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Global Patterns of Predator Diversity in the Open Oceans

Boris Worm, Marcel Sandow, Andreas Oschlies, Heike K. Lotze, Ransom A. Myers

Supporting Online Material

Materials and Methods

Diversity data. Tuna and billfish diversity was calculated from 1990-99 Japanese longlining logbook data binned on a global $5^\circ \times 5^\circ$ grid. These data yielded information on 62,092,629 individual fish caught on 4.8 billion longline hooks (Table S1). This data set covers the global range of all tuna and billfish species with the exception of coastal areas that are protected by individual countries Exclusive Economic Zones. Countries such as Australia, New Zealand and other Pacific nations however have granted coastal access to Japanese vessels through joint agreements. The rationale for using the 1990s was that fishing techniques did not change significantly during this period, as they had earlier with an increase in average fishing depth during the 1970s and 80s (*SI*). Furthermore, independent scientific observer data from U.S. and Australian longline fisheries were available to cross-validate the Japanese data for that period (Table S1). Species richness was expressed as the expected number of species from a standardized subsample of size n , which is computed as

$$E(S_n) = \sum_{i=1}^S \left[1 - \frac{\binom{N - m_i}{n}}{\binom{N}{n}} \right], \quad (1)$$

where N is the total number of individuals in the sample, S is the total number of species in the sample, m_i is the number of individuals of species i in the sample (S_2). Species density was calculated as the expected number of species standardized to $k=1000$ hooks. In this case, the number of individuals per 1000 hooks determines n , and hence diversity is also dependent on the abundance of species. We chose 50 individuals and 1000 hooks as standardized subsample sizes because these correspond roughly to the average number of individuals and hooks sampled by a single longlining set. Using other subsample sizes ($n=20, 100, 500, k=500, 2000, 5000$) did not change diversity patterns. Similarly, checking robustness by randomly deleting single species and re-calculating diversity did not change the results. This means that diversity patterns were not driven by any particular species.

Using the same methods as outlined above, total predator diversity was derived from U.S. and Australian scientific observer data as supplied by the U.S. National Marine Fishery Service (NOAA/NMFS) in the Northwest Atlantic (Atlantic observer data, since 1991, $N=1962$ longline sets) and around Hawaii (Hawaiian observer data, since 1994, $N= 3290$ sets), and by the Australian Fisheries Management Authority (AFMA; Australian observer data, since 1991, $N= 3127$ sets). These data yielded information on 439,136 individual fish, turtles, mammals and birds caught on 12.06 million longline hooks (Table S1).

Foraminiferan zooplankton data as used by Rutherford et al. (S_3) were retrieved from the Brown University Foraminifera Database, and binned across a global $5^\circ \times 5^\circ$ grid. Diversity was expressed as species richness per sample. Regression analyses were reported for the Atlantic foraminiferan data (Fig. 1G), as only the Atlantic data were deemed reliable

enough for analysis (S3). Yet the relationship between the global foraminiferan and tuna and billfish data set was equally strong ($r=0.63$, $P<0.0001$).

Oceanographic analysis. To obtain global coverage at a spatial resolution high enough to resolve mesoscale variability of the upper ocean, we based our analysis of oceanographic variables on fine-scale satellite data covering 1998-2002. Five-daily maps of sea surface temperature (SST) at 0.5° resolution were provided by the NOAA/NASA AVHRR Oceans Pathfinder project. Error estimates for this data set range from 0.3 - 0.5°C . Weekly maps of satellite-derived sea surface height (SSH) anomalies at 0.35° resolution were derived from the TOPEX/Poseidon altimeter provided by the French Aviso. SSH anomalies were used to calculate eddy kinetic energy according to (S4). Weekly surface chlorophyll *a* fields at 0.35° resolution were derived from SeaWiFS satellite ocean colour data. The error level of these data is estimated as 35%. Oxygen data at 100 m depth (corresponding to the average depth of a longline) were derived from the Levitus data set (NOAA National Oceanographic Data Center, Silver Springs, Maryland). Bathymetric data at 0.08° resolution were derived from the ETOPO5 data set (NOAA National Geophysical Data Center, Boulder, Colorado). Spatial gradients in SST ($^\circ\text{C km}^{-1}$), chlorophyll *a* ($\text{mg m}^{-3} \text{ km}^{-1}$), and bathymetry (m km^{-1}) were estimated by calculating the maximum absolute slope of each data point (at original resolution of 0.5° , 0.35° , or 0.08° , respectively) to its eight surrounding points. Slopes were subsequently averaged across $5^\circ \times 5^\circ$ grid cells. Alternatively, we calculated frontal density from slope data by using a lower cut-off of 0.01 or $0.02^\circ\text{C km}^{-1}$ (S5). This gave similar results as the mean slope which we report here. We

then fitted spatial regression models to these data in an attempt to predict diversity from oceanographic data. Eddy kinetic energy, chlorophyll a and depth gradient data were log-transformed to improve linearity. Spatial regression models accounted for possible spatial dependence among cells by using a conditional autoregressive model (S6). The spatial covariance between two $5^\circ \times 5^\circ$ cells y_i and y_j was assumed to decline with distance d in an anisotropic exponential decay function, such that

$$\text{cov}(y_i, y_j) = \sigma^2 \exp(-(\theta_1 d_{i,j,1} + \theta_2 d_{i,j,2})), \quad (2)$$

where θ_1 describes the latitudinal and θ_2 the longitudinal covariance parameter, $d_{i,j,1}$ is the latitudinal distance and $d_{i,j,2}$ the longitudinal distance between cells. Covariance parameters were estimated from the data using maximum likelihood (Procedure MIXED in SAS V.8). Cells from different oceans were assumed independent. We first fitted this model to the 1990s data, and then confirmed its robustness by fitting it to diversity and SST data from previous decades (1960-99). In these cases we used extended reconstructed sea surface temperature data (ERSST) as provided by the NOAA-CIRES climate diagnostic center (University of Colorado, Boulder, CO, USA). These analyses produced very consistent results across decades (Table S3).

Historic trends in diversity. Using mixed effects models we estimated long-term trends and short-term variability in tuna and billfish diversity and examined relationships with fishing and climate for each ocean. Trends in tuna and billfish diversity over time were estimated from 1952-99 Japanese longlining data. Using recently derived correction factors

for each species ($S7$), we first standardized Japanese longline data for historic changes in fishing practices, particularly the increase in longline depth during the 1970s and 1980s to target deeper-swimming species such as bigeye tuna (*Thunnus obesus*). Species richness and species density by year were calculated from these data by rarefaction as outlined above. The resulting data sets are displayed in Movies S1 and S2, respectively. From these data sets we estimated trends in species richness and species density for each ocean using linear mixed effects models that accounted for any changes in the coverage and seasonality of fished cells. We fitted the model

$$\alpha_{j,m,t} = \mu + month_m + year_t + lat_j + lon_j + lat \times lon_j + lat_j \times month_m + \varepsilon_{j,m,t}, \quad (3)$$

where $\alpha_{j,m,t}$ refers to diversity (species richness or species density) in cell j (defined by its latitude and longitude), month m , year t , and where μ describes the mean across all cells, months and years, and $\varepsilon_{i,k,l,m}$ the random error. Year and month were fixed categorical effects, while the other terms were modeled as random effects with normal distribution, zero mean and variances σ_j^2 , σ_m^2 , and σ_t^2 , respectively. Alternative analyses treating latitude and longitude as fixed effects yielded similar results. For further analysis we calculated the estimated least square means for the year effects in diversity D_t across each ocean. The first years in the Atlantic (1956-60) were excluded due to low sample size and latitudinal coverage.

Long-term changes in diversity were plotted against total catches of tuna and billfish (all gear types combined), compiled from the Food and Agriculture Organization (FAO) database. Year-to-year variation in diversity, i.e. the first difference in species richness $\Delta_t = D_{t+1} - D_t$ was calculated from the mixed effects model output for each ocean. Those

time series were initially correlated at zero lag with the multivariate El Niño Southern Oscillation (ENSO) index (Dec-Mar average) provided by the NOAA-CIRES climate diagnostic center (University of Colorado, Boulder, CO, USA). Longer time lags attenuated the correlation. Similar analyses were performed using the Pacific Decadal Oscillation Index (*S8*) supplied by the Joint Institute for the Study of the Atmosphere and the Ocean (Washington University, Seattle, WA, USA), the North Atlantic Oscillation Index (*S9*) supplied by the Climate Research Unit (University of East Anglia, Norwich, UK), and the Indian Ocean Dipole Index (*S10*) supplied by the Japanese Agency for Marine-Earth Science and Technology (Tokyo, Japan). Here, temporal autocorrelation was effectively removed by first-differencing, as confirmed by the Durbin-Watson test. Spatial variation among cells in response to ENSO across the Pacific was estimated using a mixed effects model for the first difference in diversity

$$\Delta_{j,t} = \beta ENSO_t + \beta_j ENSO_t + \varepsilon_{j,t}, \quad (4)$$

where β is the slope parameter that describes the mean rate of change in diversity with ENSO, β_j is the random slope component for cell j , which is assumed normal with zero mean and variance σ_β^2 , and $\varepsilon_{i,j}$ is the random error also assumed normal with zero mean and variance σ^2 . Best linear unbiased predictions for β_j were calculated and plotted for each cell to describe the local variation in the response in the change in diversity to the ENSO index. Similar analysis was carried out for the change in log catch rates for each species. Simple linear correlations of $\Delta_{j,t}$ with ENSO yielded index very similar results.

References

- S1. Y. Uozumi, H. Nakano, in *Collective Volume of Scientific Papers. Report of the second ICCAT Billfish Workshop*. (International Commission for the Conservation of Atlantic Tunas, Madrid, Spain, 1996) pp. 233–243.
- S2. N. J. Gotelli, G. R. Graves, *Null Models in Ecology* (Smithsonian Institution Press, Washington D.C., 1996).
- S3. S. Rutherford, S. D'Hondt, W. Prell, *Nature* **400**, 749-753 (1999).
- S4. A. Oschlies, V. Garçon, *Nature* **394**, 266-269 (1998).
- S5. P. Etnoyer, D. Canny, B. Mate, L. Morgan, *Oceanography* **17**, 90-101 (2004).
- S6. N. A. C. Cressie, *Statistics for Spatial Data* (John Wiley & Sons, New York, 1993).
- S7. P. Ward, R. A. Myers, *Can. J. Fish. Aquat. Sci.* **62**, 1130-1142 (2005).
- S8. N. J. Mantua, S. R. Hare, Y. Zhang, J. M. Wallace, R. C. Francis, *Bull. Am. Meteorol. Soc.* **78**, 1069-1079 (1997).
- S9. J. W. Hurrell, *Science* **269**, 676-679 (1995).
- S10. N. H. Saji, B. N. Goswami, P. N. Vinayachandran, T. Yamagata, *Nature* **401**, 360 - 363 (1999).

Table S1. Sample sizes of species identified in the Japanese and regional observer data sets 1990-99

Category	Common Name	Scientific Name	Global Japanese	Atlantic observer	Hawaii observer	Australia observer
Billfish	Atlantic blue marlin	<i>Makaira nigricans</i>	106944	554	-	-
	Black marlin	<i>Makaira indica</i>	40116	-	37	251
	Indo-Pacific blue marlin	<i>Makaira mazara</i>	997978	-	1334	295
	Longbill spearfish	<i>Tetrapturus pfluegeri</i>	-	72	-	-
	Marlin	<i>Makaira</i> sp.	-	-	-	4
	Roundscale spearfish	<i>Tetrapturus georgei</i>	-	8	-	-
	Sailfish	<i>Istiophorus platypterus</i>	96265	514	104	203
	Shortbill spearfish	<i>Tetrapturus angustirostris</i>	-	-	2146	1090
	Spearfish	<i>Tetrapturus</i> sp.	94582	67	-	-
	Striped marlin	<i>Tetrapturus audax</i>	1152396	-	3640	1505
	Swordfish	<i>Xiphias gladius</i>	2310633	28621	17121	3686
	White marlin	<i>Tetrapturus albidus</i>	32060	762	-	-
Tuna	Albacore tuna	<i>Thunnus alalunga</i>	13853138	1020	14669	48010
	Atlantic bluefin tuna	<i>Thunnus thynnus</i>	298617	396	-	-
	Bigeye tuna	<i>Thunnus obesus</i>	26304855	3039	13007	6485
	Blackfin tuna	<i>Thunnus atlanticus</i>	-	131	-	-
	Bullet tuna	<i>Auxis rochei rochei</i>	-	-	1	-
	Little tuna	<i>Euthynnus alletteratus</i>	-	66	-	-
	Kawakawa	<i>Euthynnus affinis</i>	-	-	4	1
	Pacific bluefin tuna	<i>Thunnus orientalis</i>	13398	-	72	12
	Skipjack tuna	<i>Katsuwonus pelamis</i>	135394	42	2097	1507
	Slender tuna	<i>Allothunnus fallai</i>	-	-	-	72
	Southern bluefin tuna	<i>Thunnus maccoyii</i>	1434572	-	-	31231
Yellowfin tuna	<i>Thunnus albacares</i>	15221681	3208	5651	23244	
Other bony fish	Amberjack	<i>Seriola</i> sp.	-	1	-	-
	Atlantic cutlassfish	<i>Trichiurus lepturus</i>	-	2	-	-
	Banded rudderfish	<i>Seriola zonata</i>	-	-	-	-
	Barracouta	<i>Thyrsites</i> sp.	-	-	-	100
	Barracuda	<i>Sphyrænidæ</i>	-	108	-	-
	Bigeye cigarfish	<i>Cubiceps</i> sp.	-	55	-	-
	Bigeye scad	<i>Selar crumenophthalmus</i>	-	-	7	-
	Black sea bass	<i>Centropristis striata</i>	-	1	-	-
	Blackfin snapper	<i>Lutjanus buccanella</i>	-	1	-	-
	Blue grenadier	<i>Macruronus novaezealandiae</i>	-	-	-	11
	Bluefish	<i>Pomatomus saltatrix</i>	-	44	-	-
	Bonito	<i>Sarda sarda</i>	-	19	-	-
	Butterfly mackerel	<i>Gasterochisma melampus</i>	-	-	-	1440
	Chub mackerel	<i>Scomber japonicus</i>	-	6	1	-
	Cobia	<i>Rachycentron canadum</i>	-	1	-	-
	Common dolphinfish	<i>Coryphaena hippurus</i>	-	5070	14563	822
	Common sunfish	<i>Mola ramsayi</i>	-	-	126	925
	Conger eel	Congridae	-	-	-	1
	Crestfish	<i>Lophotus lacepede</i>	-	-	23	-
	Cutlassfishes	Trichiuridae	-	111	-	-
	Dagger pomfret	<i>Taractes rubescens</i>	-	-	51	-
	Dealfish	Trachipteridae	-	1	4	-
	Deep sea trevalla	<i>Hyperoglyphe antarctica</i>	-	-	-	11
	Escolar	<i>Lepidocybium flavobrunneum</i>	-	1253	1359	4010

	Flying Fish	Exocoetidae	-	-	1	3
	Frigate mackerel	<i>Auxis thazard</i>	-	4	-	-
	Gemfish	<i>Rexea solandri</i>	-	-	-	16
	Goosefish	Lophiidae	-	1	-	-
	Great barracuda	<i>Sphyræna barracuda</i>	-	-	235	111
	Jack	<i>Caranx</i> sp.	-	1	-	-
	King mackerel	<i>Scomberomorus cavalla</i>	-	5	-	-
	Lancetfish	<i>Alepisaurus</i> sp.	-	1038	7453	-
	Long-finned bream	<i>Taractichthys longipinnis</i>	-	-	-	742
	Long-nosed lancet fish	<i>Alepisaurus ferox</i>	-	-	-	7884
	Louvar	<i>Luvarus imperialis</i>	-	-	1	-
	Oarfish	<i>Regalecus glesne</i>	-	-	6	-
	Oilfish	<i>Ruvetus pretiosus</i>	-	404	623	4960
	Opah	<i>Lampris guttatus</i>	-	1	1207	990
	Pacific pomfret	<i>Brama japonica</i>	-	-	237	-
	Pelagic puffer	<i>Lagocephalus lagocephalus</i>	-	-	32	-
	Pomfret	Bramidae	-	22	-	202
	Puffer	Tetraodontidae	-	45	-	-
	Rainbow runner	<i>Elagatis bipinnulatus</i>	-	1	6	-
	Ray's Bream	<i>Brama brama</i>	-	-	-	27278
	Remora	Echeneidae	-	8	9373	-
	Ribbonfishes	Trachipteridae	-	-	-	114
	Rudderfish	<i>Centrolophus niger</i>	-	-	-	239
	Short-nosed lancet fish	<i>Alepisaurus brevirostris</i>	-	-	-	723
	Sickle pomfret	<i>Taractichthys steindachneri</i>	-	-	1659	-
	Slender barracuda	<i>Sphyræna jello</i>	-	-	-	185
	Slender sunfish	<i>Ranzania laevis</i>	-	-	43	-
	Snake mackerel	<i>Gempylus serpens</i>	-	-	2683	50
	Southern ray's bream	<i>Brama</i> sp.	-	-	-	91
	Sunfish	<i>Mola</i> sp.	-	101	-	-
	Triggerfish	Balistidae	-	3	-	-
	Tripletail	<i>Lobotes surinamensis</i>	-	1	-	-
	Wahoo	<i>Acanthocybium solandri</i>	-	192	1233	474
	Yellowtail kingfish	<i>Seriola lalandi</i>	-	-	1	57
Turtles	Green turtle	<i>Chelonia mydas</i>	-	12	10	-
	Hawksbill turtle	<i>Eretmochelys imbricata</i>	-	3	-	-
	Leatherback turtle	<i>Dermochelys coriacea</i>	-	164	44	-
	Loggerhead turtle	<i>Caretta caretta</i>	-	287	166	-
	Olive ridley turtle	<i>Lepidochelys olivacea</i>	-	-	36	-
Sharks and rays	Atlantic sharpnose shark	<i>Rhizoprionodon terraenovae</i>	-	15	-	-
	Bigeye thresher shark	<i>Alopias superciliosus</i>	-	205	591	-
	Bignose shark	<i>Carcharhinus altimus</i>	-	30	26	-
	Blacktip shark	<i>Carcharhinus limbatus</i>	-	70	-	-
	Blue shark	<i>Prionace glauca</i>	-	26757	33346	37310
	Bronze whaler shark	<i>Carcharhinus brachyurus</i>	-	-	-	202
	Bull shark	<i>Carcharhinus leucas</i>	-	26	-	-
	Common thresher shark	<i>Alopias vulpinus</i>	-	37	-	144
	Cookie cutter shark	<i>Isistius brasiliensis</i>	-	2	18	62
	Crocodile shark	<i>Pseudocarcharias kamoharai</i>	-	156	170	921
	Dogfish	Squalidae	-	1	-	118
	Dusky shark	<i>Carcharhinus obscurus</i>	-	649	26	313
	Galapagos shark	<i>Carcharhinus galapagensis</i>	-	-	5	-

	Great hammerhead shark	<i>Sphyrna mokarran</i>	-	49	-	-
	Great white shark	<i>Carcharodon carcharias</i>	-	-	3	-
	Hammerhead sp.	<i>Sphyrna</i> sp.	-	111	4	57
	Lemon shark	<i>Negaprion brevirostris</i>	-	1	-	-
	Longfin mako shark	<i>Isurus paucus</i>	-	47	14	4
	Mako sp.	<i>Isurus</i> sp.	-	238	10	-
	Manta ray	Mobulidae	-	-	12	22
	Night shark	<i>Carcharhinus signatus</i>	-	310	-	-
	Nurse shark	<i>Ginglymostoma cirratum</i>	-	1	-	-
	Oceanic whitetip shark	<i>Carcharhinus longimanus</i>	-	278	1067	246
	Pelagic stingray	<i>Pteroplatytrygon violacea</i>	-	39	2851	1906
	Pelagic thresher shark	<i>Alopias pelagicus</i>	-	-	-	1
	Porbeagle shark	<i>Lamna nasus</i>	-	14	-	2421
	Ray	Chondrichthyes	-	1452	-	-
	Reef shark	<i>Carcharhinus perezii</i>	-	7	-	-
	Salmon shark	<i>Lamna ditropis</i>	-	-	65	-
	Sandbar shark	<i>Carcharhinus plumbeus</i>	-	188	25	1
	Scalloped hammerhead shark	<i>Sphyrna lewini</i>	-	356	-	-
	School shark	<i>Galeorhinus galeus</i>	-	-	-	224
	Shortfin mako shark	<i>Isurus paucus</i>	-	1051	519	1516
	Silky shark	<i>Carcharhinus falciformis</i>	-	1789	183	11
	Smooth hammerhead shark	<i>Sphyrna zygaena</i>	-	4	17	-
	Spinner shark	<i>Carcharhinus brevipinna</i>	-	12	-	-
	Spiny dogfish	<i>Squalus acanthias</i>	-	18	-	-
	Thresher sp.	<i>Alopias</i> sp.	-	15	111	257
	Tiger shark	<i>Galeocerdo cuvieri</i>	-	284	6	61
	Velvet dogfish	<i>Zameus squamulosus</i>	-	-	-	236
Mammals	Australian fur seal	<i>Arctocephalus pusillus</i>	-	-	-	3
	Beaked whale	Ziphiidae	-	1	-	-
	Bottlenose dolphin	<i>Tursiops truncatus</i>	-	4	2	-
	Dolphin	<i>Stenella</i> sp.	-	1	2	1
	False killer whale	<i>Pseudorca crassidens</i>	-	-	2	-
	Killer whale	<i>Orcinus orca</i>	-	1	-	-
	Pantropic spotted dolphin	<i>Stenella attenuata</i>	-	2	-	-
	Pilot whale sp.	<i>Globicephala</i> sp.	-	12	-	-
	Risso's dolphin	<i>Grampus griseus</i>	-	4	6	-
	Short spinner dolphin	<i>Stenella clymene</i>	-	1	-	-
	Shortfin pilot whale	<i>Globicephala macrorhynchus</i>	-	1	-	-
	Sperm whale	<i>Physeter macrocephalus</i>	-	-	1	-
	Whale	Cetacea	-	-	5	3
Seabirds	Albatross sp.	<i>Diomedidae</i> sp.	-	-	-	261
	Black-footed albatross	<i>Phoebastria nigripes</i>	-	-	624	-
	Gull	Larinae	-	1	-	-
	Laysan albatross	<i>Diomedea immutabilis</i>	-	-	437	-
	Other seabirds	Aves	-	12	4	791
	Petrel sp.	Procellariidae	-	-	-	73
Number of individuals			62092629	81718	141218	216200
Number of species			15	90	71	67
Number of sets			-	1962	3290	3127
Number of hooks (x1000)			4801751	1116	3835	7109
Mean hooks per set			-	569	1166	2273
Mean individuals per 1000 hooks			12.9	73.2	36.8	30.4

Table S2. Mixed model results for trends in diversity over time

Variable	Species richness Atlantic Ocean				Species density Atlantic Ocean			
	df (num.)	df (denom.)	F	P	df (num.)	df (denom.)	F	P
Month	11	211	2.8	0.0024	11	211	2.0	0.0295
Year	43	22000	50.0	<0.0001	43	22000	234.5	<0.0001
Covariance parameters	estimate	s.e.	Z	P	estimate	s.e.	Z	P
Latitude (Lat)	0.766	0.242	3.2	0.0008	0.405	0.127	3.2	0.0007
Longitude (Lon)	0.343	0.110	3.1	0.0009	0.314	0.097	3.2	0.0006
Lat x Lon	0.147	0.015	9.6	<0.0001	0.097	0.010	9.6	<0.0001
Lat x Month	0.033	0.004	7.7	<0.0001	0.020	0.003	7.7	<0.0001
Residual	0.645	0.006	105.5	<0.0001	0.422	0.004	105.5	<0.0001

Variable	Species richness Indian Ocean				Species density Indian Ocean			
	df (num.)	df (denom.)	F	P	df (num.)	df (denom.)	F	P
Month	11	135	4.6	<0.0001	11	135	4.1	<0.0001
Year	46	28000	27.6	<0.0001	46	28000	439.7	<0.0001
Covariance parameters	estimate	s.e.	Z	P	estimate	s.e.	Z	P
Latitude (Lat)	1.975	0.769	2.6	0.0051	1.061	0.414	2.6	0.0052
Longitude (Lon)	0.134	0.048	2.8	0.0028	0.098	0.034	2.9	0.0020
Lat x Lon	0.139	0.017	8.3	<0.0001	0.084	0.010	8.4	<0.0001
Lat x Month	0.025	0.004	6.4	<0.0001	0.011	0.002	5.9	<0.0001
Residual	0.673	0.006	119.1	<0.0001	0.391	0.003	119.1	<0.0001

Variable	Species richness Pacific Ocean				Species density Pacific Ocean			
	df (num.)	df (denom.)	F	P	df (num.)	df (denom.)	F	P
Month	11	205	1.9	0.0454	11	205	3.8	<0.0001
Year	47	93000	91.1	<0.0001	47	93000	377.1	<0.0001
Covariance parameters	estimate	s.e.	Z	P	estimate	s.e.	Z	P
Latitude (Lat)	0.846	0.291	2.9	0.0018	0.623	0.202	3.1	0.0010
Longitude (Lon)	0.026	0.012	2.2	0.0150	0.065	0.020	3.2	0.0006
Lat x Lon	0.177	0.013	13.3	<0.0001	0.088	0.007	13.1	<0.0001
Lat x Month	0.111	0.012	9.3	<0.0001	0.040	0.005	8.1	<0.0001
Residual	0.535	0.002	215.8	<0.0001	0.316	0.001	215.7	<0.0001

Table S3. Spatial regression models for depth-corrected decadal data 1960-1999

Variable	Species richness 1960-69				Species density 1960-69			
	coefficient	s.e.	t	P	coefficient	s.e.	t	P
Intercept	2.510	0.862	2.9	0.1005	1.551	0.724	2.1	0.1655
SST	-0.453	0.153	-3.0	0.0032	-0.313	0.128	-2.5	0.0143
(SST) ²	0.034	0.009	3.6	0.0004	0.028	0.008	3.6	0.0004
(SST) ³	-0.001	0.0002	-3.2	0.0015	-0.001	0.0001	-3.6	0.0004
SST gradient	52.438	12.044	4.4	<0.0001	37.586	10.304	3.7	0.0003
Dissolved oxygen	0.081	0.047	1.7	0.0853	0.090	0.041	2.2	0.0276
Covariance parameters	θ_1	θ_2	σ^2		θ_1	θ_2	σ^2	
Estimate	0.227	0.042	0.473		0.191	0.046	0.336	
Likelihood ratio test	df=2	$X^2=248.4$	P<0.0001		df=2	$X^2=272.2$	P<0.0001	
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Variable	Species richness 1970-79				Species density 1970-79			
	coefficient	s.e.	t	P	coefficient	s.e.	t	P
Intercept	2.763	0.869	3.2	0.0863	1.119	0.681	1.6	0.2421
SST	-0.543	0.154	-3.5	0.0004	-0.340	0.121	-2.8	0.0050
(SST) ²	0.043	0.009	4.6	<0.0001	0.030	0.007	4.1	<0.0001
(SST) ³	-0.001	0.0002	-4.5	<0.0001	-0.001	0.0001	-4.2	<0.0001
SST gradient	31.861	13.684	2.3	0.0201	28.938	10.567	2.7	0.0063
Dissolved oxygen	0.083	0.048	1.7	0.0870	0.160	0.038	4.2	<0.0001
Covariance parameters	θ_1	θ_2	σ^2		θ_1	θ_2	σ^2	
Estimate	0.280	0.084	0.519		0.269	0.076	0.316	
Likelihood ratio test	df=2	$X^2=88.3$	P<0.0001		df=2	$X^2=117.7$	P<0.0001	
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Variable	Species richness 1980-89				Species density 1980-89			
	coefficient	s.e.	t	P	coefficient	s.e.	t	P
Intercept	1.727	1.158	1.5	0.2744	0.554	0.914	0.6	0.6062
SST	-0.402	0.199	-2.0	0.0436	-0.150	0.158	-1.0	0.3424
(SST) ²	0.038	0.012	3.3	0.0012	0.020	0.009	2.1	0.0334
(SST) ³	-0.001	0.0002	-3.7	0.0003	0.000	0.0002	-2.5	0.0133
SST gradient	28.695	14.936	1.9	0.0551	18.552	11.737	1.6	0.1144
Dissolved oxygen	0.160	0.052	3.1	0.0022	0.108	0.043	2.5	0.0118
Covariance parameters	θ_1	θ_2	σ^2		θ_1	θ_2	σ^2	
Estimate	0.220	0.082	0.529		0.188	0.071	0.346	
Likelihood ratio test	df=2	$X^2=85.3$	P<0.0001		df=2	$X^2=132.7$	P<0.0001	
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Variable	Species richness 1990-99				Species density 1990-99			
	coefficient	s.e.	t	P	coefficient	s.e.	t	P
Intercept	1.291	0.852	1.5	0.2689	0.644	0.637	1.0	0.4184
SST	-0.427	0.152	-2.8	0.0050	-0.323	0.115	-2.8	0.0050
(SST) ²	0.040	0.009	4.3	<0.0001	0.030	0.007	4.2	<0.0001
(SST) ³	-0.001	0.0002	-4.7	<0.0001	-0.001	0.0001	-4.5	<0.0001
SST gradient	48.697	14.107	3.5	0.0006	34.613	10.136	3.4	0.0007
Dissolved oxygen	0.181	0.050	3.6	0.0004	0.177	0.040	4.5	<0.0001
Covariance parameters	θ_1	θ_2	σ^2		θ_1	θ_2	σ^2	
Estimate	0.241	0.086	0.481		0.178	0.070	0.272	
Likelihood ratio test	df=2	$X^2=69.2$	P<0.0001		df=2	$X^2=142.8$	P<0.0001	

Table S4. Data sources

Variable	Source	Web access
Atlantic Ocean longline data	International Commission for the Conservation of Atlantic Tunas	http://iccat.es/
Indian Ocean longline data	Indian Ocean Tuna Commission	http://www.iotc.org/English/data/databases.php
Pacific Ocean longline data (1950-80)	Oceanic Fisheries Program, Secretariat of the Pacific Community	http://www.spc.org.nc/OceanFish/html/SC/TB/Data/Index.asp
Pacific Ocean longline data (post 1980)	Japanese Fishery Agency	not available
North Atlantic observer data	NOAA-NMFS Southeast Fishery Science Center	http://www.sefsc.noaa.gov/pop.jsp
Hawaiian observer data	NOAA-NMFS Pacific Area Islands Office	not available
Australian observer data	Australian Fishery Management Agency	not available
Global tuna and billfish catch data	FAO; The Sea Around Us Project, University of British Columbia	http://www.fao.org/ffi/statist/statist.asp ; http://www.seaaroundus.org/
Sea surface temperature (SST) 1998-2002	NASA Physical Oceanography Distributed Active Archive Center	http://podaac.jpl.nasa.gov/sst/
Chlorophyll <i>a</i>	NASA Goddard Space Flight Center	http://oceancolor.gsfc.nasa.gov/SeaWIFS/
Historic SST (1950-2000)	NOAA-CIRES Climate Diagnostic Center	http://www.cdc.noaa.gov/cdc/data.noaa.ersst.html
Sea surface height (SSH)	CLS Space Oceanography Division	http://www.cls.fr/html/oceano/welcome_en.html
Oxygen at 100 m depth	NOAA National Oceanographic Data Center	http://www.nodc.noaa.gov/General/oxygen.html
Foraminiferan zooplankton diversity	Brown University Foraminiferan database	not available
Bathymetry	NOAA National Geophysical Data Center	http://www.ngdc.noaa.gov/mgg/global/etopo5.html
El Niño Southern Oscillation (ENSO) Index	NOAA-CIRES Climate Diagnostic Center	http://www.cdc.noaa.gov/ENSO/enso_mei_index.html
North Atlantic Oscillation Index (NAO)	Climate Research Unit, University of East Anglia	http://www.cru.uea.ac.uk/cru/data/nao.htm
Indian Ocean Dipole Index (IOD)	Japanese Agency for Marine-Earth Science and Technology	http://www.jamstec.go.jp/frcgc/research/d1/iod/
Pacific Decadal Oscillation Index (PDO)	Joint Institute for the Study of the Atmosphere and the Ocean	http://jisao.washington.edu/pdo/PDO.latest

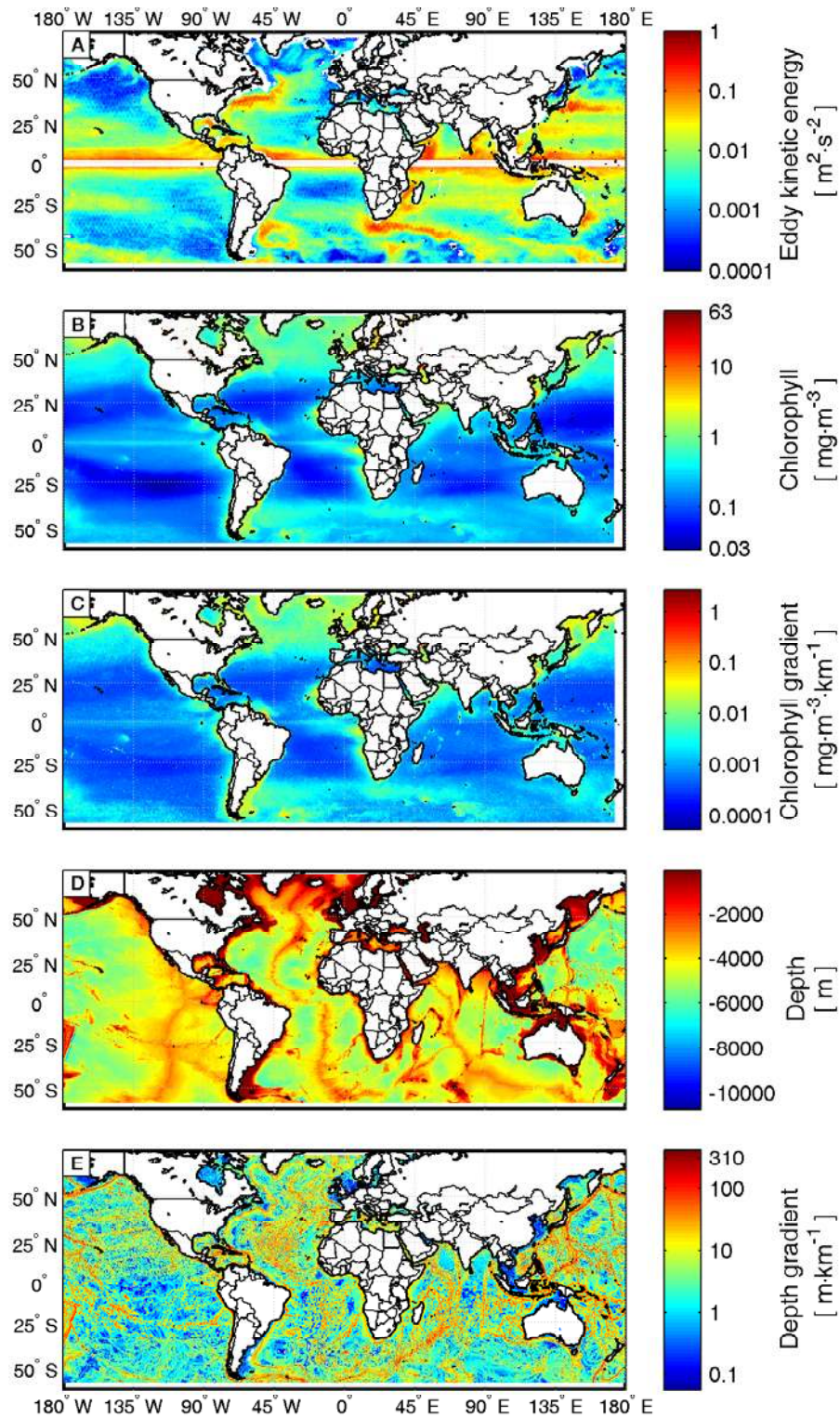


Fig. S1. Additional oceanographic variables used in the analysis. (A) eddy kinetic energy as derived from altimeter data, (B) mean chlorophyll a concentrations, (C) spatial chlorophyll a gradient, (D) depth, and (E) spatial bathymetric gradient.