and corresponded to the maximum swept area within the dataset. Annual mean projections were obtained from the 50 projected richness rasters.

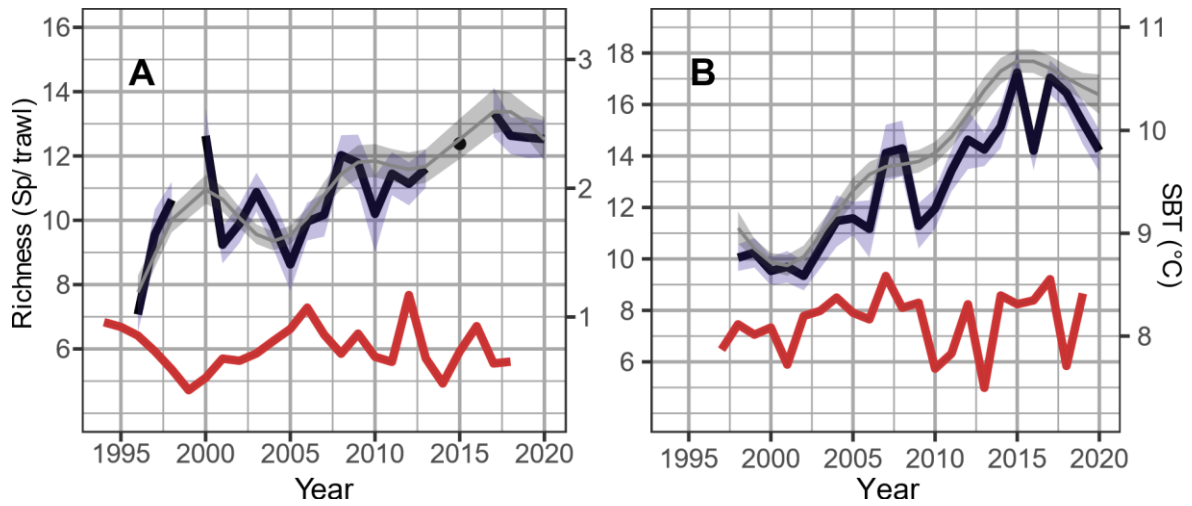


Figure S1. Average species per trawl (alpha diversity) across time in adjacent areas A: Around Svalbard; B: North Sea. Black line represents mean species richness per trawl with 95% CI in blue. Grey smoothed line and light grey 95 %CI represents the marginal effect of Year for constant sampling effort from a GAM model using Year and swept area as an offset (**Table 1**). Red line indicates changes in mean Sea Bottom Temperature across the whole area (correlation with SBT; $p > 0.05$).

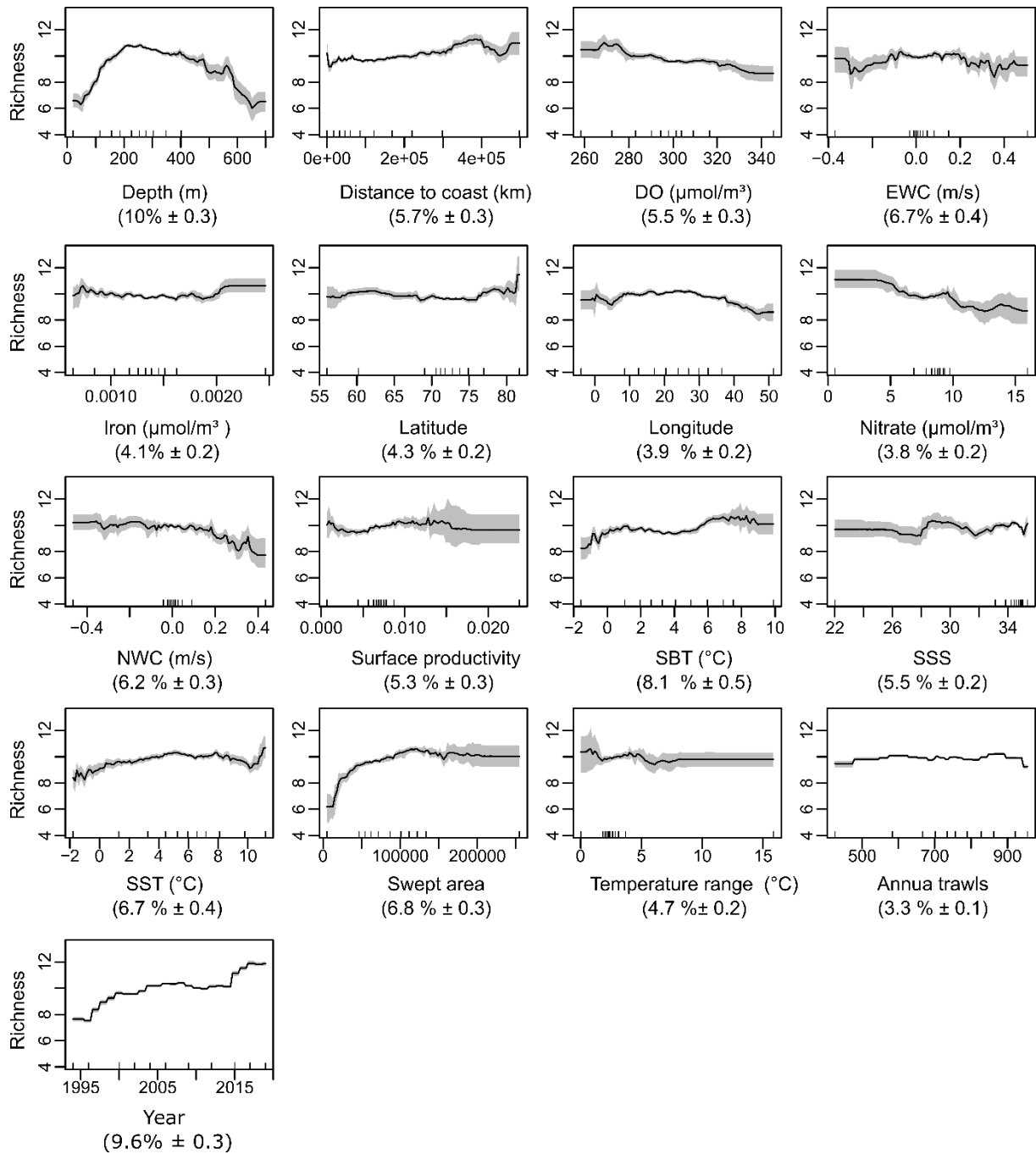


Figure S2. Partial dependence plots of the BRT model from 1994 to 2019. Between parenthesis is the relevance of each variable in the model.

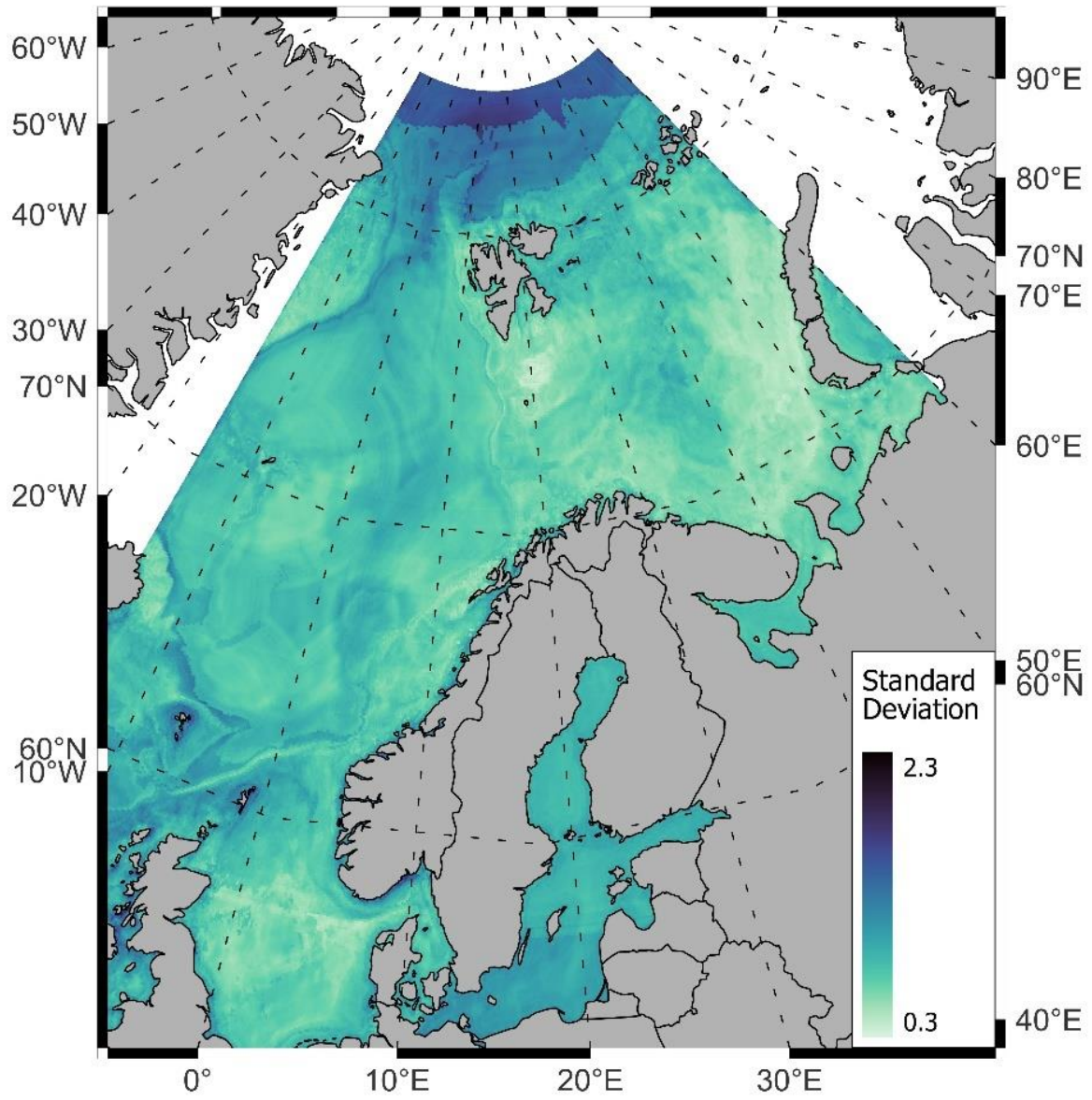


Figure S3. Overall mean standard deviation from BRT annual species richness predictions.

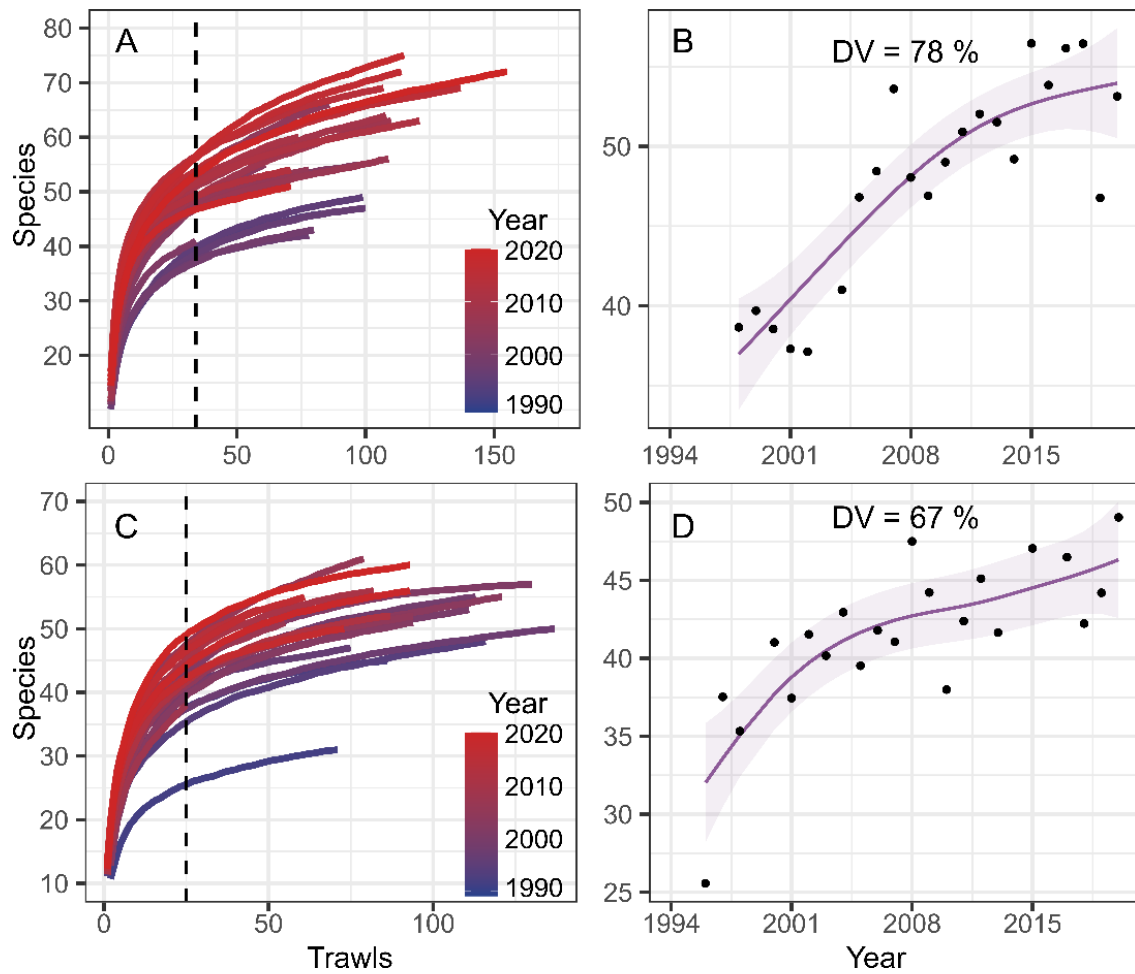


Figure S4. Gamma diversity across time in adjacent areas A: North Sea annual (rarefacted) SACs; B: North Sea species richness at minimum common number of sites ($n = 34$); C: Svalbard annual (rarefacted) SACs; D: Svalbard species richness at minimum common number of sites ($n = 25$).

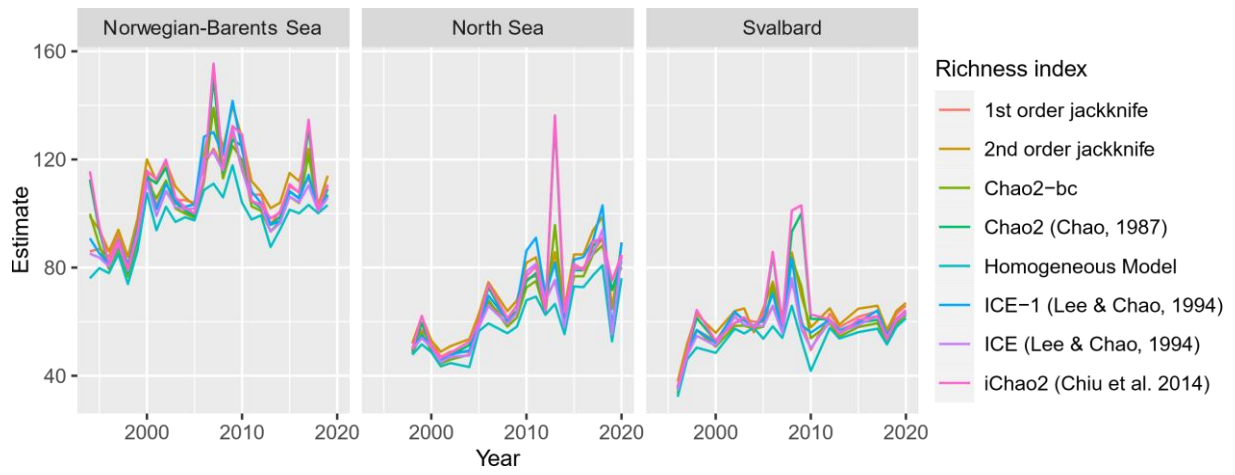


Figure S5. Chao indices change across study areas and years.

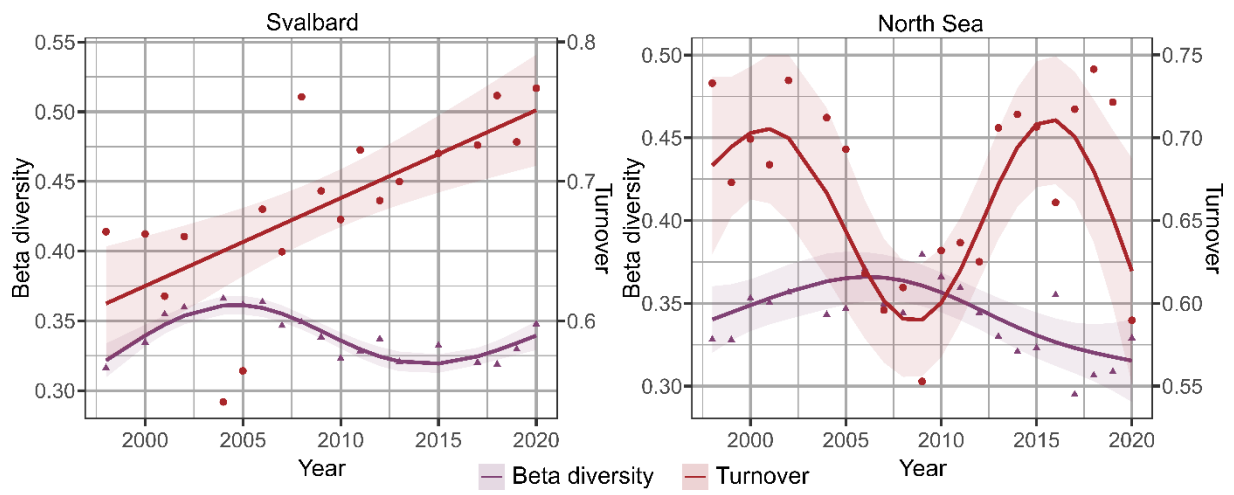
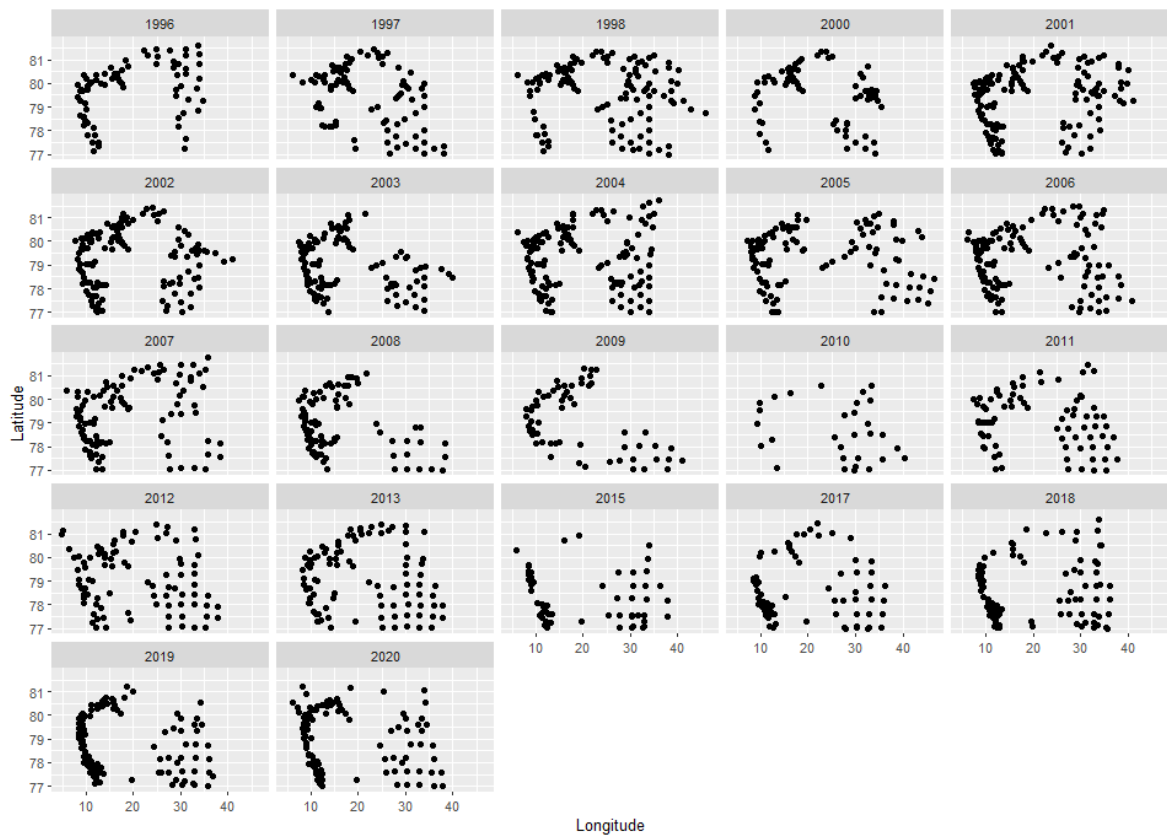
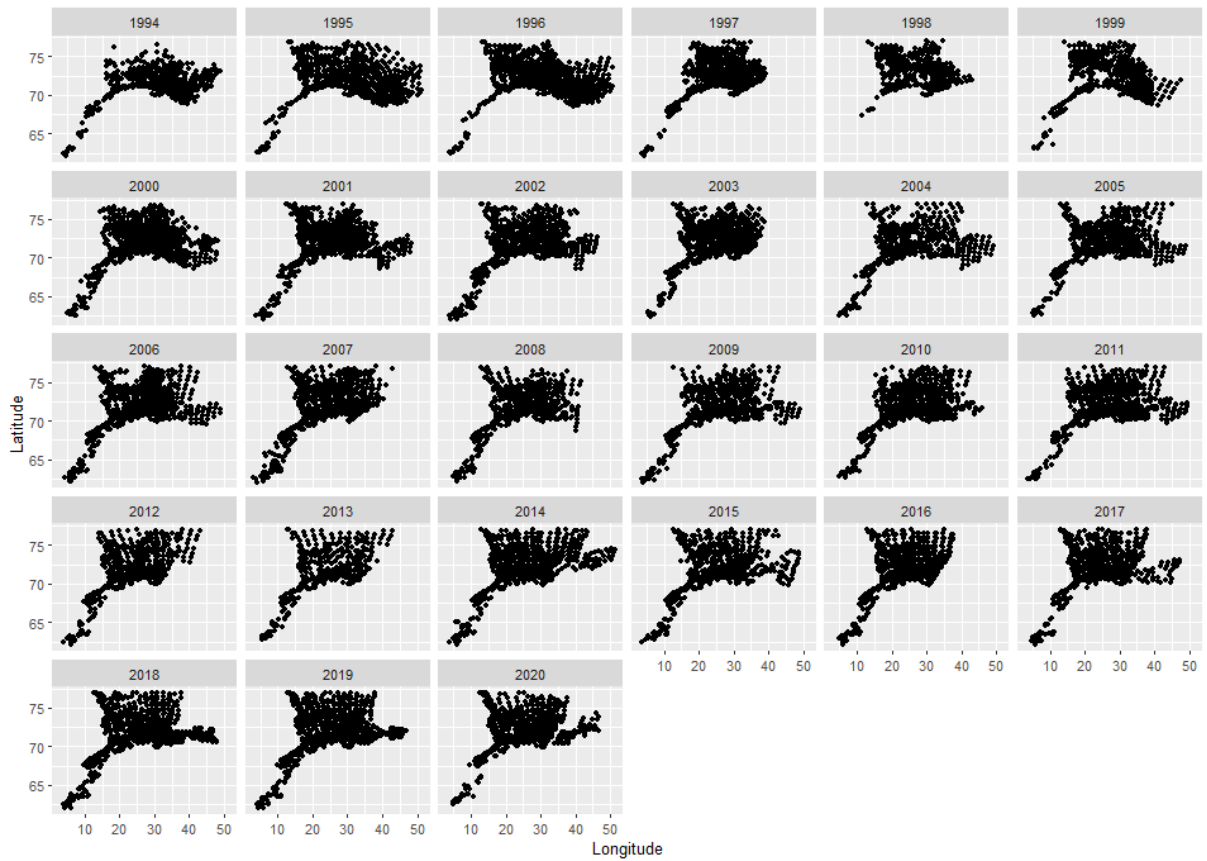


Figure S6. Annual change in beta diversity and turnover at adjacent regions, using mean pairwise Jaccard dissimilarity index.

(A)



(B)



(C)

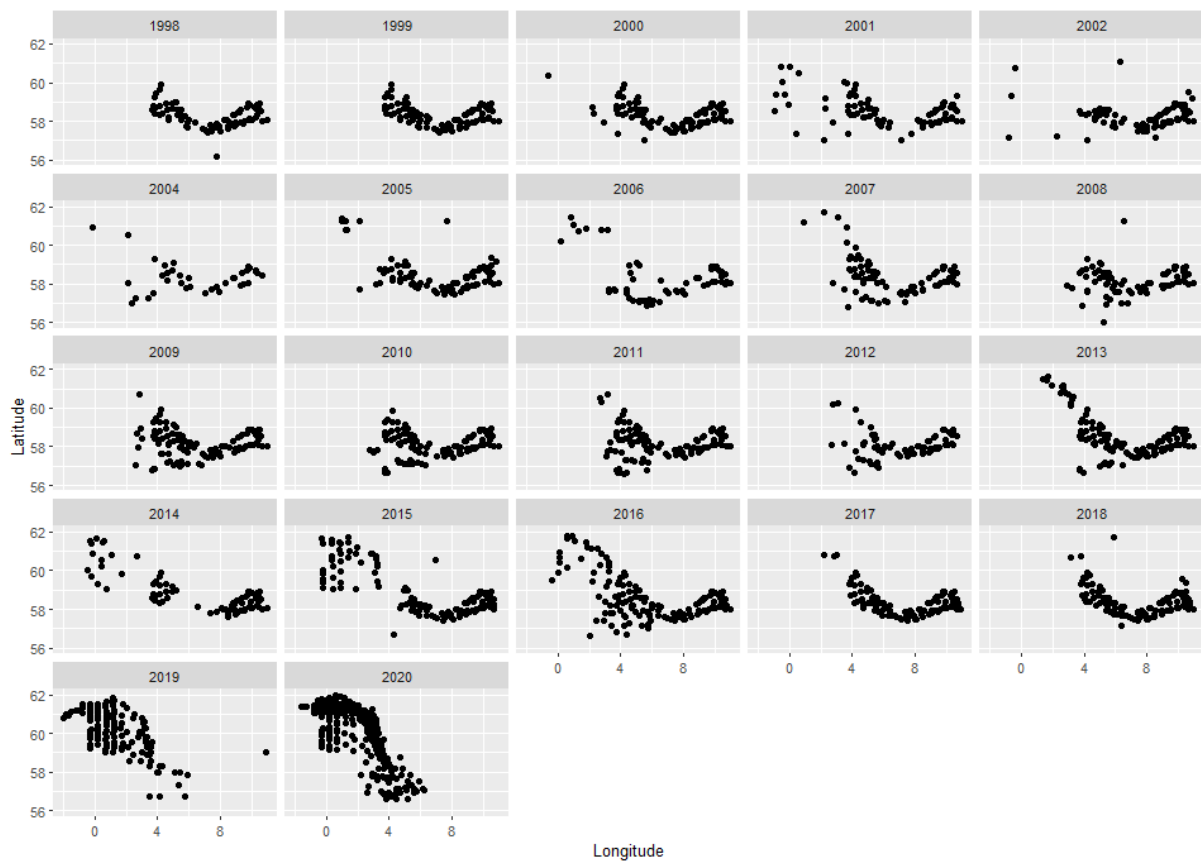


Figure S7. Spatial and temporal distribution of the sampling trawls. A: Main study area Norwegian-Barents Sea; B: Adjacent region around Svalbard; C: Adjacent region in the North Sea.

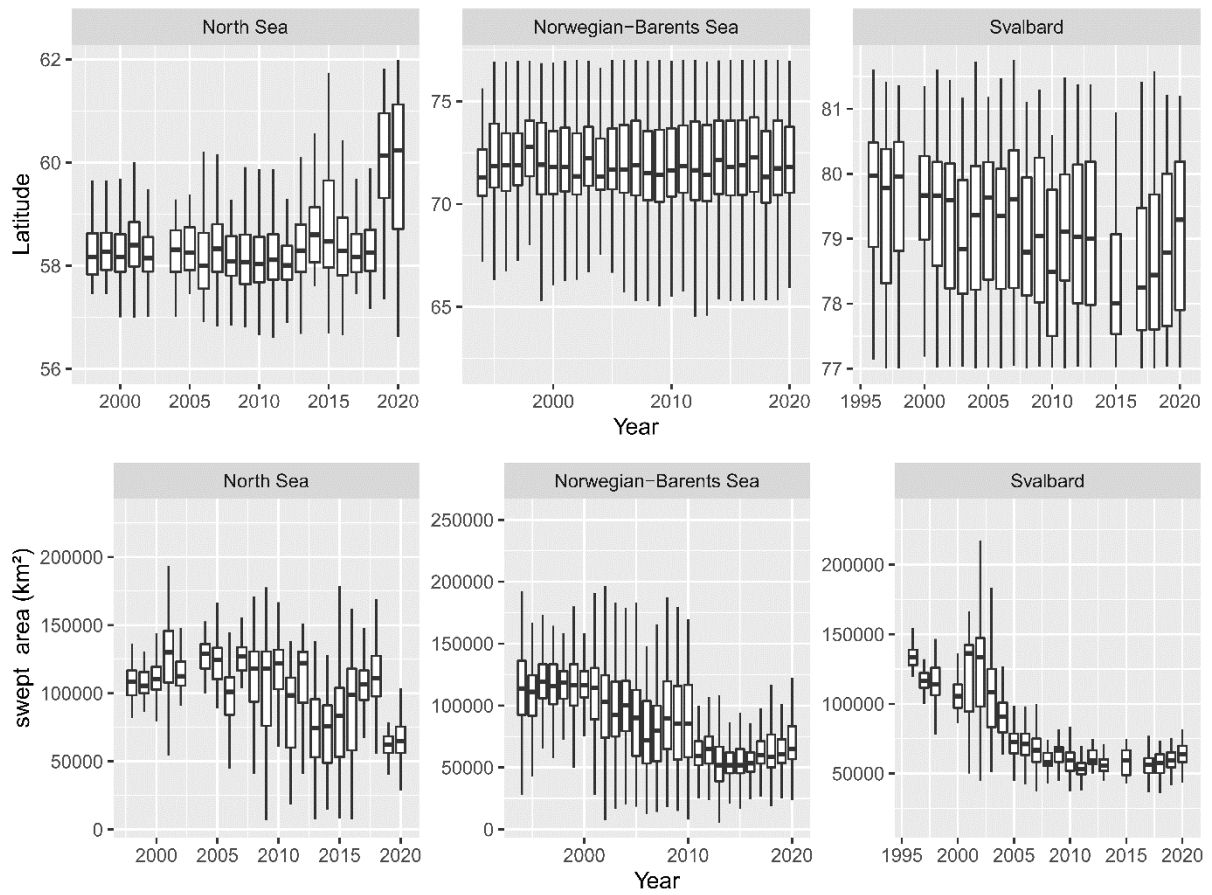


Figure S8. Dataset exploration graphics. Top: Latitudinal distribution of trawls, per year; Bottom: swept area (effort) at each trawl, per year.

Table S1. Existing studies of fish species richness changes in the Arctic Oceans.

Ref	Region	Low lat (° N)	High lat (° N)	No. spp	Years	Comments
Batt et al., 2017	East Bering Sea (1984–2014, n = 31), Aleutian Islands (1983–2014, n = 12), Gulf of Alaska (1984–2013, n = 13), West Coast US (1977–2004, n = 10), Gulf of Mexico (1984–2000, n = 17), Southeast US (1990–2014, n = 25), Northeast US (1982–2013, n = 32), Scotian Shelf (1970–2010, n = 41), Newfoundland (1996–2011, n = 16)	20	60	581	1970-2013	No Arctic latitudes. Regional increases of 30.
Chaudhary et al., 2021	Global			50,000 globally	1955-2019	Suggested poleward shift spp. in northern hemisphere but high variability in data due to diversity of datasets used. Species shifting not reported.
Burrows et al., 2019	North Atlantic and Pacific	20	62	> 80		Report general increase in community thermal index in the North Atlantic, though mixed effects at 2 degrees latitudinal cells. Community level, no taxonomic resolution.
Sunday et al., 2012	Global	-	-	142 marine and terrestrial	1650 - 2011	Shifts at both range boundaries. No marine shifts reported in polar latitudes.
Pinsky et al., 2013	East Bering Sea (1982–2011), Aleutian Islands (1980–2010), Gulf of Alaska (1984–2011), West Coast US (1977–2004), Gulf of Mexico (1987–2011), Southeast US (1971–2009), Northeast US (1968–2008), Scotian Shelf (1970–2011), Newfoundland (1995–2011)	27	60	360 (maximum 107 spp. per region)	1968 - 2011	Marine taxa distribution shifts follow local climate velocities instead of a general pattern. No reference to richness.
Poloczanska et al., 2013	Global	-	-	857		No studies reporting fish distributional shifts in polar regions.
Fosheim et al., 2015	Barents Sea	68	81	74	2004, 2012	Increase in species richness between two years. No comparison to temperature.
Kortsch et al., 2015	Barents Sea	68	81	233	2004, 2012	Food-web structure analysis of changes reported in Fosheim et al. 2015.
Frainer et al., 2017	Barents Sea	68	81	52	2004, 2012	Same dataset than Fosheim et al. 2015. Analysis of functional traits.
Frainer et al., 2021	Barents Sea	68	81	49	2004-2017	They report an increase in Arctic Barents Sea and stable richness in boreal Barents Sea, though only 49 species selected for the analyses, limited to the species with known functional traits.
Husson et al., 2022	Barents Sea	68	81	33	2004-2017	Increase in abundance and extent of most species during 2/3 extremely warm periods within this time period. Change in mean long and lat in the last 1/3.
Pecuchet et al., 2020	Barents Sea	68	81	239	2014-2017	11 boreal species observed in the Arctic region of the Barents Sea
Hiddink & ter Hofstede, 2008	North Sea	51	62	118	1985-2006	Similar research trawl data to present study, and similar magnitude.
Fisher et al., 2008	North-western pacific	35	55	133	1973 - 2003	Correlation of -0.45 between richness and NAO. No long-term trend

Drinkwater & Kristiansen, 2018	North Atlantic and Arctic	35	81	12 fish species	1950-2000	Links changes in recruitment to AMO index and cold period during 1970s – 1980s
Tittensor et al., 2021	Global	-	-	many taxa, depending on model used	2000-2100	Ensemble of 9 Marine Ecosystem Models. No species taxonomic resolution. Predict a decline in biomass in the Norwegian and boreal Barents Sea. Increase in biomass in the Arctic Barents.
Coll et al., 2020	Global	-	-	~ 3400 taxa	1950-2100	EcoOcean Marine Ecosystem Model with 3400 species organized in functional groups. Predict a decline in consumers' biomass in the North Atlantic and increase in biomass in the Arctic Ocean using IPSL model forcings.
Cheung et al., 2013	Global	-	-	990	1970-2006	No taxonomic resolution. Increase in mean temperature of the catch worldwide.
Cheung et al., 2009	Global	-	-	836 fish + 230 inverts	2050	Model projection of species invasion in the arctic region of the Barents Sea, and species extinction in the Norwegian Sea and south of Svalbard by 2050.
Skaret et al., 2015	Norwegian Sea	66	69		2013	Mackerel north expansion.
Druon et al., 2016	Mediterranean Sea, North Atlantic and Gulf of Mexico	12	72	1	2003-2012	Ecological niche modelling of Atlantic bluefin tuna.
Alabia et al., 2021	Eastern Bering Sea	55	62	159 (66 fish, 93 inverts)	1990 - 2018	Very similar trend than ours in Alpha diversity, but in markedly smaller latitudinal range, and not polar.
(Brunel & Boucher, 2007)	North-east Atlantic	45	70	9 fish (4 species at high latitudes)	1970-1998	Most recruitment declining in the Baltic Sea, north Sea, west of Scotland and Irish populations. Herring and populations of boreal ecosystems followed an increasing trend.
Mueter & Litzow, 2008	Berings Sea	54	61	46 fish and inverts		Links community changes to sea ice retreat. Reports an increase in sp richness < 20 %.
Magurran et al., 2015	North Sea	55	59	131 (126 fish)	1985-2013	No change in species richness, though increase in turnover (beta diversity), with time.
Molinos et al., 2016	Global	-	-	13,000 marine species	2006-2100	Projected increase in richness (alpha diversity) across our study area until 2100. Unclear trend in dissimilarity (beta diversity).
Sunday et al., 2015	Eastern Australia	20	45	50 fish + 54 inverts	1945-2005	Poleward species shifts.
Morley et al., 2018	Northeastern Pacific & Northwestern atlantic	27	60	686 species	2007-2100	Mostly poleward shifts projected. Projections mostly based on the data from Batt et al. 2017 and Pinsky et al. 2013.
Pilotto et al., 2020	North Atlantic	47	61	6200 marine, freshwater and terrestrial		Increases in richness and abundance with increasing temperatures in most biogeoregions of Northern and Eastern Europe.
Pereira et al., 2010	Global	-	-	1066 fish and inverts	2005-2050	Rate of projected poleward shift among the demersal community are highest in the North Atlantic and Barents Sea.

Table S2. Taxonomic classification of the species found.

Class	Order	Family	N especies
Actinopteri	Perciformes/Cottoidei	Agonidae	3
Actinopteri	Alepocephaliformes	Alepocephalidae	1
Actinopteri	Perciformes/Uranoscoipoidei	Ammodytidae	5
Actinopteri	Perciformes/Zoarcoidei	Anarhichadidae	3
Actinopteri	Anguilliformes	Anguillidae	1
Actinopteri	Argentiniformes	Argentinidae	2
Elasmobranchii	Rajiformes	Arhynchobatidae	1
Actinopteri	Beloniformes	Belonidae	1
Actinopteri	Pleuronectiformes	Bothidae	1
Actinopteri	Callionymiformes	Callionymidae	3
Actinopteri	Acanthuriformes	Caproidae	1
Actinopteri	Carangiformes	Carangidae	1
Actinopteri	Syngnathiformes	Centriscidae	1
Actinopteri	Ophidiiformes	Carapidae	1
Actinopteri	Scombriformes	Centrolophidae	1
Elasmobranchii	Squaliformes	Centrophoridae	1
Holocephali	Chimaeriformes	Chimaeridae	1
Actinopteri	Clupeiformes	Clupeidae	4
Actinopteri	Anguilliformes	Congridae	1
Actinopteri	Perciformes/Cottoidei	Cottidae	11
Actinopteri	Perciformes/Cottoidei	Cyclopteridae	4
Actinopteri	Clupeiformes	Engraulidae	1
Elasmobranchii	Squaliformes	Etmopteridae	1
Actinopteri	Gadiformes	Gadidae	14
Actinopteri	Perciformes/Gasterosteoides	Gasterosteidae	1
Actinopteri	Gobiiformes	Gobiidae	4
Actinopteri	Perciformes/Cottoidei	Liparidae	16
Actinopteri	Lophiiformes	Lophiidae	1
Actinopteri	Gadiformes	Lotidae	9
Actinopteri	Gadiformes	Macrouridae	4
Actinopteri	Gadiformes	Merlucciidae	1
Actinopteri	Argentiniformes	Microstomatidae	1
Actinopteri	Eupercaria/misc	Moronidae	1
Actinopteri	Mulliformes	Mullidae	1
Actinopteri	Myctophiformes	Myctophidae	3
Myxini	Myxiniformes	Myxinidae	1
Actinopteri	Osmeriformes	Osmeridae	1
Actinopteri	Aulopiformes	Paralepididae	2
Elasmobranchii	Carcharhiniformes	Pentanchidae	1
Petromyzonti	Petromyzontiformes	Petromyzontidae	1
Actinopteri	Perciformes/Zoarcoidei	Pholidae	1
Actinopteri	Gadiformes	Phycidae	2
Actinopteri	Pleuronectiformes	Pleuronectidae	8
Actinopteri	Perciformes/Cottoidei	Psychrolutidae	2

Elasmobranchii	Rajiformes	Rajidae	13
Actinopteri	Salmoniformes	Salmonidae	2
Actinopteri	Beloniformes	Scomberesocidae	1
Actinopteri	Scombriformes	Scombridae	1
Actinopteri	Pleuronectiformes	Scophthalmidae	6
Elasmobranchii	Carcharhiniformes	Scyliorhinidae	2
Actinopteri	Perciformes/Scorpaenoidei	Sebastidae	4
Actinopteri	Pleuronectiformes	Soleidae	3
Elasmobranchii	Squaliformes	Somniosidae	1
Elasmobranchii	Squaliformes	Squalidae	1
Actinopteri	Stomiiformes	Sternoptychidae	2
Actinopteri	Perciformes/Zoarcoidei	Stichaeidae	5
Actinopteri	Syngnathiformes	Syngnathidae	2
Actinopteri	Perciformes/Percoidei	Trachinidae	2
Elasmobranchii	Carcharhiniformes	Triakidae	1
Actinopteri	Perciformes/Scorpaenoidei	Triglidae	3
Actinopteri	Zeiformes	Zeidae	1
Actinopteri	Perciformes/Zoarcoidei	Zoarcidae	18
			193

Table S3. Variables used in the BRT model. Variables with a (*) were excluded after proving not relevant in the exploration partial dependence plots. (< 3 % of DV explained).

Layer name	Layer code	Units	Origin	Temporal resolution
Sea surface temperature	SST	°C	Copernicus	Yes
Sea surface salinity	SSS	psu	Copernicus	Yes
Sea bottom temperature	SBT	°C	Copernicus	Yes
Northward currents	NWC	m/s	Copernicus	Yes
Eastward currents	EWC	m/s	Copernicus	Yes
Ice concentration *	ICC	Area fraction 0 to 1	Copernicus	Yes
Bottom nitrate concentration	Nitrate	µmol/m ³	Bio Oracle	No
Bottom oxygen concentration	DO	µmol/m ³	Bio Oracle	No
Bottom iron concentration	Iron	µmol/m ³	Bio Oracle	No
Surface productivity	Prod.Surface	g/m ³ /day	Bio Oracle	No
Temperature Range	Temp. range	°C	Bio Oracle	No
Bottom productivity *	Bot. Prod	g/m ³ /day	Bio Oracle	No
Bathymetry	Depth	M	MARSPEC	No
Distance to coast	Dist_to_coast	M	Self made	No
Longitude	Longitude	°	Self made	No
Latitude	Latitude	°	Self made	No
Year	Year	yr	Self made	Yes
Swept area	swept_area	Km ²	Self made	No
Annual trawl	Annual_trawls	Trawls	Self made	No

