



Supplementary Materials for

Marine Taxa Track Local Climate Velocities

Malin L. Pinsky,* Boris Worm, Michael J. Fogarty, Jorge L. Sarmiento, Simon A. Levin

*Corresponding author. E-mail: malin.pinsky@rutgers.edu

Published 13 September 2013, *Science* **341**, 1239 (2013)
DOI: 10.1126/science.1239352

This PDF file includes:

Materials and Methods
Figs. S1 to S6
Tables S1 to S5
References (22–26)

Materials and Methods

Survey data

We compiled long-term, spatially extensive, scientific bottom trawl surveys from North America (Table S1). When two surveys were available in the same region, we chose the one with more consistent survey timing (spring rather than fall in the northeast U.S.) or the one that was more spatially extensive (fall rather than spring in Newfoundland).

To ensure that changes in survey extent did not influence our estimates of distribution shift, we standardized each survey to a consistent spatial and depth extent based on the statistical strata that each survey uses (Fig. S1). Years with particularly sparse sampling were dropped (e.g., 1978 and 2003 in the Southern Gulf of St. Lawrence). Consistent strata do not exist for the west coast U.S. triennial survey, and so we defined strata on a $1^\circ \times 1^\circ$ latitude-longitude grid by a 100 m depth grid.

We also trimmed surveys to periods in which they had relatively consistent survey design and sampling gear (Table S1). For example, Newfoundland surveys extend back to 1971, but had a major change in trawl nets beginning in 1995 that cannot be easily corrected. We therefore begin our Newfoundland analysis in 1995. Similarly, we end our analysis of northeast U.S. trawls in 2008, before a large change in the survey vessel occurred. In general, changes in survey gear affect the catchability of particular species, and therefore have particularly large impacts on attempts to estimate overall biomass or to assess stock status. Such changes, however, have less impact on the spatial distributions of biomass that are the focus of our study. For smaller changes in survey methods, we therefore used the correction factors for biomass developed by each agency conducting the surveys (e.g., in the Southern Gulf of St. Lawrence and the northeast U.S.).

Surveys usually recorded biomass, bottom temperature, and surface temperature, though the latter measure was not available for Newfoundland. While surveys were conducted in a variety of seasons (Table S1), we analyze each survey separately and use season-specific temperature data to account for these differences. We restricted our analysis to tows without gear and duration problems, to taxa that were resolved at least to genus, and to taxa that were sampled at least once per year to reduce effects from changes in taxonomic recording or resolution.

Rates of range shift, temperature change, and assemblage offsets

We calculated the centroid of each taxon's distribution in each year of each survey as its biomass-weighted average latitude, longitude, and depth. We treated each taxon in each survey as an independent data point because they are typically considered demographically independent and in many cases are separate populations. We also calculated mean bottom and surface temperatures in each year of each survey. We used linear regressions of mean latitude, depth, or temperature against year to estimate the rate of change, and verified that changes in season-specific survey timing did not explain variation in temperature trends (bottom temperature: $p=0.32$, $n=9$; surface temperature: $p=0.25$, $n=8$).

Latitude and depth rates were averaged across taxa to estimate the mean and standard error of the shift in the assemblage in each region. We also calculated the mean

offset in each assemblage for each year by normalizing each taxon's mean latitude to start at 0 and then averaging the normalized timeseries.

Taxon-specific climate velocity

While climate velocity has most often been calculated on a grid (16, 17), it is difficult to compare grid values to observed shifts of irregular and spatially extensive species distributions. Instead, we need to average the climate velocities across each species distribution to create a taxon-specific version of climate velocity. We did so by recording spatial shifts in the thermal conditions most favorable to each taxon. This approach in effect averaged the climate velocity of those isotherms associated with individual taxa, which allowed us to compare climate velocities directly to observed shifts in taxon distributions.

Because we had temperature data from each survey tow, this definition differed in method from other definitions that start from gridded temperature data (16, 17). However, both definitions of climate velocity (the traditional definition and our taxon-specific version) record the rate at which a given set of thermal conditions shifts across the landscape. The benefit of using survey temperatures is that they corresponded directly to the conditions experienced by the taxa, rather than to remote or interpolated measures. The shifts in thermal conditions that we recorded, however, are limited by the extent and duration of the surveys whose data we used. We used a bootstrap resampling procedure to account for these constraints (see “Analyzing climate velocities” below).

As a first step towards taxon-specific climate velocities, we estimated thermal envelopes for well-sampled taxa (sampled at least ten times each year in a survey) by fitting Generalized Additive Models (GAMs) to biomass data in the surveys. We used a commonly applied statistical approach, a two-part GAM, to account for the large number of zeros in the data (22). Part one of the GAM was fit to presence/absence data and had binomial errors. Part two was fit to log(biomass) data for non-zero observations and had Gaussian errors. Explanatory factors in each model included bottom temperature, surface temperature, survey stratum, and average biomass for the year. Penalized regression splines were used for each temperature term, as is typical in GAMs (22). The stratum effect accounts for consistent differences in habitat quality between locations within a survey, while the average biomass term corrects for survey-wide changes in abundance, such as from overfishing or recovery, that are not relevant to our focus on spatial shifts. We explored including depth as a fifth explanatory factor, but model performance was worse. Models were fit with the mgcv 1.7-18 package in R 2.15.1 (22).

Basic model diagnostics revealed reasonable fits to the data, despite the models' simple form. Area Under the Curve (AUC) evaluation of taxa presence/absence model accuracy (part one of the GAM) revealed a range of 0.65 to 0.996 with a mean of 0.85. Models of non-zero observations (part two of the GAM) explained 5–93% of the deviance in the data, with a mean of 42%.

Thermal envelope predictions (\hat{b}) were calculated as

$$\hat{b} = \hat{p}e^{\hat{u}}\phi$$

where \hat{p} was the prediction from part one, \hat{u} was the prediction from part two, and ϕ was a correction factor. The exponential of a log transformation (used in part two) is

known to produce a biased estimate of the untransformed expectation (23), a problem known as the re-transformation bias problem. We used Duan's smearing estimate of the correction factor, calculated as

$$\phi = \frac{\sum_{i=1}^n e^{\varepsilon_i}}{n}$$

where ε_i were the n residuals from part two of the GAM for a given taxon (23).

Once fit, each model was used to project the thermal envelope onto the seascape in each year (i.e., onto the temperatures observed at the surveys locations in that year). We then calculated the centroid of each thermal envelope in each year by calculating the mean latitude and depth of the survey locations, weighted by the model predictions. This procedure mirrors the approach used to calculate the observed taxon centroids, but considers the location of the thermal envelope instead of the observed distribution of biomass. Next, we calculated the rate and direction at which the centroid of the thermal envelope shifted across latitudes and depths by regressing the latitude or depth of the centroid against year. The slope is the climate velocity in °N/yr or m/yr. We call this a taxon-specific version of climate velocity because it records the rate at which a particular set of thermal conditions shift through space.

Analyzing climate velocities

We compared climate velocities to the observed rates and directions of shifts in taxon distributions (°N/yr or m/yr) with a linear regression. To account for correlated responses within regions, we also fit mixed effects models with the *nlme* package in R 2.15.1 (24). These models had climate velocity as a fixed effect and region as a random effect both for intercept and slope.

In addition, we used a bootstrap resampling procedure to test the null hypothesis that our observed correlation between climate velocity and taxon shifts could occur even if there is no effect of climate velocity on taxa. For each bootstrap, we re-sampled the biomass values within each taxon before re-calculating distribution centroids, rates of distribution shift, and the correlation between climate velocity and distribution shifts. We repeated this procedure 1000 times to generate a null distribution of correlations under the hypothesis of no relationship. We then compared our observed correlation to this null distribution and calculated a p -value as the proportion of bootstrapped correlations larger than our observed correlation.

We next evaluated whether taxa were shifting faster or slower than climate velocity by evaluating the bias (B) and relative bias (RB) between observed and predicted velocities:

$$B = \text{sign}(\hat{y}) \cdot (y - \hat{y})$$

$$RB = \frac{y - \hat{y}}{\hat{y}}$$

where y is the observed rate of shift and \hat{y} is the predicted climate velocity (both in °N/year or m/year). Bias is multiplied by the sign of the predicted velocity (positive is north or deeper, negative is south or shallower) so that positive bias always indicates taxa shifting faster but in the same direction as their thermal envelopes, while negative values indicate taxa shifting slower or in the opposite direction.

Taxon characteristics

We used a model choice framework to test whether taxon and regional characteristics could explain the rate and direction of taxon shifts. We fit multiple linear regression models to the observed rate and direction of shift for each taxon (°N/yr or m/yr) and selected the minimally adequate models with Akaike's Information Criterion (AIC). Negative rates of shift indicated shifts towards the south or towards shallower water.

For models involving all taxa, independent variables included climate velocity, the length of the survey in years, the latitudinal extent of the survey, whether the taxon was a fish or an invertebrate, whether the taxon was commercially fished or not, the survey-wide trend in biomass, and whether the taxon was pelagic or demersal. While spatio-temporal data on the magnitude of fishing effort for each species would have been ideal, such data were not available for the large majority of species in our dataset. Co-linearity among variables was low, and the highest correlation among variables was 26% for survey extent and survey duration (Table S2).

For models involving all fish, we also included the latitudinal range of the taxon (globally), log(maximum length), trophic level, and log(individual growth rate) measured as the von Bertalanffy K parameter. These variables were primarily derived from Fishbase (25). Co-linearity among variables was low, and the highest correlations among variables were 32% for maximum length and growth rate, and 30% for survey extent and survey duration (Table S3).

To identify a minimally adequate model, we first fit linear regressions with all possible combinations of independent variables (128 models for all taxa, 1024 models for fishes). Next, we selected the model with the lowest AIC. Because other models may be nearly as good (AIC nearly as low), we also calculated a multi-model average following standard procedures (26). We also calculated Akaike weights for each model and Relative Variable Importance for each variable included in the models (26). The latter is the sum of Akaike weights across all models that included a particular variable. Redoing our analysis with AICc (the small-sample version of AIC) produced equivalent results, largely because AIC and AICc values were strongly correlated for these models ($p < 0.0001$ and $r^2 > 99.99\%$).

In addition, we fit models for the log-transformed absolute value of distribution shift to examine our ability to explain just the speed of shift, regardless of its direction. For these models, we used a directional version of climate velocity, which we defined as climate velocity times the sign of the observed shift. This ensured that positive values indicated predictions that matched the direction of the observed shift while negative values indicated predictions in the opposite direction.

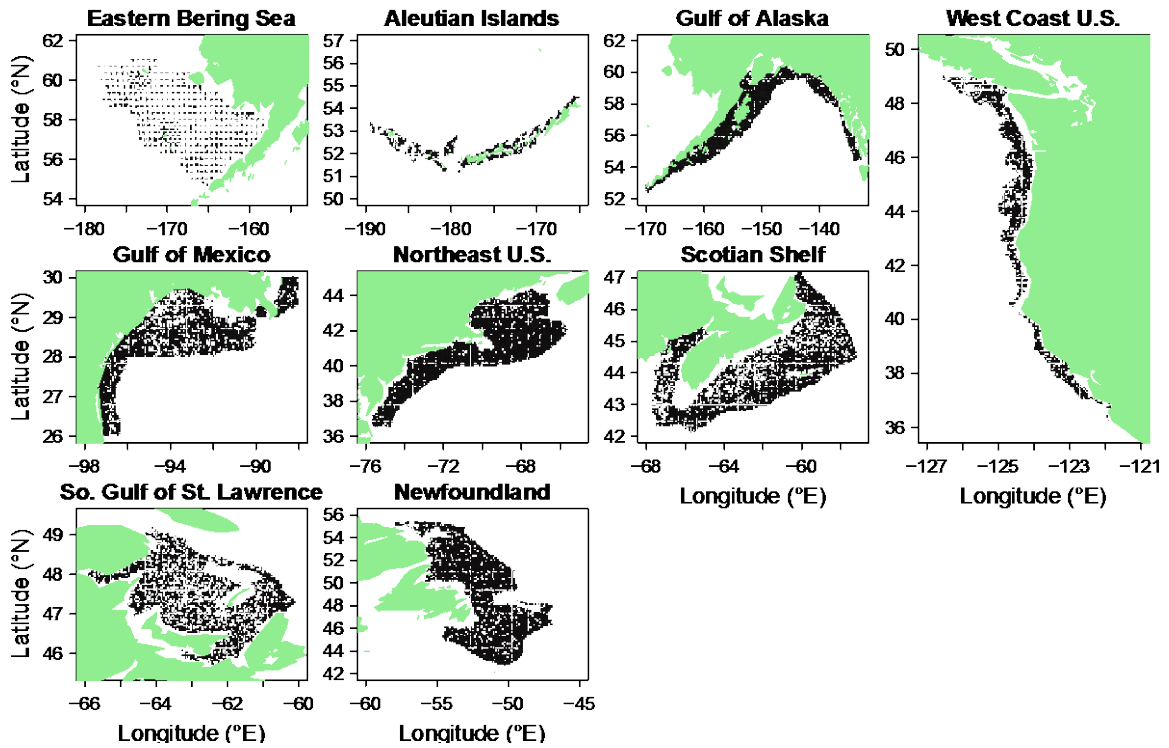


Fig. S1.

Maps of all survey locations (bottom trawl tows) used in our analysis, divided by region. Each black dot represents a bottom trawl tow.

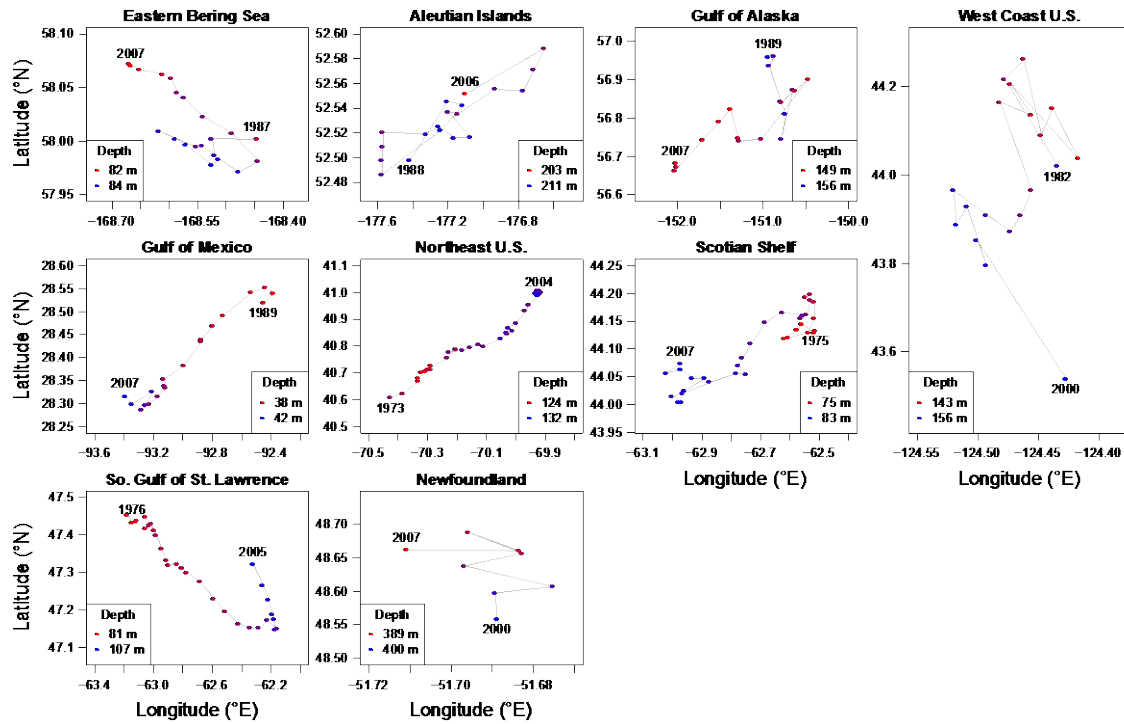


Fig. S2

Assemblage positions through time. Average latitude, longitude, and depth are calculated as 10-year running means centered on the focal year. Color represents depth, from red (shallow) to blue (deep). The depth range of each color gradient is indicated in the inset for each graph.

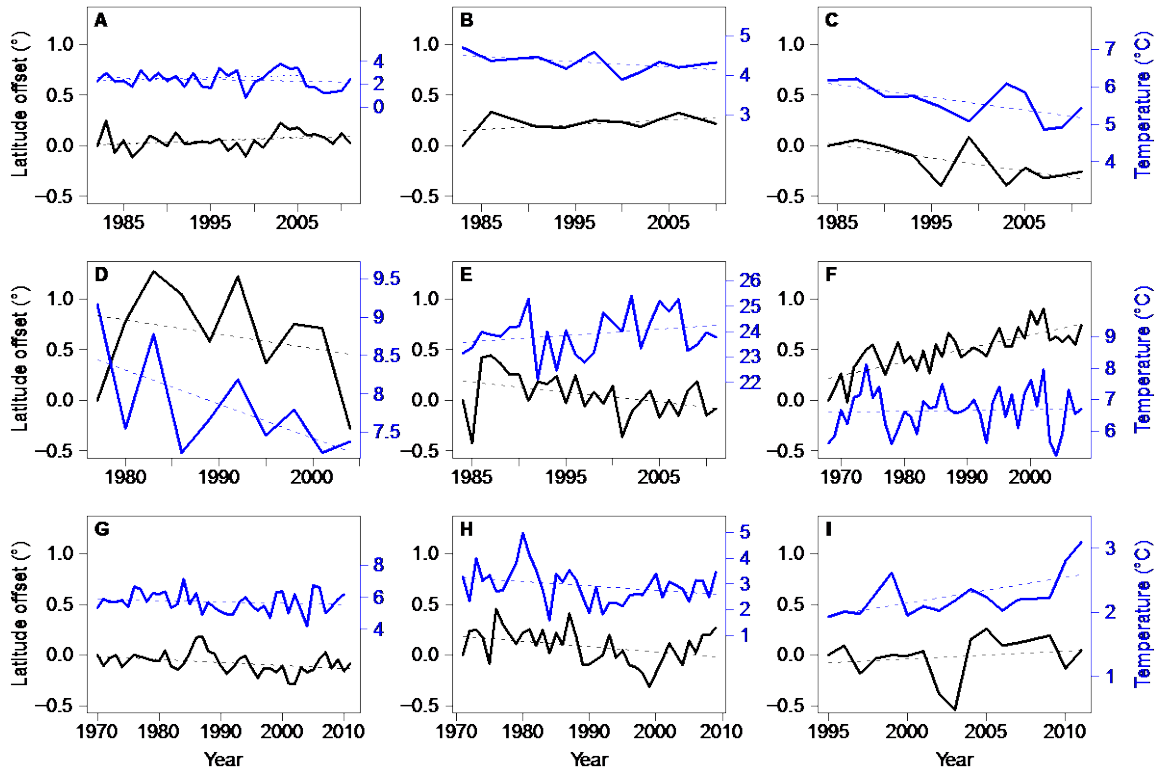


Fig. S3

Average offset in mean latitude (black) of taxa and mean bottom temperature (blue) in each region through time. (A) Eastern Bering Sea, (B) Aleutian Islands, (C) Gulf of Alaska, (D) West Coast U.S., (E) Gulf of Mexico, (F) Northeast U.S., (G) Scotian Shelf, (H) Southern Gulf of St. Lawrence, and (I) Newfoundland. Dashed regression lines are for full time period in each region. Dotted regression lines in the Eastern Bering Sea are for 1982-2006 during a period of warming and northward shifts (as published in Mueter & Litzow 2008). In this region, compare dotted lines to dashed lines (full period) to see how the rapid cooling in recent years has led to an overall cooling trend in this region. Southward shifts in taxon distributions in the Eastern Bering Sea, in contrast, have been of lower magnitude and so the latitudinal trend for the full period remains positive.

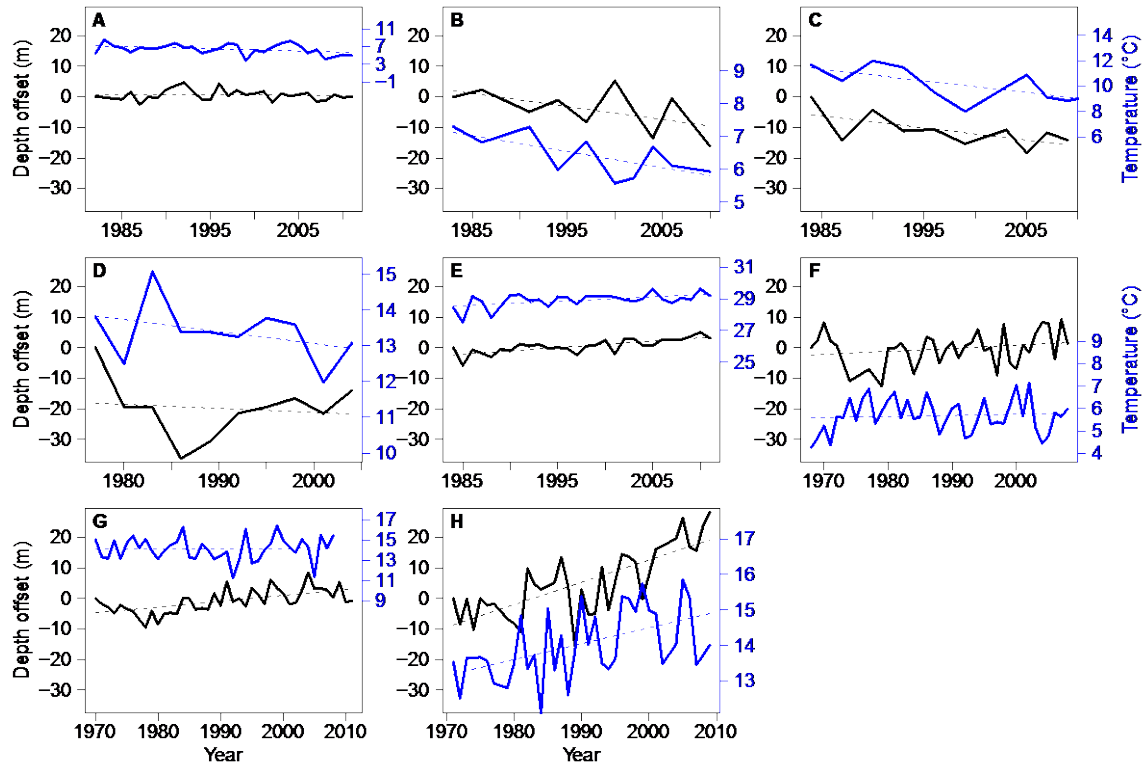


Fig. S4

Average offset in mean depth (black) of taxa and mean surface temperature (blue) in each region through time. (A) Eastern Bering Sea, (B) Aleutian Islands, (C) Gulf of Alaska, (D) West Coast U.S., (E) Gulf of Mexico, (F) Northeast U.S., (G) Scotian Shelf, and (H) Southern Gulf of St. Lawrence. Dashed regression lines are for full time period in each region.

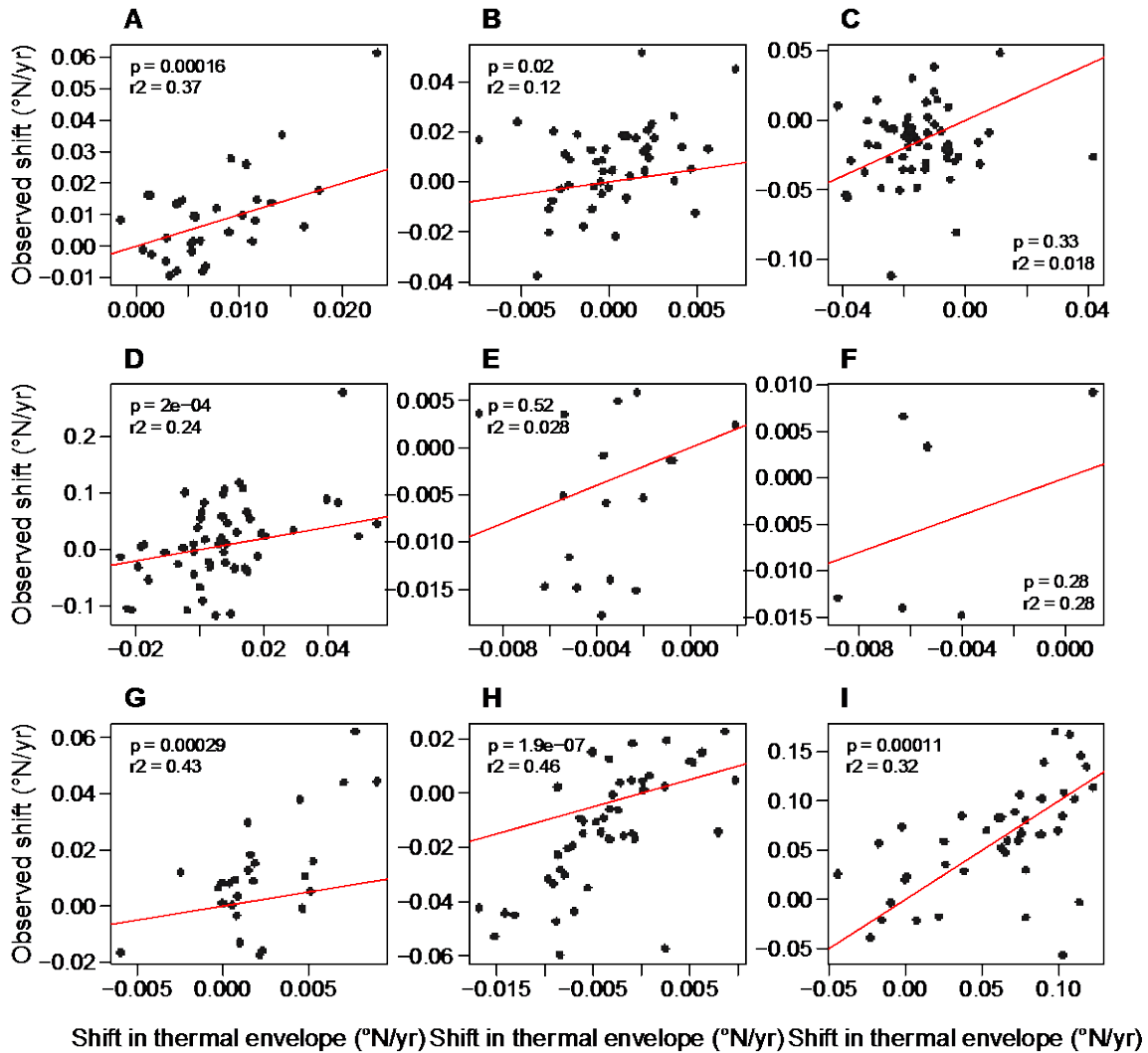


Fig. S5

Relationship between climate velocity and observed shifts in taxon latitude (measured as range centroid) for each survey separately. (A) Aleutian Islands, (B) Eastern Bering Sea, (C) Gulf of Alaska, (D) Newfoundland, (E) Scotian Shelf, (F) Southern Gulf of St. Lawrence, (G) Northeast U.S., (H) Gulf of Mexico, and (I) West Coast U.S. Results from correlations between velocity and observed shifts are printed on each graph (p-values and r² values). The red line is a 1:1 line.

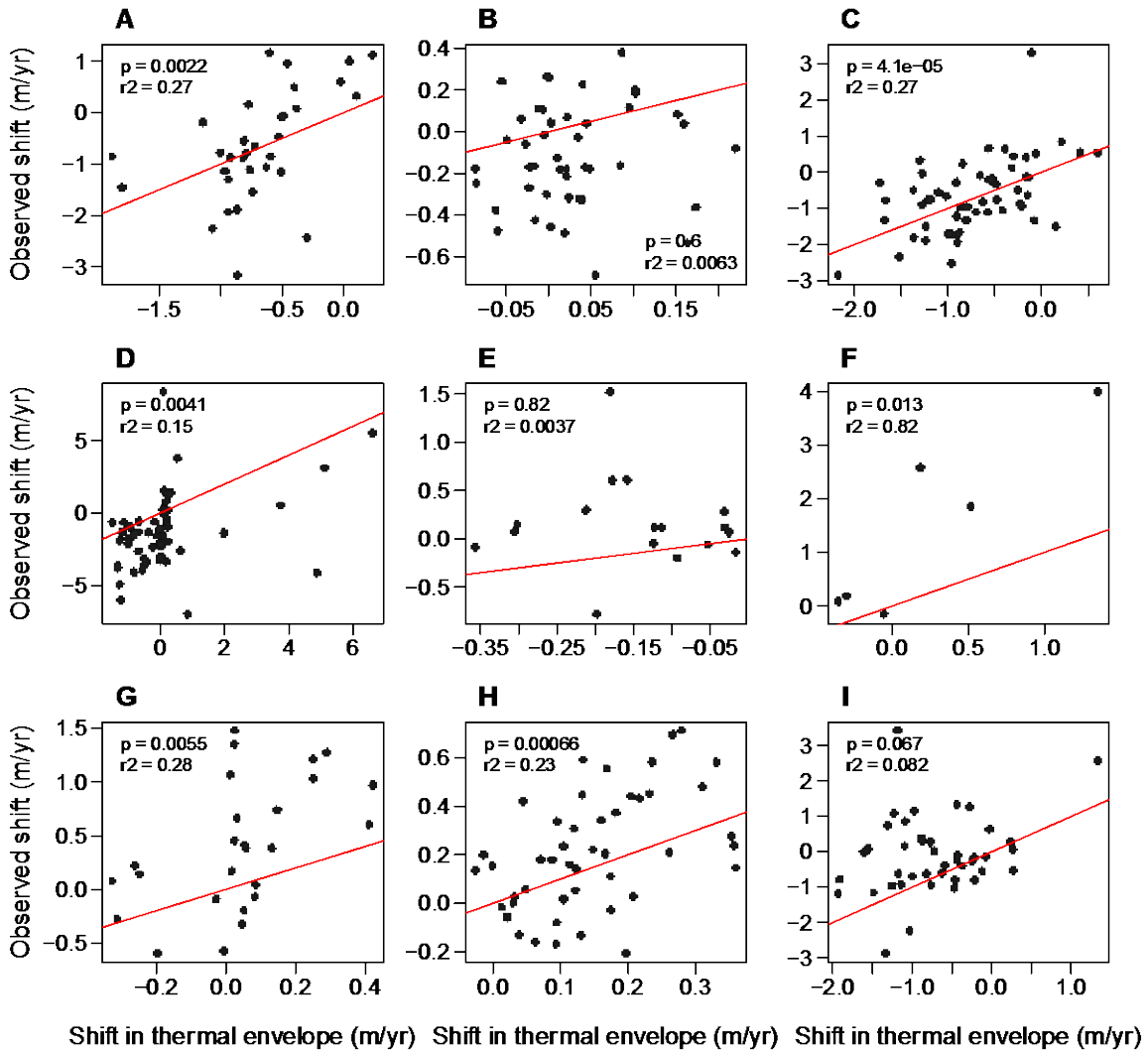


Fig. S6

Relationship between climate velocity and observed shifts in taxon depth (measured as range centroid) for each survey separately. Sub-graphs are the same as in Fig. S5.

Table S1.

North American bottom trawl surveys compiled for this analysis, including season of the survey, time span, frequency of the surveys (years between surveys), number of taxa sampled at least once every year or at least ten times every year.

Region	Season	Years	Freq.	Taxa \geq 1x/yr	Taxa \geq 10x/yr	Source
Eastern Bering Sea	Summer	1982-2011	1	74	45	Bob Lauth, AFSC*
Aleutian Islands	Summer	1980-2010	2-5	58	33	Bob Lauth, AFSC*
Gulf of Alaska	Summer	1984-2011	2-4	107	56	Bob Lauth, AFSC*
West Coast Triennial	Summer	1977-2004	3	69	42	Beth Horness, NMFS†
Gulf of Mexico SEAMAP	Summer	1987-2011	1	106	47	GSMFC‡
Northeast U.S.	Spring	1968-2008	1	41	26	NEFSC§
Scotian Shelf	Summer	1970-2011	1	28	17	Don Clark, DFO
Southern Gulf of St. Lawrence	Fall	1971-2009	1	14	6	Hugues Benoît, DFO¶
Newfoundland	Fall	1995-2011	1	83	53	Bill Brodie, DFO**

* Alaska Fisheries Science Center (AFSC) Resource Assessment and Conservation Engineering (RACE) Groundfish Survey. Data available from http://www.afsc.noaa.gov/RACE/groundfish/survey_data/default.htm.

† West Coast Groundfish Bottom Trawl Survey Program NOAA Fisheries 2725 Montlake Blvd. Seattle, WA 98112. Requests for data should be directed to the NWFSC/FRAM Division Director (Dr. Michelle McClure, Michelle.Mcclure@noaa.gov) or data manager (Beth Horness, Beth.Horness@noaa.gov).

‡ Gulf States Marine Fisheries Commission (GSMFC) Summer SEAMAP Groundfish Survey. Data available from <http://seamap.gsmfc.org>.

§ Northeast Fisheries Science Center (NEFSC) Spring Bottom Trawl Survey. Data available from <http://www.iobis.org>.

|| Department of Fisheries and Oceans (DFO) Scotian Shelf Groundfish Survey. Requests for data should be directed to the Ecosystem Survey Biologist, St. Andrews Biological Station (Don Clark, Don.Clark@dfo-mpo.gc.ca).

¶ Gulf Region September Bottom-Trawl survey Database, Aquatic Resources Division, Science Branch, Department of Fisheries and Oceans, 343 Université Avenue, Moncton, New Brunswick, E1C 9B6. Database query: December 11, 2011. Requests for data should be directed to Hugues Benoît (Hugues.Benoit@dfo-mpo.gc.ca).

** Newfoundland and Labrador Autumn multispecies trawl surveys, Science Branch, Department of Fisheries and Oceans, P.O Box 5667, St. John's, Newfoundland, A1C 5X1. Requests for data should be directed to Bill Brodie (Bill.Brodie@dfo-mpo.gc.ca).

Table S2.

Correlations among predictor variables for all taxa. Table cells show r^2 values from linear correlations.

	Survey duration	Survey extent	Fish/ Invertebrate	Fished/ Unfished	Pelagic/ Demersal	Biomass trend
Climate velocity	0.00	0.17	0.02	0.00	0.01	0.00
Speed of climate velocity	0.01	0.09	0.01	0.00	0.00	0.00
Survey duration		0.26	0.01	0.09	0.00	0.01
Survey extent			0.01	0.00	0.01	0.00
Fish/Invertebrate				0.00	0.00	0.00
Fished/Unfished					0.03	0.00
Pelagic/Demersal						0.02

Table S3.

Correlations among predictor variables for just fishes. Table cells show r^2 values from linear correlations.

	3	4	5	6	7	8	9	10	11. Range size
1. Climate velocity	0.01	0.10	0.00	0.01	0.00	0.01	0.00	0.01	0.00
2. Speed of climate velocity	0.01	0.21	0.00	0.02	0.00	0.01	0.00	0.01	0.01
3. Survey duration		0.30	0.13	0.02	0.01	0.08	0.04	0.01	0.02
4. Survey extent			0.01	0.02	0.01	0.00	0.01	0.02	0.00
5. Fished/Unfished				0.02	0.00	0.13	0.01	0.01	0.01
6. Pelagic/ Demersal					0.03	0.03	0.04	0.05	0.03
7. Biomass trend						0.00	0.00	0.00	0.00
8. Maximum length							0.27	0.32	0.04
9. Trophic level								0.08	0.05
10. Growth rate									0.00

Table S4. Models explaining the speed (absolute value of °N/year) of taxon shifts. The Taxa column indicates whether models were fit to data for all taxa ($n=325$) or just fishes ($n=199$). Relative Variable Importance (RVI) ranks all explanatory variables from high to low importance. The model coefficients associated with each variable are shown for the most parsimonious model with the lowest AIC value (Best Model), a model with all factors retained (Full Model), a multi-model average (Model Average), and models with only climate velocity, only survey characteristics (Survey char.), or only species characteristics (Species char.) retained as explanatory variables. The Δ AIC indicates the difference in model parsimony as explained by AIC relative to the Best Model; a Δ AIC value <10 indicates higher support for a model. Values of r^2 and Akaike weight for each model are also shown. RVI and Akaike weights are calculated across all possible models (128 for all taxa, 1024 for just fishes).

Taxa	Variable	RVI	Best Model	Full Model	Model Average	Climate velocity	Survey char.	Species char.
All Taxa	Climate velocity	1	15	14	14	19		
	Survey extent	1	0.1	0.1	0.1		0.14	
	Survey duration	0.995	-0.032	-0.036	-0.035		-0.03	
	Fish/Invertebrate	0.663	-0.26	-0.26	-0.17			-0.14
	Fished/Unfished	0.431		0.13	0.061			0.04
	Pelagic/Demersal	0.382		0.21	0.082			0.5
	Biomass trend	0.329		-0.098	-0.03			-0.012
	Δ AIC		0	2.98		73.1	42	138
	r^2		0.35	0.36		0.18	0.26	0.013
	Akaike weight		0.15	0.034		2.00×10^{-17}	1.20×10^{-10}	1.70×10^{-31}
Only Fishes	Climate velocity	1	14	14	14	19		
	Survey extent	1	0.13	0.13	0.13		0.16	
	Survey duration	0.95	-0.031	-0.037	-0.032		-0.03	
	Growth rate	0.603	0.19	0.2	0.12			-0.037
	Fished/Unfished	0.287		0.049	0.016			0.27
	Pelagic/Demersal	0.363		0.28	0.088			0.79
	Range size	0.382		-0.0047	-0.0014			-0.00043
	Biomass trend	0.336		-0.11	-0.034			-0.012
	Trophic level	0.31		0.17	0.035			0.043
	Maximum length	0.297		0.042	0.00054			-0.03
Δ AIC		0	8.57		57.6	26.5	106	
r^2		0.42	0.43		0.2	0.32	0.033	
Akaike weight		0.057	0.00078		1.80×10^{-14}	1.00×10^{-7}	4.40×10^{-25}	

Table S5.

Single-variable predictors of taxon shifts. Taxon characteristics were related to speed and direction ($^{\circ}\text{N}/\text{year}$) or only to speed (absolute value of $^{\circ}\text{N}/\text{year}$), and models were fit to all taxa ($n=325$) or to all fishes ($n=199$). Column shows estimated coefficient (Coef.), difference in AIC from the best model (ΔAIC), r^2 values, and AIC model weight. Weight and ΔAIC values are calculated across all 128 possible models for all taxa or across all 1024 possible models for just fishes.

Taxa	Factor	Speed and direction				Speed			
		Coef.	ΔAIC	r^2	Weight	Coef.	ΔAIC	r^2	Weight
All	Climate velocity	0.96	11.1	0.38	0.00041	19	73.1	0.18	2.00×10^{-17}
All	Survey extent	0.0038	134	0.096	7.80×10^{-31}	0.17	48.7	0.24	4.10×10^{-12}
All	Survey duration	-0.00012	167	0.00034	6.70×10^{-38}	-0.066	88.3	0.14	1.00×10^{-20}
All	Fish/ Invertebrate	0.021	155	0.037	2.90×10^{-35}	-0.14	136	0.0019	5.50×10^{-31}
All	Fished/ Unfished	-0.013	160	0.022	2.20×10^{-36}	0.0034	136	1.90×10^{-6}	4.00×10^{-31}
All	Pelagic/ Demersal	0.029	157	0.031	1.00×10^{-35}	0.48	133	0.011	2.30×10^{-30}
All	Biomass trend	0.0084	164	0.0078	2.30×10^{-37}	0.017	136	4.20×10^{-5}	4.10×10^{-31}
Fish	Climate velocity	0.93	20.4	0.36	2.60×10^{-6}	19	57.6	0.2	1.80×10^{-14}
Fish	Survey extent	0.0055	72.5	0.17	1.30×10^{-17}	0.2	30.8	0.3	1.20×10^{-8}
Fish	Survey duration	-9.00×10^{-4}	106	0.021	5.60×10^{-25}	-0.073	62.2	0.18	1.80×10^{-15}
Fish	Growth rate	-0.012	105	0.028	1.10×10^{-24}	0.062	101	0.001	6.80×10^{-24}
Fish	Fished/ Unfished	-0.014	107	0.019	4.60×10^{-25}	0.21	100	0.0056	1.10×10^{-23}
Fish	Pelagic/ Demersal	0.037	100	0.05	1.10×10^{-23}	0.69	96.6	0.023	6.10×10^{-23}
Fish	Range size	3.00×10^{-4}	107	0.017	3.80×10^{-25}	8.00×10^{-4}	101	0.00016	6.20×10^{-24}
Fish	Biomass trend	0.0082	109	0.0097	1.80×10^{-25}	0.048	101	0.00043	6.40×10^{-24}
Fish	Trophic level	0.005	110	0.002	8.30×10^{-26}	-0.12	101	0.0014	7.10×10^{-24}
Fish	Maximum length	0.014	103	0.039	3.70×10^{-24}	-0.13	100	0.0041	9.20×10^{-24}

References and Notes

1. C. Parmesan, G. Yohe, A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003). [doi:10.1038/nature01286](https://doi.org/10.1038/nature01286) [Medline](#)
2. I.-C. Chen, J. K. Hill, R. Ohlemüller, D. B. Roy, C. D. Thomas, Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011). [doi:10.1126/science.1206432](https://doi.org/10.1126/science.1206432) [Medline](#)
3. A. L. Perry, P. J. Low, J. R. Ellis, J. D. Reynolds, Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915 (2005). [doi:10.1126/science.1111322](https://doi.org/10.1126/science.1111322) [Medline](#)
4. K. Zhu, C. W. Woodall, J. S. Clark, Failure to migrate: Lack of tree range expansion in response to climate change. *Glob. Change Biol.* **18**, 1042–1052 (2012). [doi:10.1111/j.1365-2486.2011.02571.x](https://doi.org/10.1111/j.1365-2486.2011.02571.x)
5. N. K. Dulvy, S. I. Rogers, S. Jennings, V. Stelzenmüller, S. R. Dye, H. R. Skjoldal, Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *J. Appl. Ecol.* **45**, 1029–1039 (2008). [doi:10.1111/j.1365-2664.2008.01488.x](https://doi.org/10.1111/j.1365-2664.2008.01488.x)
6. J. M. Sunday, A. E. Bates, N. K. Dulvy, Thermal tolerance and the global redistribution of animals. *Nat. Clim. Change* **2**, 686 (2012).
7. J. A. Nye, J. S. Link, J. A. Hare, W. J. Overholtz, Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol. Prog. Ser.* **393**, 111–129 (2009). [doi:10.3354/meps08220](https://doi.org/10.3354/meps08220)
8. F. J. Mueter, M. A. Litzow, Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecol. Appl.* **18**, 309–320 (2008). [doi:10.1890/07-0564.1](https://doi.org/10.1890/07-0564.1) [Medline](#)
9. C. Moritz, J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, S. R. Beissinger, Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261–264 (2008). [doi:10.1126/science.1163428](https://doi.org/10.1126/science.1163428) [Medline](#)
10. F. A. La Sorte, W. Jetz, Tracking of climatic niche boundaries under recent climate change. *J. Anim. Ecol.* **81**, 914–925 (2012). [doi:10.1111/j.1365-2656.2012.01958.x](https://doi.org/10.1111/j.1365-2656.2012.01958.x) [Medline](#)
11. J. Lenoir *et al.*, Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* **33**, 295 (2010).
12. R. K. Heikkinen, M. Luoto, R. Virkkala, R. G. Pearson, J.-H. Körber, Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Glob. Ecol. Biogeogr.* **16**, 754–763 (2007). [doi:10.1111/j.1466-8238.2007.00345.x](https://doi.org/10.1111/j.1466-8238.2007.00345.x)
13. M. W. Tingley, M. S. Koo, C. Moritz, A. C. Rush, S. R. Beissinger, The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Glob. Change Biol.* **18**, 3279–3290 (2012). [doi:10.1111/j.1365-2486.2012.02784.x](https://doi.org/10.1111/j.1365-2486.2012.02784.x)
14. A. L. Angert, L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, A. J. Chuncó, Do species' traits predict recent shifts at expanding range edges? *Ecol. Lett.* **14**, 677–689 (2011). [doi:10.1111/j.1461-0248.2011.01620.x](https://doi.org/10.1111/j.1461-0248.2011.01620.x) [Medline](#)
15. L.-M. Chevin, R. Lande, G. M. Mace, Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biol.* **8**, e1000357 (2010). [doi:10.1371/journal.pbio.1000357](https://doi.org/10.1371/journal.pbio.1000357) [Medline](#)

16. M. T. Burrows, D. S. Schoeman, L. B. Buckley, P. Moore, E. S. Poloczanska, K. M. Brander, C. Brown, J. F. Bruno, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, W. Kiessling, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. B. Schwing, W. J. Sydeman, A. J. Richardson, The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652–655 (2011). [doi:10.1126/science.1210288](https://doi.org/10.1126/science.1210288) [Medline](#)
17. S. R. Loarie, P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, D. D. Ackerly, The velocity of climate change. *Nature* **462**, 1052–1055 (2009). [doi:10.1038/nature08649](https://doi.org/10.1038/nature08649) [Medline](#)
18. R. Ohlemüller, Running out of climate space. *Science* **334**, 613–614 (2011). [doi:10.1126/science.1214215](https://doi.org/10.1126/science.1214215) [Medline](#)
19. W. W. L. Cheung, V. W. Y. Lam, J. L. Sarmiento, K. Kearney, R. Watson, D. Pauly, Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish.* **10**, 235–251 (2009). [doi:10.1111/j.1467-2979.2008.00315.x](https://doi.org/10.1111/j.1467-2979.2008.00315.x)
20. Materials and methods are available as supplementary materials on *Science* Online.
21. F. P. Chavez, M. Messié, J. T. Pennington, Marine primary production in relation to climate variability and change. *Annu. Rev. Mar. Sci.* **3**, 227–260 (2011). [doi:10.1146/annurev.marine.010908.163917](https://doi.org/10.1146/annurev.marine.010908.163917) [Medline](#)
22. S. N. Wood, Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B (Stat. Method.)* **73**, 3 (2011).
23. N. Duan, Smearing estimate: A nonparametric retransformation method. *J. Am. Stat. Assoc.* **78**, 605–610 (1983). [doi:10.1080/01621459.1983.10478017](https://doi.org/10.1080/01621459.1983.10478017)
24. J. Pinheiro, D. Bates, S. DebRoy, D. Sarkar, *nlme: Linear and Nonlinear Mixed Effects Models* (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria, 2011).
25. R. Froese, D. Pauly, Fishbase. www.fishbase.org (2012).
26. K. P. Burnham, D. R. Anderson, *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, New York, ed. 2, 2002).