Climate Change and Distribution Shifts in Marine Fishes

Allison L. Perry,[1]* Paula J. Low,[2]† Jim R. Ellis,[2] John D. Reynolds[1]*

We show that the distributions of both exploited and nonexploited North Sea fishes have responded markedly to recent increases in sea temperature, with nearly two-thirds of species shifting in mean latitude or depth or both over 25 years. For species with northerly or southerly range margins in the North Sea, half have shown boundary shifts with warming, and all but one shifted northward. Species with shifting distributions have faster life cycles and smaller body sizes than nonshifting species. Further temperature rises are likely to have profound impacts on commercial fisheries through continued shifts in distribution and alterations in community interactions.

Climate change is predicted to drive species ranges toward the poles (*1*), potentially resulting in widespread extinctions where dispersal capabilities are limited or suitable habitat is unavailable (*2*). For fishes, climate change may strongly influence distribution and abundance (*3*, *4*) through changes in growth, survival, reproduction, or responses to changes at other trophic levels (*5*, *6*). These changes may have impacts on the nature and value of commercial fisheries. Species-specific responses are likely to vary according to rates of population turnover. Fish species with more rapid turnover of generations may show the most rapid demographic responses to temperature changes, resulting in stronger distributional responses to warming. We tested for large-scale, long-term, climate-related changes in marine fish distributions and examined whether the distributions of species with fast generation times and associated life history characteristics are particularly responsive to temperature changes.

We studied the demersal (bottom-living) fish assemblage in the North Sea. This group is composed of more than 90 species with varied biogeographical origins and distribution patterns. North Sea waters have warmed by an average of 0.6°C between 1962 and 2001, based on four decadal means before 2001, and by 1.05°C from 1977 to 2001 (*7*), which correspond with our fish survey time series. Survey data were used to calculate catch per unit effort to determine centers of abundance (mean latitudes and depths) for all species and boundary latitudes for those species that have either northerly or southerly range limits in the North Sea (*7*). No species range was entirely confined to the North Sea. Measures of distribution were regressed against same-year and time-lagged bottom temperatures, and also a composite measure of temperatures, the North Atlantic Oscillation Index, the Gulf Stream Index, and the ratio of abundances of northern and southern calanoid copepod species (*7*). We also controlled for changes in abundance that may have influenced species distributions (*7*).

Centers of distribution as measured by mean latitudes shifted in relation to warming for 15 of 36 species (Table 1). These trends were shown by both commercially exploited species [such as Atlantic cod (*Gadus morhua*) and the common sole (*Solea solea*)], and by species that are not targeted by fisheries [such as scaldfish (*Arnoglossus laterna*) and snake-blenny (*Lumpenus lampretaeformis*)]. Distances moved ranged from 48 to 403 km (average distance $\bar{x}$ = 172.3 ± 98.8 km, n = 15 species) (Fig. 1) and most of these shifts (13 of 15) were northward (Table 1). The spatial temperature gradient of the North Sea is somewhat unusual; water temperatures become colder with increasing latitude in the southern North Sea but become slightly warmer with increasing latitudes in the north (*8*), where warm North Atlantic Current waters enter the region (*9*). This temperature pattern may explain one of the two exceptional species that moved south, the Norway pout (*Trisopterus esmarkii*). Its distribution was centered in the northern North Sea, and its southern movement brought it into cooler waters. The other exception was the common sole. We speculate that the southward shift in its distribution may have been caused by the fact that the cleanup of the Thames estuary led to its emergence as a major sole nursery ground during the study period (*10*).

Most species that showed climate-related latitudinal changes also shifted in depth, which was unsurprising because North Sea depths are roughly positively correlated with latitude (*8*). A further six species, including plaice (*Pleuronectes platessa*) and cuckoo ray (*Leucoraja*

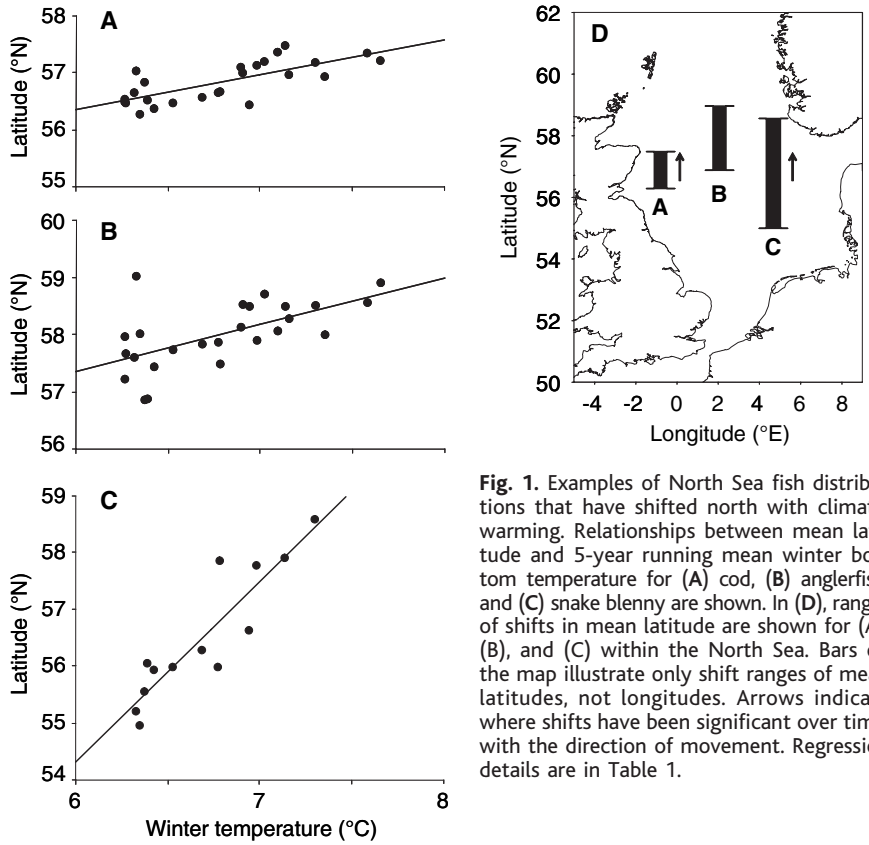

Fig. 1. Examples of North Sea fish distributions that have shifted north with climatic warming. Relationships between mean latitude and 5-year running mean winter bottom temperature for (**A**) cod, (**B**) anglerfish, and (**C**) snake blenny are shown. In (**D**), ranges of shifts in mean latitude are shown for (A), (B), and (C) within the North Sea. Bars on the map illustrate only shift ranges of mean latitudes, not longitudes. Arrows indicate where shifts have been significant over time, with the direction of movement. Regression details are in Table 1.

[1]Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK. [2]Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, UK.

*To whom correspondence should be addressed. E-mail: a.perry@uea.ac.uk (A.L.P.); reynolds@uea.ac.uk (J.D.R.).

†Present address: University Marine Biological Station Millport, Isle of Cumbrae KA28 0EF, UK.

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naevus), moved deeper with warming but did not change in latitude, suggesting that they may have responded to climatic variation through local movements offshore or into pockets of deeper water. Considering both latitude and depth, nearly two-thirds of species (n = 21 out of 36) have shown distributional responses to climatic warming (table S1).

We tested whether species boundaries have also been displaced by warming, by examining those 20 species from our data set with a southern or a northern range limit in the North Sea. The boundaries of half of these fishes moved significantly with warming (Fig. 2 and table S2). Southern boundaries shifted in 6 of 12 cases, and all shifts were northward. Four of eight northern boundaries also moved with warming. All but one of these species shifted north, despite the fact that their northern range limits lay in the relatively intensively fished southern North Sea (*11*). Shifting species again included both exploited and nonexploited fishes. Boundaries moved over distances ranging from 119 to 816 km ($\bar{x}$ = 304 ± 196 km, n = 10), with the highest value describing the range of movement of the southern boundary of blue whiting (*Micromesistius poutassou*), which is the target of the largest fishery in the Atlantic (*12*). In the case of bib (*Trisopterus luscus*), the northern boundary shifted by 342 km from 1978 to 2001, a trend that is supported by observations that North Sea catches of this species have been increasing (*13*).

To identify shifts that may have been driven by fishing or other nonclimatic influences, we also examined distribution changes over time. Fishing pressure could not be included explicitly in our analyses because reliable fishing effort data on a comparable spatial and temporal scale do not exist for the North Sea. However, during at least the last decade of the 25-year period of analysis, the spatial distribution of effort remained relatively constant (*11*), and total fishing effort may have declined slightly (*14*). Temporal trends in distribution suggested that fishing alone could not explain climate-related shifts; despite the general increase in temperature over the study period, warming-related shifts occurred independently of time for centers of distribution in 8 of 36 species and for range limits in 4 of 20 species (table S3). Such shifts may have reflected year-to-year environmental variability, with northward movement during warm years cancelled by southward movement during cool years. If so, long-term distribution shifts could depend strongly on future climatic variability, in addition to longer-term average conditions.

The examination of temporal trends also allowed for rough comparisons to be drawn with rates of warming-related distribution shifts in other taxa. A recent meta-analysis of climate-change impacts on natural systems estimated the mean annual rate of boundary movement for 99 species of birds, butterflies, and alpine herbs at 0.6 km northward or 0.6 m upward (*1*). From the current study, the mean rate of movement for the six fish species whose boundaries shifted in relation to both climate and time [bib, blue whiting, lesser weever

Table 1. Statistically significant multiple regressions of the effects of three measures of North Sea warming on mean latitudes of 36 demersal fishes from 1977 to 2001. PC1, first principal component from principal components analysis (PCA) of eight environmental variables (PC1 generally describes warming). Winter temp. and summer temp. indicate 5-year running mean bottom temperatures for December to March and June to September, respectively.

Species	Common name	df	Mean latitude (°N)	SD	PC1	r^2	P	Winter temp.	r^2	P	Summer temp.	r^2	P
Agonus cataphractus	Pogge	22	54.67	0.90									
Anarhichus lupus	Atlantic wolffish	21	58.14	0.46									
Argentina spp.	Argentines	24	59.59	0.30									
Arnoglossus laterna	Scaldfish	15	54.17	0.31				0.456	0.43	0.006			
Buglossidium luteum	Solenette	23	54.14	0.28									
Callionymus lyra	Dragonet	23	55.40	0.65	0.265	0.16	0.049	0.937	0.34	0.002			
Echiichthys vipera	Lesser weever	24	53.30	0.13				0.191	0.39	0.001			
Eutrigla gurnardus	Grey gurnard	23	56.13	0.35	0.194	0.30	0.006	0.651	0.61	<0.001	0.402	0.17	0.040
Gadiculus argenteus	Silvery pout	23	59.83	0.41									
Gadus morhua	Atlantic cod	23	56.81	0.34	0.256	0.58	<0.001	0.534	0.38†	<0.001	0.578	0.33†	<0.001
Glyptocephalus cynoglossus	Witch	24	58.22	0.42									
Hippoglossoides platessoides	Long rough dab	24	57.62	0.21				0.304	0.40	0.001			
Lepidorhombus boscii	Fourspot megrim	24	60.51	0.37									
Leucoraja naevus	Cuckoo ray	19	58.06	0.57									
Limanda limanda	Dab	24	55.86	0.13				0.180	0.35†	0.001			
Lophius piscatorius	Anglerfish	23	57.99	0.58	0.254	0.19	0.032	0.818	0.37	0.001			
Lumpenus lampretaeformis	Snake blenny	12	56.52	1.15				3.174	0.81	<0.001			
Melanogrammus aeglefinus	Haddock	24	57.91	0.16									
Merlangius merlangus	Whiting	23	56.57	0.15	0.066	0.19	0.034						
Merluccius merluccius	Hake	24	58.84	0.59									
Micromesistius poutassou	Blue whiting	21	60.13	0.48									
Microstomus kitt	Lemon sole	24	57.06	0.24									
Molva molva	Ling	24	59.26	0.74									
Myxine glutinosa	Hagfish	11	57.51	0.62									
Pleuronectes platessa	Plaice	24	55.52	0.18									
Pollachius virens	Saithe	24	59.44	0.20									
Psetta maxima	Turbot	13	54.73	0.31									
Rhinonemus cimbrius	Four-bearded rockling	22	56.05	0.68	0.419	0.40	0.001	1.147	0.53	<0.001	0.950	0.28	0.008
Scyliorhinus canicula	Small-spotted catshark	20	58.34	0.89									
Sebastes spp.	Redfish	18	59.89	0.49									
Solea solea	Common sole	13	53.68	0.66				–0.941	0.38	0.020	–0.963	0.34	0.028
Squalus acanthias	Spurdog	19	56.29	0.68									
Trigla lucerna	Tub gurnard	19	53.89	0.50									
Trisopterus esmarkii	Norway pout	23	58.59	0.26	–0.190	0.52	<0.001	–0.304	0.25	0.010	–0.429	0.37	0.001
Trisopterus luscus	Bib	9	53.29	0.51				0.489*	0.45	0.035			
Trisopterus minutus	Poor cod	23	55.63	0.66	0.334	0.26	0.012	0.877	0.33	0.003	0.753	0.18	0.035

*A relationship with annual mean summer or winter temperature. †To identify the proportion of variance in distribution accounted for by warming, r^2 and P describe the squared semi-partial correlation coefficient, where abundance was also a significant predictor of distribution.

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(*Echiichthys vipera*), Norway pout, scaldfish, and witch (*Glyptocephalus cynoglossus*)] was 2.2 km per year. It is perhaps unsurprising that the rate of shift might be higher for marine fishes than for alpine herbs and butterflies, given that marine fish may generally face fewer constraints on movement. However, if such a difference is indicative of more widespread trends in marine fishes, climate change could pose a greater threat to fish populations that are constrained by their dispersal capabilities or habitat requirements.

If the differences in rates of movement among the taxa documented here result from differential rates of population turnover, we would expect species with life history traits associated with fast population growth to have responded most strongly to climate change. To test this prediction, we compared life history traits between shifting and nonshifting species (*7*). As predicted, shifting species tend to have faster life histories than do nonshifting species, with significantly smaller body sizes, faster maturation, and smaller sizes at maturity (Fig. 3). Body growth rates did not differ significantly between shifting and nonshifting species ($P = 0.19$). These relationships therefore provide a starting point for predicting species' responses to future climate change. These predictions could be refined, through detailed studies of the relative sensitivities of different life history stages, to uncover the specific mechanisms driving the patterns.

Our study shows that climate change is having detectable impacts on marine fish distributions, and observed rates of boundary movement with warming indicate that future distribution shifts could be pronounced. Mean annual surface temperatures in the North Sea are predicted to increase by 0.5 to 1.0°C by 2020, 1.0 to 2.5°C by 2050, and 1.5 to 4.0°C by 2080 (*15*). We used the midpoints of these temperature ranges as the basis for a rough approximation, which suggested that two types of commercial fishes, blue whiting and redfishes (*Sebastes* spp.), may retract completely from the North Sea by 2050, and by 2080, bib may extend its range northward to encompass the entire region. Such changes will clearly also depend on the responses of their predators and prey to increases in bottom temperature and on the availability of suitable habitat.

These findings may have important impacts on fisheries. For example, species with slower life histories are already more vulnerable to overexploitation (*16–18*) and may also be less able to compensate for warming through rapid demographic responses. A further concern is that differential rates of shift could result in altered spatial overlap among species, thereby disrupting interactions and also potentially compounding the decoupling effects of climate-driven changes in phenology (*19*). Previous work off the eastern United States has shown that fishes with the most temperature-sensitive distributions included key prey species of nonshifting predators (*20*). Such changes could have unpredictable effects in an ecosystem already under heavy anthropogenic pressure.

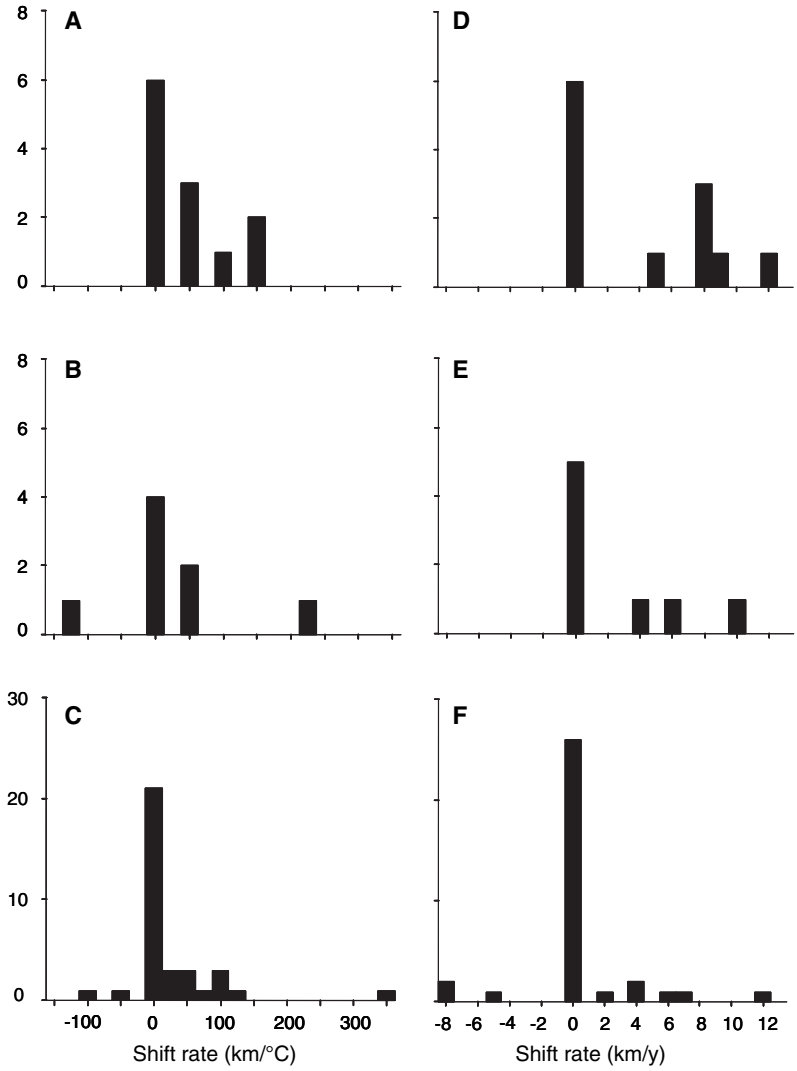

Fig. 2. Frequency distributions of fish species shift rates in relation to warming and time. (**A**) Rates of shift for northerly species' (southern) boundaries with climate. (**B**) Southerly species' (northern) boundaries with climate. (**C**) All species' mean latitudes with climate. (**D**) Northerly species'(southern) boundaries over time. (**E**) Southerly species' (northern) boundaries over time. (**F**) All species' mean latitudes over time. Rates for shifting species are slopes from regressions.

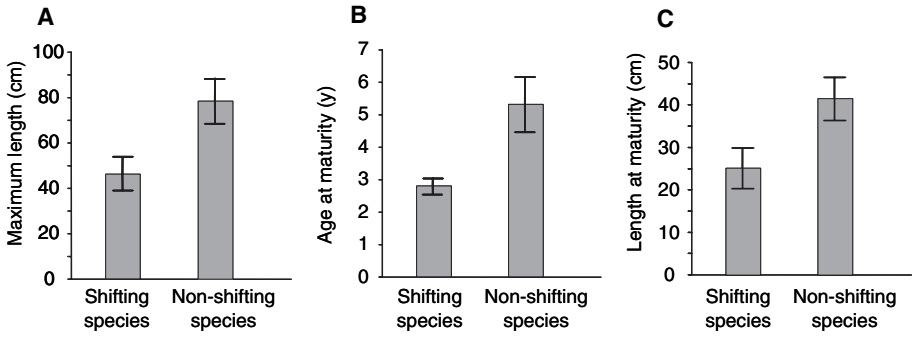

Fig. 3. Differences in life-history traits between shifting ($n = 15$) and nonshifting ($n = 21$) species with respect to centers of distribution (mean latitudes). (**A**) Maximum body size [$t = -2.41$, degrees of freedom (df) = 34, $P = 0.02$]. (**B**) Age at maturity ($t = -2.86$, df = 27, $P = 0.01$). (**C**) Length at maturity ($t = -2.29$, df = 29, $P = 0.03$). Means are shown with standard errors.

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Community Proteomics of a Natural Microbial Biofilm

Rachna J. Ram,[1] Nathan C. VerBerkmoes,[3,4] Michael P. Thelen,[1,6] Gene W. Tyson,[1] Brett J. Baker,[2] Robert C. Blake II,[7] Manesh Shah,[5] Robert L. Hettich,[4] Jillian F. Banfield[1,2]*

Using genomic and mass spectrometry–based proteomic methods, we evaluated gene expression, identified key activities, and examined partitioning of metabolic functions in a natural acid mine drainage (AMD) microbial biofilm community. We detected 2033 proteins from the five most abundant species in the biofilm, including 48% of the predicted proteins from the dominant biofilm organism, *Leptospirillum* group II. Proteins involved in protein refolding and response to oxidative stress appeared to be highly expressed, which suggests that damage to biomolecules is a key challenge for survival. We validated and estimated the relative abundance and cellular localization of 357 unique and 215 conserved novel proteins and determined that one abundant novel protein is a cytochrome central to iron oxidation and AMD formation.

Microbial communities play key roles in the Earth's biogeochemical cycles. Our knowledge of the structure and activities in these communities is limited, because analyses of microbial physiology and genetics have been largely confined to studies of organisms from the few lineages for which cultivation conditions have been determined (*1*). An additional limitation of pure culture–based studies is that potentially critical community and environmental interactions are not sampled. Recent acquisition of genomic data directly from natural samples has begun to reveal the gene content of communities (*2*) and environments (*3*). Here we combined "shotgun" mass spectrometry (MS)–based proteomics (*4–6*) with community genomic analysis to evaluate in situ microbial activity of a low-complexity natural microbial biofilm.

The biofilm samples used in this study and prior work (*2*) were collected from underground sites in the Richmond mine at Iron Mountain, near Redding, California (USA). These pink biofilms grew on the surface of sulfuric acid–rich (pH ~0.8), ~42°C solutions that contain near-molar concentrations of Fe and millimolar concentrations of Zn, Cu, and As (*7*) (Fig. 1). We used oligonucleotide probes (*8*) to demonstrate that *Leptospirillum* group II dominated the sample, but it also contained *Leptospirillum* group III, *Sulfobacillus*, and Archaea related to *Ferroplasma acidarmanus* and "G-plasma" (Fig. 2). This was similar in structure and composition to the community previously used as a source of genomic sequence (*2*).

In general, proteins could be assigned to organisms, because the genes that encode them are on DNA fragments (scaffolds) that have been assigned to different organism types (*2*). From the genomic dataset (*2*), we created a database of 12,148 proteins (Biofilm_db1) that was used to identify two-dimensional (2D) nano–liquid chromatography (nano-LC) (200 to 300 nl/min) tandem mass spectrometry (MS/MS) spectra (*8–13*) from different biofilm fractions. One or more peptides were assigned to ~5994 proteins (Table 1). This corresponds to ~49% of all proteins encoded by the genomes of the five most abundant organisms. We estimated the likelihood of false-positive protein identification using a variety of detection criteria and databases derived from organisms not present in this environment (*8*). Because of these results, for all subsequent analyses, we required matching of two or more peptides per protein for confident detection (*8*). After removal of duplicates, we detected 2003 different proteins (table S1). An additional 30 proteins were found that were encoded by alternative or overlapping open reading frames (*8*).

We detected 48% of the predicted proteins (i.e., 1362 of 2862) from *Leptospirillum* group II (table S2). This percentage exceeded those of most prior proteomic studies of microbial isolates (*10*, *12*, *13*). In part, this may reflect the presence of cells in many different growth stages, as well as microniches within the biofilm (*14*). We also detected 270 *Leptospirillum* group III, 84 *Ferroplasma* type I, 99 *Ferroplasma* type II, and 122 "G-plasma" proteins. In addition, we found 30 proteins on unassigned archaeal scaffolds and 36 on unassigned bacterial scaffolds. The proportion of proteins detected from each organism type was similar to the proportion of cells from each organism type in the biofilm (*8*). Most proteins from low-abundance members were probably in concentrations too low to be detected by the presence of two peptides.

[1]Department of Environmental Science, Policy, and Management, [2]Department of Earth and Planetary Science, University of California at Berkeley, Berkeley, CA 94720, USA. [3]Graduate School of Genome Science and Technology University of Tennessee–Oak Ridge National Laboratory, 1060 Commerce Park, Oak Ridge, TN 37830, USA. [4]Chemical Sciences Division, [5]Life Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA. [6]Biosciences Directorate, Lawrence Livermore National Laboratory, Livermore, CA 94551, USA. [7]College of Pharmacy, Xavier University, New Orleans, LA, 70125, USA.

*To whom correspondence should be addressed. E-mail: jill@seismo.berkeley.edu

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