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Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change

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Table S1 – Aggregation of species into multi-species groups

Table S1. Multi-species groups of demersal North Sea fish. Several species in the survey have been aggregated because of difficulties in the identification of species and/or because of probable misidentifications in the past. Grouping has been done as suggested by Heessen et al. (2015).

Species	**Multi-species group**
Mustelus mustelus *Mustelus asterias*	*Mustelus* spp.
Callionymus lyra *Callionymus maculatus* *Callionymus reticulates* *Callionymidae*	*Callionymus* spp.
Aphia minuta *Crystallogobius linearis*	Translucent gobies
Liparis liparis *Liparis montagui*	*Liparis* spp.
Syngnathus acus *Syngnathus rostellatus* *Syngnathus typhle* *Nerophis ophidion*	*Syngnathidae/*Other pipefishes*
Ammodytes marinus *Ammodytes tobianus* *Hyperoplus immaculatus* *Hyperoplus lanceolatus*	*Ammodytidae*
Argentina silus *Argentina sphyraena*	*Argentina* spp.

* *Entelurus aequoreus*, another pipefish, is not included in this group.

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Table S2 – Species list and trait values

Table S2. Species list and trait values of the demersal North Sea fish species retained in the analysis.
Length was calculated as the mean length over all length classes present for each species retained from the survey data (North Sea International Bottom Trawl Survey; https://datras.ices.dk). All trophic level data were taken from FishBase (1). References for the remaining traits are given in the last column.

Species	Common name	Length	Length at maturity	Age at maturity	Lifespan	K	Trophic level	Fecundity	Offspring size	References
Agonus cataphractus	Hooknose	12.8	9.5	1.0	3	0.48	3.43	3000	2	(1–3)
Amblyraja radiata	Starry ray	42.0	37.2	3.5	20	0.13	4.20	17	110	(1, 2, 4)
Ammodytidae	Sandeels	22.9	17.8	2.3	7.5	0.78	3.37	21613	0.8	(1, 2, 5–8)
Ammodytes marinus	Lesser sandeel		14.0	2.6	4	0.89	2.71	8225		(1, 2, 5, 7, 8)
Ammodytes tobianus	Common sandeel			1.5	7	0.68	3.08			(1, 2)
Anarhichas lupus	Atlantic wolffish	74.1	55.0	6.5	20	0.12	3.55	10000	5	(1, 2, 6, 9, 10)
Anguilla anguilla	European eel	72.7	46.3	12.9	44	0.10	3.55	2500000	1	(1, 6, 11)
Aphia minuta	Transparent goby		3.6	0.6	0.7	1.87	3.10	1800	0.34	(1, 2, 6)
Argentina spp.	Argentines	19.1	23.3	4.5	26	0.24	3.47	15239	2.53	(1, 2, 12, 13)
Argentina silus	Greater argentine		33.0	6.5	35	0.19	3.32	15239	1.8	(1, 2, 12, 13)
Argentina sphyraena	Lesser argentine		13.6	2.5	17	0.28	3.62		3.25	(1, 2)
Arnoglossus laterna	Mediterranean scaldfish	12.4	7.5	1.5	8	0.94	3.59	33333	0.7	(1, 2, 6, 14)
Brosme brosme	Tusk	56.4	40.0	6.5	20	0.08	3.90	2500000	1.4	(1–3, 6, 8)
Buglossidium luteum	Solenette	10.1	7.0	3.0	14	0.58	3.31	13400	0.8	(2, 6, 9, 15)
Callionymus spp.	Dragonets	18.2	11.5	1.9	5	0.55	3.29	10228[a]	0.8	(1, 2, 6, 8, 16)
Callionymus lyra	Dragonet		16.3	3.5	6.6	0.55	3.27		0.9	(1, 2, 6, 8)
Callionymus maculatus	Spotted dragonet		10.7	1.3	5		3.31		0.7	(1, 6)
Callionymus reticulatus	Reticulated dragonet		7.6	1.0	3.3		3.28		0.8	(1, 6)
Capros aper	Boarfish	10.1	9.0	3.0	30	0.17	3.14	87720[b]	1.	(2, 17)
Chelidonichthys cuculus	Red gurnard	27.1	25.6	3.7	21	0.49	3.81	100000[c]	1.55	(2, 6, 18)
Chelidonichthys lucerna	Tub gurnard	34.7	37.5	3.5	14	0.39	3.98	100000	1.3	(2, 6, 19)
Ciliata mustela	Fivebeard rockling	18.6	13.0	1.0	4	0.65	3.50	19500	0.8	(2, 6, 20)
Ciliata septentrionalis	Northern rockling	11.6	12.9	1.0	2	0.79	3.50	19500[d]	0.8[d]	(1, 2)
Crystallogobius linearis	Crystal goby		2.7	0.4		0.97	3.40	450	0.4	(1, 2)
Cyclopterus lumpus	Lumpfish	38.9	29.4	3.5	6	0.26	3.89	194112	2.6	(1, 2, 6)

Species	Common name	Length	Length at maturity	Age at maturity	Lifespan	K	Trophic level	Fecundity	Offspring size	
Dicentrarchus labrax	European seabass	46.5	37.0	5.5	30	0.14	3.47	520278	1.3	(1, 2, 6, 8, 21, 22)
Dipturus batis	Blue skate	76.4	130.0	11.0	23	0.06	3.52	40	170	(1, 2, 6)
Echiichthys vipera	Lesser weever	12.5	10.0	1.0[e]	14	0.33	4.41	57600	1.2	(1, 2, 6)
Enchelyopus cimbrius	Fourbeard rockling	21.6	15.0	3.0	9	0.20	3.53	25000	0.9	(1, 2, 6, 8)
Entelurus aequoreus	Snake pipefish	35.7	23.8	2.0	8	0.36	3.54	1000	1	(1, 23)
Eutrigla gurnardus	Grey gurnard	29.4	23.0	2.5	14	0.81	3.87	250000	1.45	(2, 6)
Gadiculus argenteus	Silvery pout	11.2	10.2	1.6	3	0.50	3.60	2763809[f]	1	(1, 2, 6)
Gadus morhua	Atlantic cod	76.2	54.9	3.3	18	0.30	4.09	1000000	1.43	(1, 2, 6)
Gaidropsarus vulgaris	Three-bearded rockling	28.3	27.0	3.0	6	0.48	3.47	11018375[g]	0.8	(1, 6, 24)
Galeorhinus galeus	Tope shark	104.9	117.0	10.0	40	0.08	4.34	29	280	(2, 25, 26)
Gasterosteus aculeatus	Three-spined stickleback	6.3	4.0	1.0	3	1.79	3.31	250	1.3	(1, 2, 6, 27)
Glyptocephalus cynoglossus	Witch flounder	37.2	44.5	5.5	25	0.20	3.17	278550	1.27	(1, 2, 6, 8)
Helicolenus dactylopterus	Blackbelly rosefish	17.0	24.5	14.3	43	0.08	3.54	230055	2.8	(1, 2, 6)
Hippoglossoides platessoides	American plaice	20.5	14.0	2.6	15	0.34	4.08	1525000	2.3	(1–3, 8, 9)
Hippoglossus hippoglossus	Atlantic halibut	64.0	83.0	5.8	50	0.10	4.00	1900000	3.4	(1–3, 28)
Hyperoplus immaculatus	Corbin's sandeel		21.2	2.9	11.8		4.38		0.8	(1, 6)
Hyperoplus lanceolatus	Greater sandeel		17.6	1.8	7.1		3.98	35000	0.8	(1, 6)
Lepidorhombus whiffiagonis	Megrim	39.2	26.3	2.8	12	0.16	4.34	333523	1.1	(1, 2, 6, 29, 30)
Leucoraja fullonica	Shagreen ray	74.7	75.0	7.0[h]	24	0.12	3.50	63[h]	65	(1, 6, 31)
Leucoraja naevus	Cuckoo ray	53.2	51.5	7.0	12	0.24	4.21	63	50	(2, 6, 32)
Limanda limanda	Common dab	22.9	18.8	1.7	12	0.26	3.39	100000	1	(1–3, 6, 8, 33)
Liparis spp.	Seasnails	12.3	9.1	1.0	1	1.02	3.52	627	1.3	(1, 2, 6)
Liparis liparis	Common seasnail		10.0	1.0		0.91	3.59	460	1.5	(1, 2, 6)
Liparis montagui	Montagu's seasnail		8.2	1.0		1.12	3.45	793	1.1	(1, 2)
Lophius budegassa	Blackbellied angler	56.5	59.5	8.2	21	0.11	4.41	1550000	1.8	(1, 2, 6)
Lophius piscatorius	Anglerfish	64.3	80.0	4.5	24	0.16	4.45	1000000	2.7	(1, 2, 6, 8, 9)
Lumpenus lampretaeformis	Snakeblenny	26.4	20.0	3.0	9	0.21	3.59	1000	0.8	(1–3, 6, 8, 9)
Melanogrammus aeglefinus	Haddock	37.5	28.3	2.2	11	0.26	4.03	535000	1.5	(1, 2, 6, 8, 9, 34)
Merlangius merlangus	Whiting	31.0	20.2	1.5	10	0.29	4.36	350800	1.28	(1, 2, 6, 8, 9)
Merluccius merluccius	European hake	45.6	41.3	3.8	12	0.11	4.42	294521	1	(1, 2, 6, 8, 35, 36)
Microchirus variegatus	Thickback sole	15.4	9.0	3.0	10	0.38	3.28	500000	1.3	(2, 6, 37)

Species	Common name	Length	Length at maturity	Age at maturity	Lifespan	K	Trophic level	Fecundity	Offspring size	References
Microstomus kitt	Lemon sole	29.7	27.0	3.8	23	0.19	3.21	200000	1.2	(2, 6, 9, 38)
Molva molva	Ling	95.7	65.0	6.0	20	0.17	4.40	40000000	1	(2, 4, 6)
Mullus surmuletus	Surmullet	21.0	16.5	1.5	10	0.29	3.45	10000	0.85	(1, 2, 6)
Mustelus spp.	Smooth-hounds	72.6	82.5	5.3	20	0.18	3.69	13	345	(1, 2, 39, 40)
Mustelus asterias	Starry smooth-hound		82.5	5.3	15.5	0.18	3.62	15	300	(1, 2, 39)
Mustelus mustelus	Smooth-hound				24		3.75	11	390	(1, 39, 40)
Myxine glutinosa	Atlantic hagfish	35.1	26.5	2.7	11	0.09[i]	4.54	25	20	(1, 2, 6, 24)
Nerophis ophidion	Straight-nosed pipefish		17.9	0.7		1.05	4.01		1	(1, 23)
Pholis gunnellus	Rock gunnel	21.4	10.5	2.0	8.5	0.30	3.54	100	2	(1, 2, 6, 41)
Phrynorhombus norvegicus	Norwegian topknot	9.4	8.5	1.3	6	0.60	3.98	2666761[j]	0.8	(1, 2, 4)
Phycis blennoides	Greater forkbeard	42.6	22.5	3.5	20	0.15	3.66	1643889	0.6	(1, 2, 42)
Platichthys flesus	European flounder	31.3	23.5	3.5	9	0.26	3.32	650000	1.06	(1, 2, 6)
Pleuronectes platessa	European plaice	31.4	28.0	2.5	28	0.23	3.23	146778	1.8	(1, 2, 6, 9)
Pollachius pollachius	Pollack	69.2	41.5	3.0	15	0.19	4.32	220000	1.15	(1, 2, 6, 8, 20)
Pollachius virens	Saithe	69.6	48.7	4.6	25	0.19	4.31	4831000	1.1	(1, 2, 6, 8, 9, 43)
Pomatoschistus minutus	Sand goby	42.7	0.5	0.9	3	0.93	3.22	3654	0.8	(1, 2, 6, 8)
Raja brachyura	Blonde ray	74.1	81.5	9.0	10	0.17	3.76	65	121.5	(1, 2, 44, 45)
Raja clavata	Thornback ray	66.3	71.8	8.0	15	0.16	3.84	61	70	(1, 2)
Raja montagui	Spotted ray	56.4	56.5	5.0	7	0.20	3.88	43	65.5	(1, 2)
Raniceps raninus	Tadpole fish	11.0	18.5	1.8	8	0.46	3.77	1021420[f]	1.2[f]	(1, 2)
Scophthalmus maximus	Turbot	49.6	40.0	3.3	38	0.24	4.36	4000000	1	(2, 6)
Scophthalmus rhombus	Brill	42.9	24.5	3.0	19	0.43	4.42	5000000	1.3	(2, 6)
Scyliorhinus canicula	Lesser spotted dogfish	60.2	55.5	7.3	14.5	0.14	3.82	46	59.5	(1, 2, 46, 47)
Sebastes viviparus	Norway redfish	23.8	12.5	20.0	39	0.10	4.03	8558	5.5	(2, 6, 9, 48)
Solea solea	Common sole	27.7	28.0	2.5	39.5	0.34	3.21	118050	1.2	(1, 2, 6)
Spinachia spinachia	Sea stickleback	32.1	14.1	1.0	1	1.78	3.50	170	2	(1, 2, 49)
Spondyliosoma cantharus	Black seabream	24.8	21.0	2.5	18	0.25	3.34	61396	0.65	(1, 2, 50)
Squalus acanthias	Picked dogfish	82.2	69.8	10.5	62.5	0.11	4.37	8	245	(1, 2, 46, 51, 52)
Syngnathidae	Other pipefishes	31.9	18.7	1.2	4[k]	0.79	3.84	186	1.48	(1, 2, 6, 23)
Syngnathus acus	Greater pipefish		30.0	1.7			3.33	300	2.5	(1, 2, 23)
Syngnathus rostellatus	Nilsson's pipefish		10.0	1.0		0.75	3.69	100	1.2	(1, 2, 6, 23)

Species	Common name	Length	Length at maturity	Age at maturity	Lifespan	K	Trophic level	Fecundity	Offspring size	References
Syngnathus typhle	Deep-snouted pipefish		17.0	1.5		0.56	4.31	158	1.7	(1, 2, 23)
Trachinus draco	Greater weever	31.5	12.0	1.0	14	0.16	4.18	141273	1	(2, 6, 53, 54)
Translucent gobies	Translucent gobies	4.6	3.2	0.5	0.7	1.42	3.25	1125	0.37	(1, 2, 6)
Triglops murrayi	Moustache sculpin	11.0	12.9	3.5	10	0.19	3.45	100	1.75	(1, 4)
Trisopterus esmarkii	Norway pout	15.9	19.0	1.7	4	0.66	3.24	205595	1.1	(1, 2, 6, 9)
Trisopterus luscus	Bib	25.3	22.5	2.0	6	0.76	3.73	520238	1.1	(1, 2, 6, 9)
Trisopterus minutus	Poor cod	17.3	15.0	2.0	8	0.51	3.73	10000	1	(1, 2, 6, 8, 9, 55)
Zeugopterus punctatus	Topknot	11.0	15.7	2.4	8.8	0.31	3.99	2166761[j]	1	(1, 2, 56)
Zeus faber	John dory	29.0	30.0	3.5	14	0.43	4.50	292500[l]	2	(1, 2, 6)
Zoarces viviparus	Viviparous eelpout	15.8	17.8	1.5	6	0.43	3.47	100	3	(1, 2, 6)

[a]Inferred from *Callionymus kaianus*
[b]Order mean (Perciformes)
[c]Inferred from *Chelidonichthys lucerna*
[d]Inferred from *Ciliata mustela*
[e]Inferred from *Trachinus draco*
[f]Family mean (Gadidae)
[g]Family mean (Lotidae)
[h]Inferred from *Leucoraja naevus*
[i]Inferred from *Petromyzon marinus*
[j]Family mean (Scophthalmidae)
[k]Inferred from *Syngnathus leptorhynchus*
[l]Inferred from *Zenopsis nebulosa*

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Table S3 – Best models

Predictor variables that were selected by the corrected Akaike Information Criterion (AICc) to be in the best models for the temporal CWM traits (upper table) and spatial CWM traits (lower table). The explained deviance (adjusted R^2) of each model is given in the bottom row.

Temporal models

	Length	Length at maturity	Age at maturity	Lifespan	K	Trophic level	Fecundity	Offspring size
PCI	+	+	+	+			+	
Temperature	+	+	+	+			+	
Salinity		+	+	+	+		+	
Seasonality								+
R^2 best model	0.61	0.78	0.55	0.37	0.11	0.08	0.52	0.01

Spatial models

	Length	Length at maturity	Age at maturity	Lifespan	K	Trophic level	Fecundity	Offspring size
Depth				+	+	+	+	+
Temperature	+	+				+	+	
Seasonality			+	+		+		
Otter trawl effort					+	+		
PCI					+			
Salinity								
Substrate richness								
Beam trawl effort								
R^2 best model	0.03	0.05	0.06	0.53	0.47	0.59	0.52	0.02

Figure S1 – Size-independent growth rate

Von Bertalanffy's growth coefficient K is the rate (yr^{-1}) at which an individual fish reaches its asymptotic size (length infinity, L_∞). It follows from the Von Bertalanffy growth equation that describes body length as a function of age:

$$L_t = L_\infty - L_\infty \cdot e^{-K(t-t_0)}$$

where L_t is length (cm) at age t, L_∞ is the asymptotic length (cm), K the growth coefficient (yr^{-1}), t is age (yr) and t_0 the theoretical age at size zero (yr).

The growth coefficient K is negatively correlated to L_∞. We therefore calculated an alternative growth rate that is independent of L_∞: growth rate ω in $cm \cdot yr^{-1}$ that is calculated by multiplying K and L_∞ (Gallucci & Quinn 1979). It represents growth rate in early in life (close to t_0) and can therefore be seen as juvenile growth rate.

The temporal and spatial community weighted means (CWM) of growth rate ω are plotted below as well as the rate of change in the spatio-temporal CWMs, calculated as the slope of a linear regression of the CWM growth rates per survey grid cell.

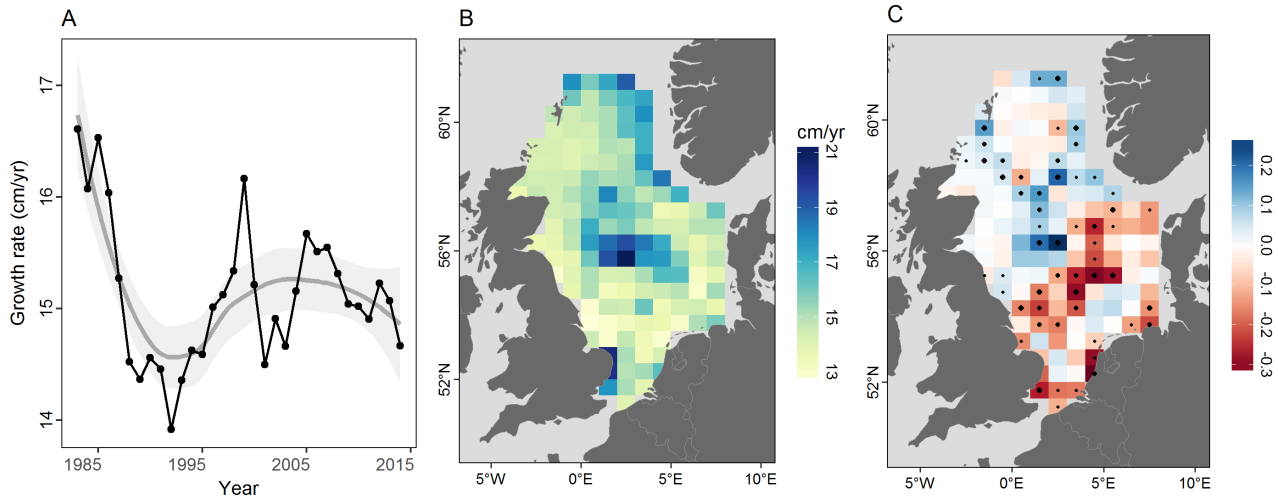

Figure S1. Time series (A), spatial patterns (B) and spatio-temporal trends (C) of the community weighted mean of growth rate ω ($cm \cdot yr^{-1}$). Grey line with shaded area in A is a loess-smoother with confidence interval to visualize the main trend. Circles in C indicate significant temporal trends (small $p < 0.05$, medium $p < 0.01$, large $p < 0.001$).

References

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Figure S2 – Modelled relationships temporal trends of traits

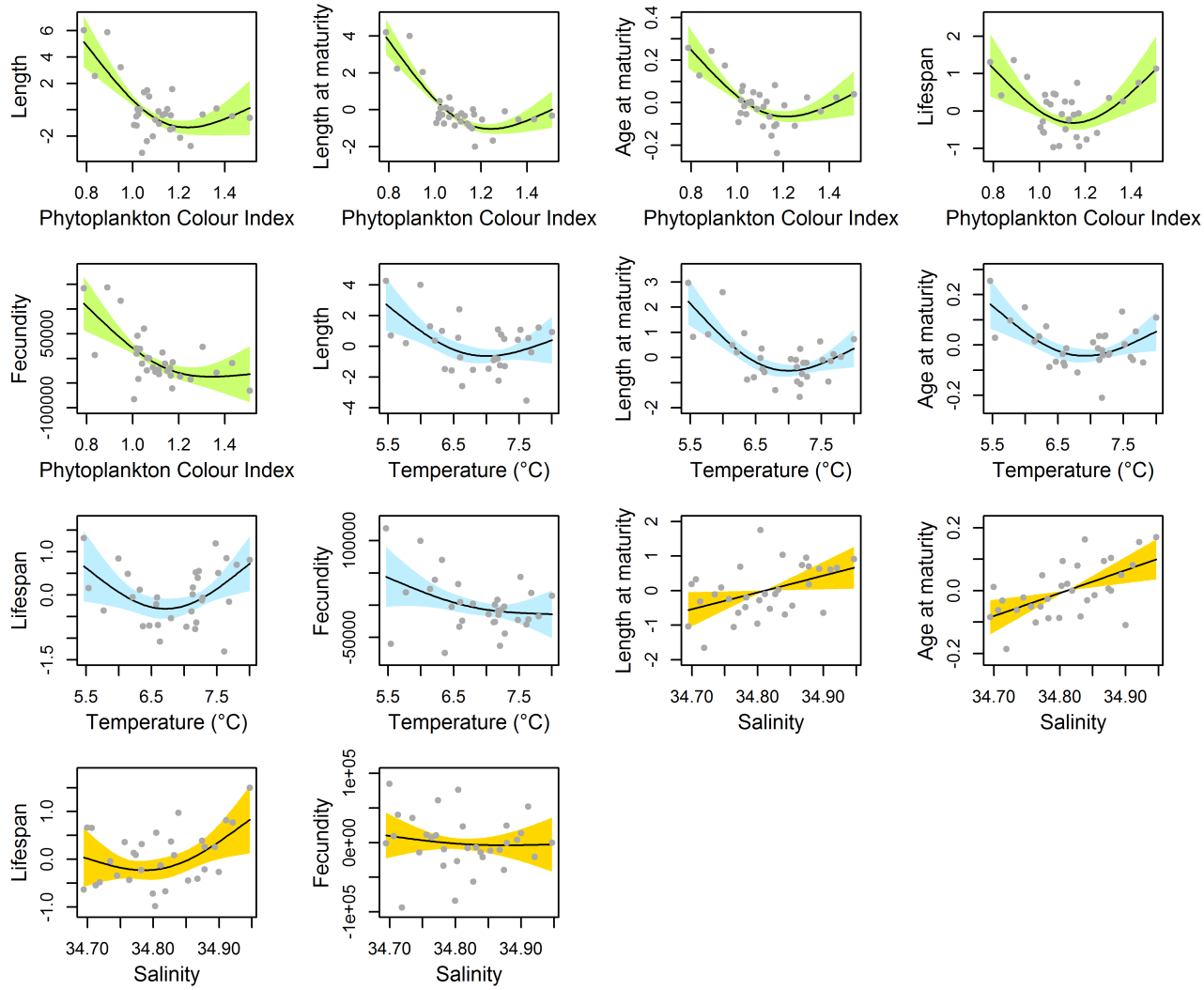

Figure S2. Selection of modelled relationships between environmental variables and temporal community weighted mean traits. Fitted lines are the modelled relationships through generalized additive models or generalized additive mixed models, grey dots are the partial residuals (plotted on y-axis) and the shaded area represents the 95% confidence interval. For plotting the partial residuals the best models were taken, i.e. models with the lowest corrected Akaike Information Criterion (AICc), see Table S3.

Figure S3 – Modelled relationships spatial trait patterns

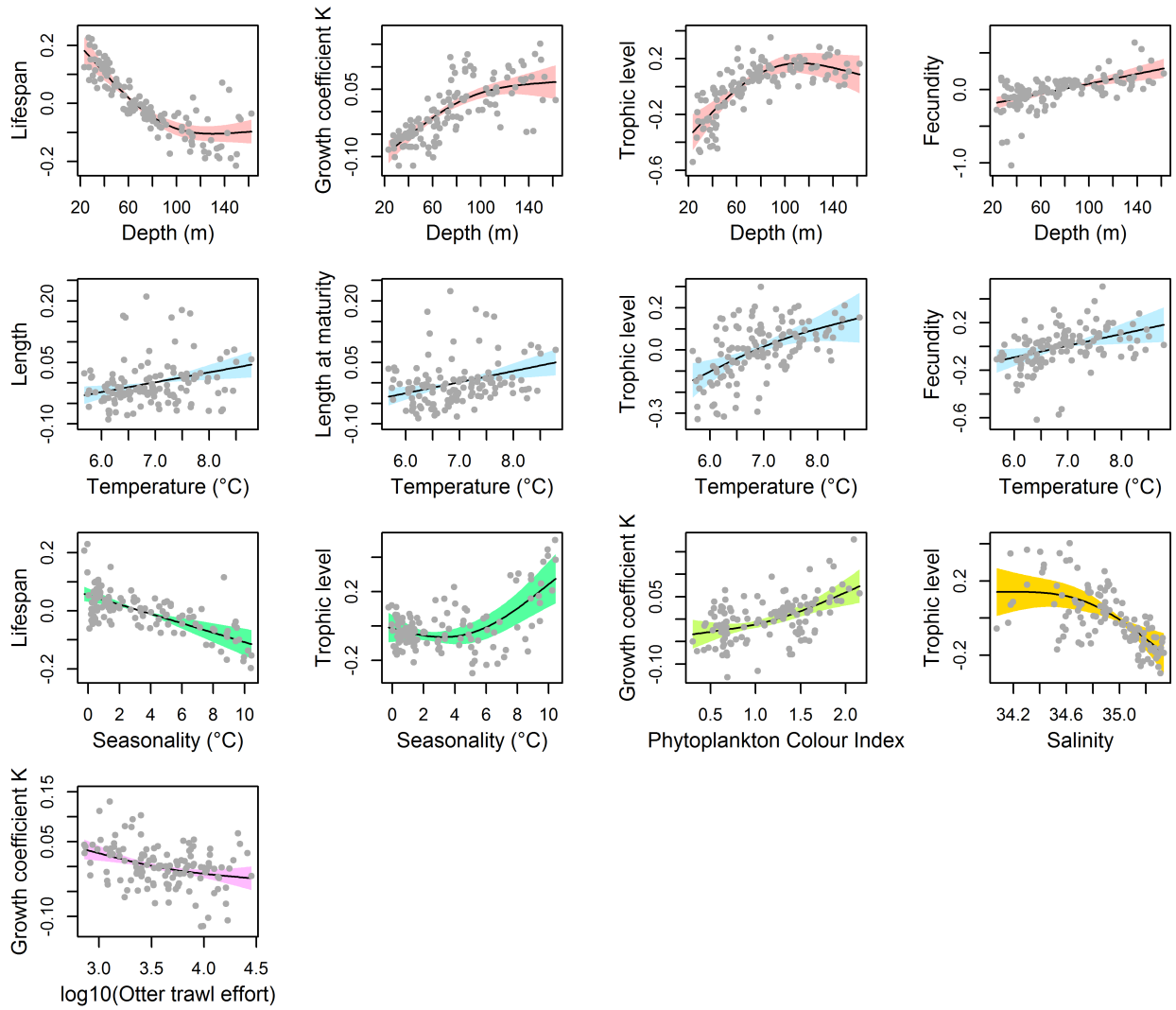

Figure S3. Selection of modelled relationships between spatial community weighted mean traits and environmental and fishing variables. Fitted lines are the modelled relationship through generalized additive mixed models, grey dots are the partial residuals (plotted on y-axis) and the shaded area represents the 95% confidence interval. For plotting the partial residuals the best models were taken, i.e. models with the lowest corrected Akaike Information Criterion (AICc), see Table S3.

Figure S4 – Time series of environmental and fishing variables

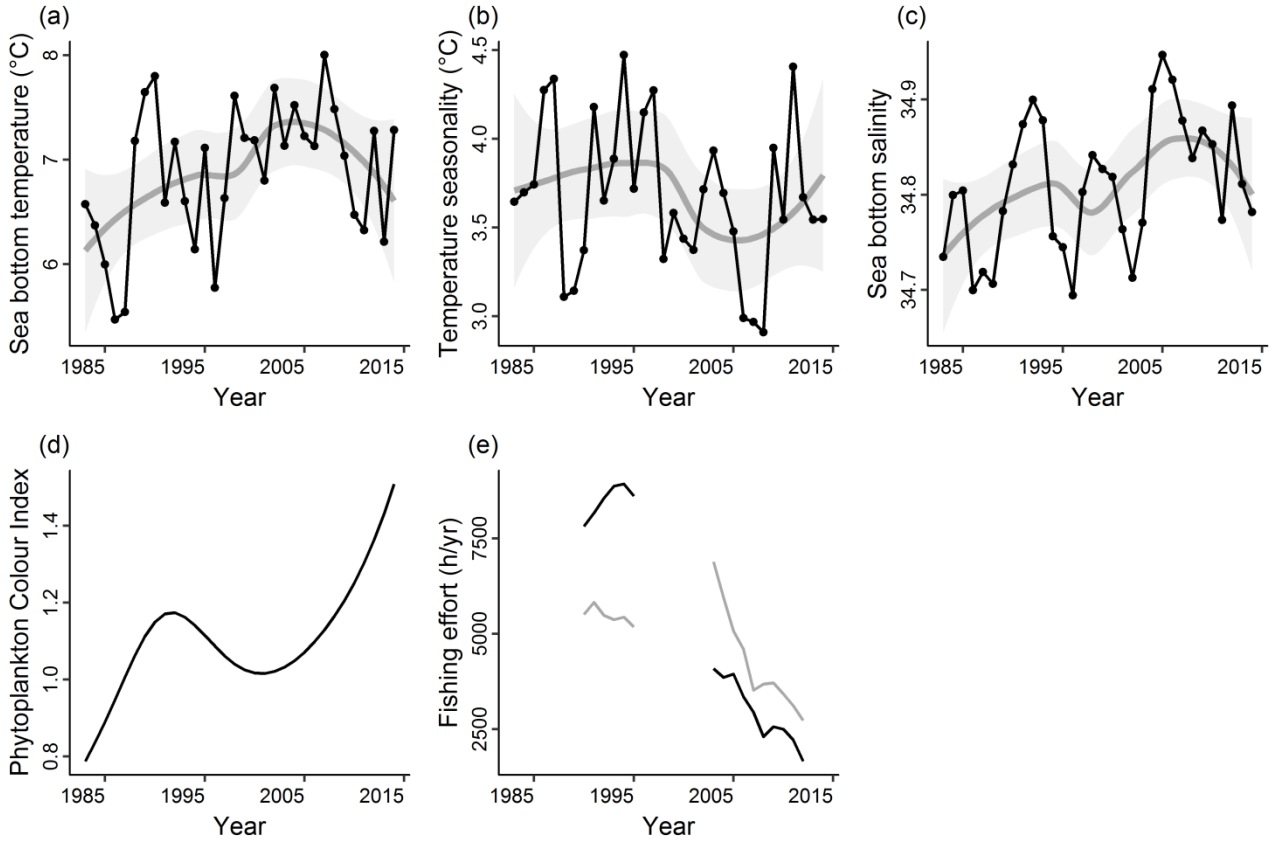

Figure S4. Time series of sea bottom temperature (a), seasonal difference in temperature (b), sea bottom salinity (c), Phytoplankton Color Index (d), and fishing effort (black = beam trawl effort, grey = otter trawl effort; e). Grey line with shaded area is a loess-smoother with confidence interval to visualize the main trend. Only temparture, salinity, seasonality and PCI were used as predictor variables to model the temporal community weighted mean traits.

Figure S5 – Spatial distribution of environmental and fishing variables

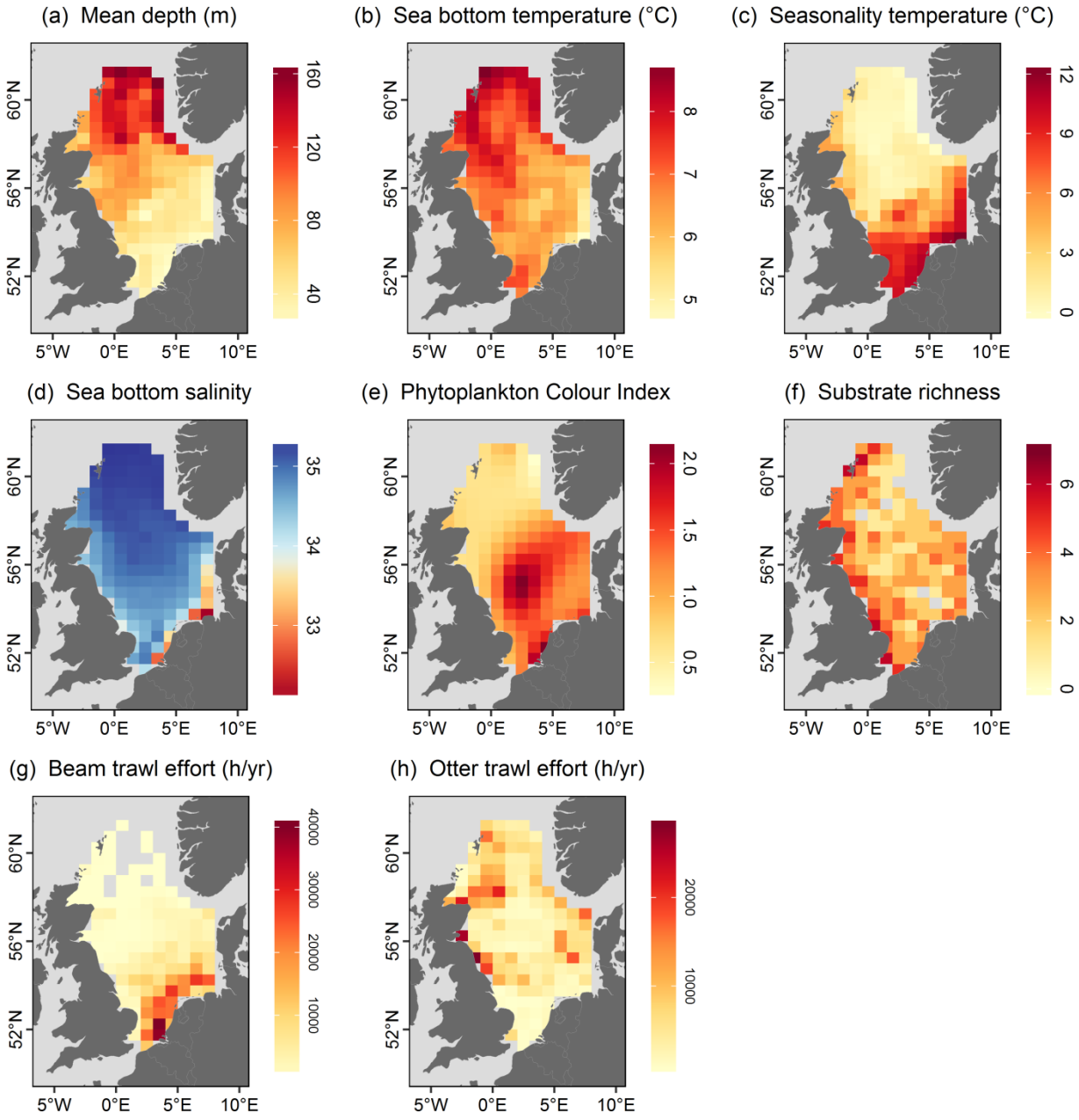

Figure S5. Spatial distribution of depth (a), sea bottom temperature (b), seasonal difference in temperature (c), sea bottom salinity (d) , Phytoplankton Colour Index (d), substrate richness (f), beam trawl effort (g) and otter trawl effort (h). All variables were used as predictors to model the spatial community weighted mean traits.