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Research

Exploring timescales of predictability in species distributions

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Accurate forecasts of how animals respond to climate-driven environmental change are needed to prepare for future redistributions, however, it is unclear which temporal scales of environmental variability give rise to predictability of species distributions. We examined the temporal scales of environmental variability that best predicted spatial abundance of a marine predator, swordfish *Xiphias gladius*, in the California Current. To understand which temporal scales of environmental variability provide biological predictability, we decomposed physical variables into three components: a monthly climatology (long-term average), a low frequency component representing interannual variability, and a high frequency (sub-annual) component that captures ephemeral features. We then assessed each component's contribution to predictive skill for spatially-explicit swordfish catch. The monthly climatology was the primary source of predictability in swordfish spatial catch, reflecting the spatial distribution associated with seasonal movements in this region. Importantly, we found that the low frequency component (capturing interannual variability) provided significant skill in predicting anomalous swordfish distribution and catch, which the monthly climatology cannot. The addition of the high frequency component added only minor improvement in predictability. By examining models' ability to predict species distribution anomalies, we assess the models in a way that is consistent with the goal of distribution forecasts – to predict deviations of species distributions from their average historical locations. The critical importance of low frequency climate variability in describing anomalous swordfish distributions and catch matches the target timescales of physical climate forecasts, suggesting potential for skillful ecological forecasts of swordfish distributions across short (seasonal) and long (climate) timescales. Understanding sources of prediction skill for species environmental responses gives confidence in our ability to accurately predict species distributions and abundance, and to know which responses are likely less predictable, under future climate change. This is important as climate change continues to cause an unprecedented redistribution of life on Earth.

Keywords: climate change, ecological forecasting, prediction, spatial ecology, species distribution models, temporal decomposition



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Introduction

Our oceans are experiencing unprecedented climate-driven changes. The magnitude and direction of these changes vary widely across space and time, causing species to respond in diverse ways (Walther et al. 2002). For example, long-term changes in temperature and other physical properties have led to documented spatial (Perry et al. 2005, Tingley et al. 2009, Pinsky et al. 2013), behavioural (Mueller et al. 2011) and phenological shifts (Edwards and Richardson 2004, Kharouba et al. 2018, Szesciorka et al. 2020) across an increasingly diverse array of species. In addition, ephemeral events such as heatwaves, storms and drought have caused catastrophic population declines and restructuring of ecological communities (Boersma and Rebstock 2014, Descamps et al. 2015, Smale et al. 2019). There remains considerable uncertainty and variability in the magnitude and direction of species' responses to climate change and extreme climate events (Parmesan and Yohe 2003, Hazen et al. 2013, Pinsky et al. 2013, Poloczanska et al. 2013, Smale et al. 2019). Accurate predictions of these responses are paramount for informing proactive climate-ready management.

Species distributions can be considered a function of multiple scales of environmental variability (Winkler et al. 2014). For example, many migratory taxa respond to environmental information over a range of timescales, including both proximate conditions resulting from short-term environmental variability (Boustany et al. 2010, Aikens et al. 2017, Snyder et al. 2017) as well as long-term historical (i.e. climatological) conditions (Abrahms et al. 2019a, Tsalyuk et al. 2019, Horton et al. 2020). Indeed, considering fine-scale environmental variability (Hazen et al. 2018, Morán-Ordóñez et al. 2018, Abrahms et al. 2019b) or seasonal to inter-annual environmental variability (Zimmermann et al. 2009, Reside et al. 2010, Descamps et al. 2015, Thorson 2019) can improve predictions of species spatial distributions in response to environmental change. There is a need to better understand and define the relative contribution of different temporal scales of environmental variability to better predict species' responses to future environmental change.

Correlative species distribution models (SDMs) have become an important tool to predict and plan for changes in species abundance and distribution under climate change (Elith and Leathwick 2009, Robinson et al. 2017, Araújo et al. 2019, Brodie et al. 2020). While correlative models provide important insights into species' realized niches under observed conditions, there is a discrepancy among studies as to whether species–environment correlations may break down (Muhling et al. 2020), or hold up (Becker et al. 2019), under novel environmental conditions (Sequeira et al. 2018, Yates et al. 2018). As climate change is driving non-stationarity in ecosystems and reducing the utility of historical climate information (Zimmermann et al. 2009, Zurell et al. 2009, Franklin 2010), there is a need to understand which scales of environmental variability contribute to predictive skill (i.e. predictive ability) in SDMs.

Ecological forecasting is gaining traction as an approach to understand, predict and project future ecosystem change (Tommasi et al. 2017, Dietze et al. 2018, Hobday et al. 2018, Jacox et al. 2020). In marine systems, ecological forecasting most often relies on correlative statistical models applied to ocean climate forecasts (Payne et al. 2017). This makes skillful ecological forecasts at a particular spatiotemporal scale reliant on skillful forecasts of environmental variables at that same spatiotemporal scale (Jacox et al. 2020). For example, if a physical ocean forecast is unable to skillfully resolve fine-scale ephemeral features such as eddies and fronts, an ecological forecast reliant on physical variables cannot skillfully predict at these fine spatiotemporal scales. Similarly, if a physical or ecological forecast derives its skill from long-term climatological conditions, then forecasting is redundant and a monthly climatology can instead be used for short-term predictive purposes. Exploring which temporal scales of environmental variability underpin our ability to predict species distributions is therefore essential to assess and improve the utility of ecological forecasting applications.

Our goal is to understand the temporal scales of environmental variability that provide predictability for spatially-explicit animal abundance. We use data from a swordfish *Xiphias gladius* fishery in the California Current System (CCS) to test the hypothesis that multiple scales of environmental variability contribute to predictive skill of species distributions. We use an approach that decomposes important environmental drivers into sub-annual, inter-annual and climatological components, to quantify which scales predictably structure distributions and movements of animals. Importantly, we quantify model performance not just for species distributions but also for species distribution anomalies (i.e. deviations from climatological fisheries catch), which is key to assessing models' capabilities to predicting future change in distributions. Our approach of modelling species distributions using abundance data is standard for fisheries datasets and for the species distribution modelling literature (Guisan and Thuiller 2005, Elith and Leathwick 2009). An improved accounting of the temporal scales of environmental forcing that drive species distributional changes will aid in prioritizing monitoring and planning adaptive management scenarios under climate variability and change.

Methods

Study system and focal species

The CCS is a highly productive and dynamic ecosystem in the northeast Pacific, dominated by seasonal upwelling that drives cool, nutrient-rich waters to the surface and stimulates extensive biological productivity (Hickey 1979, Huyer 1983). This ecosystem provides important foraging grounds for many highly migratory species, including species of importance to fisheries (Block et al. 2011). Variability in the CCS occurs across a range of spatial (meters to 1000s of km) and temporal scales, including intra-annual (e.g. upwelling,

mesoscale features), interannual (e.g. due to large-scale climate modes like El Niño-Southern Oscillation) and multi-decadal scales (e.g. due to decadal climate oscillations and secular climate change) (Checkley Jr and Barth 2009). These changes in the regional climate and oceanography can have pronounced ecological impacts; for example, a severe marine heatwave from 2014 to 2016, with positive sea surface temperature anomalies up to 6°C (Bond et al. 2015, Leising et al. 2015, Jacox et al. 2016), led to a broad range of ecosystem impacts including species redistributing across the CCS (Cavole et al. 2016, Becker et al. 2018, Muhling et al. 2020).

Swordfish are a large highly migratory predator widely distributed across the Pacific, Atlantic and Indian oceans (~50°N, 50°S). Swordfish exhibit extreme diel vertical migration, and in the CCS forage at depths up to 500 m during the day and in surface waters at night (Sepulveda et al. 2010, 2018, Dewar et al. 2011). The CCS is an important foraging ground for north Pacific swordfish, with some adults undertaking spawning migrations to tropical waters near Hawaii during May–August (Grall et al. 1983) and other adults residing in the CCS year-round (Abecassis et al. 2012, Sepulveda et al. 2020). Within the CCS, swordfish are generally distributed at higher latitudes in summer and lower latitudes in winter (Hanan et al. 1993, Sepulveda et al. 2018), with some individuals showing high site fidelity following extensive seasonal movements (Sepulveda et al. 2020). The presence and distribution of swordfish in the CCS thus depend on a complex combination of movements across multiple scales, including large-scale spawning migrations, non-spawning seasonal latitudinal movements, fine-scale foraging, diel vertical migration and site fidelity. As such, swordfish are an appropriate case study species to explore the sources of predictability in species distribution models.

Species data

Swordfish are available to U.S. fisheries in the CCS, and historically have largely been targeted with drift gillnet gear, in contrast to longlines used in other large marine ecosystems (Hanan et al. 1993, Urbisci et al. 2016). The fishery operates primarily from September to January along the U.S. West Coast, deploying drift gillnet gear at night when swordfish are shallower in the water column and susceptible to this gear type. Gear will drift on average ~10 km during sets, so we consider the resolution of catch data to be approximately 0.1°. Swordfish catch data were obtained from the NOAA National Marine Fisheries Service observer program, which has placed observers on drift gillnet vessels since 1990 (Caretta et al. 2004). Catch data were reported as the number of swordfish caught in each drift gillnet set, with multiple sets per fishing trip, and set-level effort reported as duration (h) of each set. Catch data for SDM training were temporally limited to 1998–2016 ($n=4162$ sets, totaling 8788 swordfish caught) to match the availability of satellite-derived chlorophyll-*a* from 1998, and fisheries data beyond 2016 not available for analysis.

Environmental data

Environmental data (1998–2016) were sourced from a data-assimilative configuration of the Regional Ocean Modelling System (ROMS) that covers the CCS from 30 to 48°N and from the coast to 134°W at 0.1° (~10 km) horizontal resolution (<<http://oceanmodeling.ucsc.edu/ccsrt>> version 2016a; Neveu et al. 2016; Fig. 1). Vertical structure in the ROMS model is resolved by 42 terrain-following vertical levels (Veneziani et al. 2009). Daily sea surface temperature (SST; °C) and isothermal layer depth (ILD; m), defined as the depth corresponding to a 0.5°C temperature difference relative to the surface, were sourced from ROMS. Satellite-derived chlorophyll-*a* (Chl; mg m⁻³) was a 4 km 8-day composite from GlobColour sourced from Copernicus Marine Environment Monitoring Service and interpolated to the ROMS resolution (daily and 0.1° resolution). Environmental covariates were selected based on published relationships of swordfish distribution and catch in the CCS (Scales et al. 2017b, Brodie et al. 2018, Smith et al. 2020).

For each grid cell, three environmental covariates (SST, ILD, Chl) were temporally decomposed into three component signals: 1) a monthly climatology; 2) a low-frequency component; 3) a high frequency component. The monthly climatology captures the mean historical seasonal cycle, with conditions for each month averaged across all years (1998–2016). Daily anomalies for each variable were calculated by subtracting the monthly climatology from the daily time series at each grid point. The low frequency component was calculated by smoothing the anomalies with a 12-month running mean centered on each day in the time period (1998–2016). This low frequency component captures interannual variability in the oceanic environment. The high frequency component was the component remaining after subtracting the monthly climatology and low frequency components from the daily values. This high frequency component isolates sub-annual variability including ephemeral features such as fronts and eddies. The monthly climatology, low-frequency and high-frequency components sum to the daily values of the observed environmental covariates.

Our approach to decomposing environmental variables was designed with an eye toward assessing SDMs for forecasting applications. In this sense, the monthly climatology provides a baseline against which forecasts can be measured. If the high and low frequency components do not appreciably increase model performance relative to the monthly climatology, then a forecast is unnecessary. The low frequency component isolates interannual variability (i.e. how a specific year differs from an ‘average’ year). Capturing interannual variability is the target of climate forecasts that are used as the basis for SDM forecasts, so our analysis evaluates whether timescales of predictive skill in the climate forecasts align with timescales of predictive skill in the SDM. Model performance for interannual variability is also key to informing management actions that are taken on an annual basis (e.g. seasonal closures; Welch et al. 2019, Smith et al. 2020). While high frequency environmental variability, including ephemeral

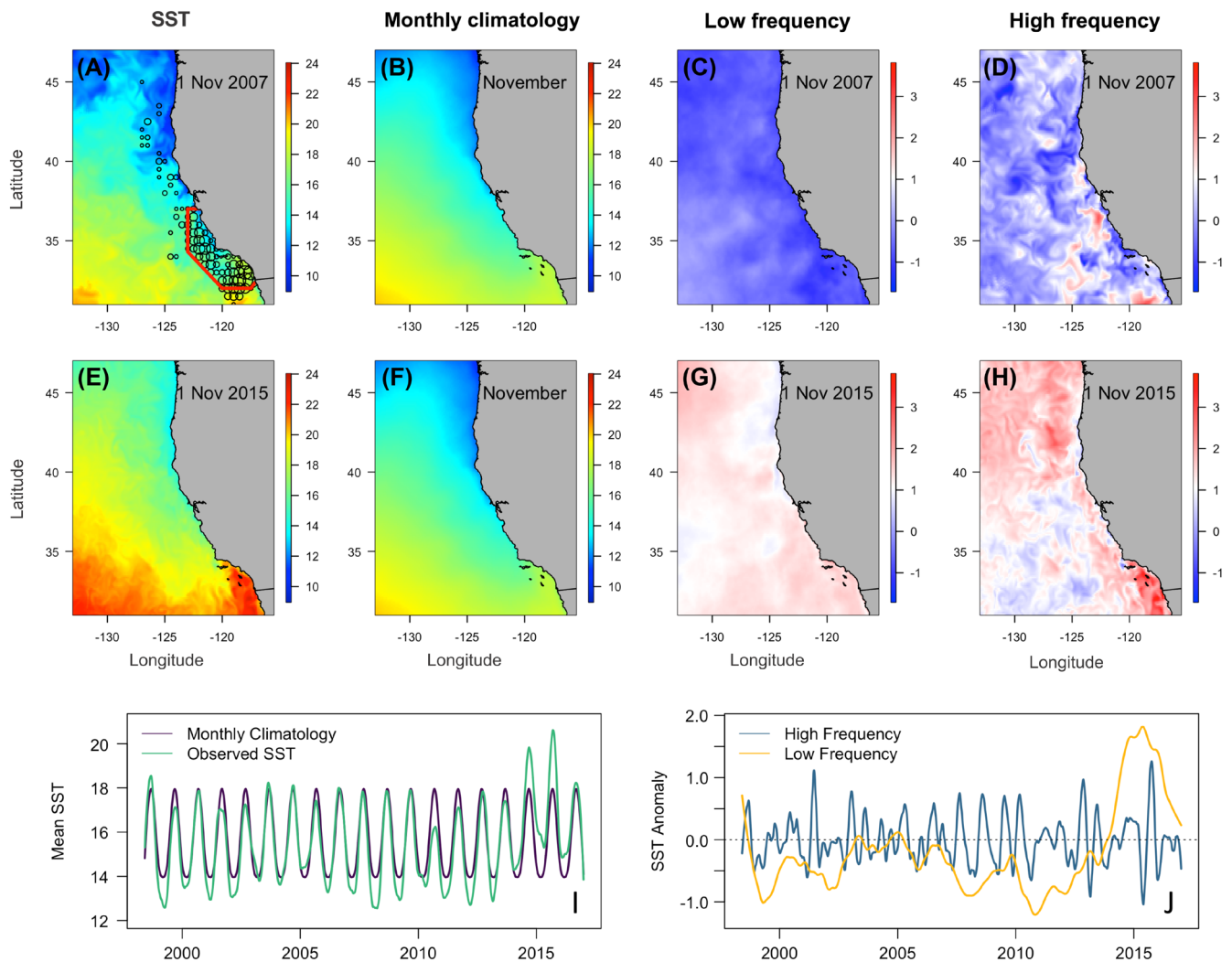


Figure 1. Map of the California Current System showing observed and decomposed sea surface temperature (SST) for two example days, 1 November 2007 (A–D), and 1 November 2015 (E–H). Swordfish catch locations aggregated to the nearest 0.5 degrees are shown, with the red polygon indicating 95% of the catch data (core fishing zone; top left). Time-series plots (I and J) show the spatially-averaged observed and decomposed sea surface temperature from 1998 to 2016, and were smoothed for illustrative purposes. Decomposition separated sea surface temperature into three component parts: a monthly climatology, a low frequency signal capturing interannual variability, and a high frequency signal capturing the remaining variability on sub-annual timescales.

features such as fronts and eddies, is commonly included when developing and predicting SDMs, in a forecasting sense this component is unlikely to be predictable except at very short lead times. Thus, if an SDM derives much of its skill from the high frequency component, it is likely to not be a good candidate for forecasts.

Species distribution models

A total of 4162 drift gillnet sets, totaling 8788 swordfish caught (mean catch of 2.11 swordfish per set) were used to build swordfish SDMs. Here we model swordfish catch per unit effort as a function of the environment. Swordfish catch was modelled as a function of the environment using a generalized additive mixed model (GAMM), using the *mgcv* R package (ver. 1.8-33; Wood 2017). GAMMs were fitted with

a negative binomial family and log link function, with fishing trip included as a random effect (using $bs = 're'$). Including fishing trip as a random effect removed temporal autocorrelation in the model residuals, according to the 'acf' function in the *stats* R package. We did not consider swordfish population biomass in the North Pacific in our modelling approach as biomass has remained relatively constant across our study period (ISC 2018). Environmental covariates (SST, ILD, Chl) were included using a thin plate regression spline, with the number of knots (which controls the degree of non-linearity) not pre-specified. Gear soak time (h) was also included as a smoother to account for variability in catch relating to the duration of each set.

Three SDMs were built to partition the relative influence of decomposed environmental covariates on model predictive performance. The first SDM included only the monthly

climatologies of each environmental covariate. The second SDM included the sum of the monthly climatology and low frequency anomalies for each environmental covariate (i.e. only the high frequency component was removed). The third SDM was built with the raw model output for each environmental covariate (i.e. including the monthly climatology, low frequency and high frequency components). The three SDMs thus incrementally increased the temporal resolution of environmental predictors and allowed us to partition the predictive performance of SDMs into climatological, low frequency and high frequency environmental processes. We did not assess the three decomposed environmental covariates individually as the low and high frequency anomalies were not individually capable of describing spatially-explicit swordfish catch. SST and ILD were correlated in the monthly climatology-only SDM and the interpretation of their response curves should be treated with caution. Environmental covariates in the other two SDMs were not correlated.

Model evaluation: mean catch and distribution

The explanatory power and predictive performance of each swordfish SDM was evaluated using a series of metrics appropriate to the integer response variable to assess model fit, bias and performance. Goodness-of-fit was compared among models using Akaike's information criterion, explained deviance (%) and *r*-squared. Model bias was assessed using the slope and intercept of a linear regression of observed and fitted abundance values. Model predictive performance was assessed using metrics of model accuracy, discrimination power, calibration and precision of predictions (Norberg et al. 2019). Specifically, accuracy measures the degree of proximity between the predicted and true value. Discrimination power considers how well predictions discern observed trends, but does not consider the absolute match between predicted and observed values. Calibration is the statistical consistency between distributional predictions and observed values, such as the proportion of observed values that fall within a model's confidence interval. Precision measures the width of the predictive distribution. For accuracy, calibration and precision, smaller values indicate better performance. Model accuracy was determined by the root mean square error between observed and predicted values. Discrimination power was determined as the Spearman correlation coefficient between observed and predicted values. Calibration was determined by finding the absolute difference between 0.5 and the proportion of predictions that fall within the 50% prediction interval (i.e. the interval within which 50% of future observations would fall) of each model (Norberg et al. 2019). Precision was determined by the standard deviation of predictions that fall within the 50% prediction interval (Norberg et al. 2019).

These measures of model performance were assessed through two types of cross-validation. First, models were trained on a random subset of 75% of the data and tested against the remaining 25%. This was repeated 10 times, and the four measures of model predictive performance (accuracy,

discrimination, calibration and precision) were each averaged. Second, models were trained on all data from 1998 to 2013, and tested against data from 2014 to 2016 when a severe marine heatwave occurred in the CCS. This out-of-sample cross-validation approach tests how well models perform under novel environmental conditions (Muhling et al. 2020). The four measures of predictive performance described above were then calculated. For all out-of-sample predictions, the fishing trip random effect was excluded and soak time was fixed at 12 h (the mean of observed effort).

Model evaluation: swordfish catch anomalies

We then assessed the ability of the three SDMs to predict swordfish catch anomalies in the core fishing zone, where 95% of drift gillnet swordfish catch was observed from 1998 to 2016 (Fig. 1). We examined catch anomalies rather than absolute catches to remove the influence of long-term average catch, and focus on the ability of models to predict changes in catch as a function of environmental change, a necessary step toward making accurate predictions under climate change. For example, using anomalies we can assess whether November in a given year has higher or lower catch than the average November, rather than whether more fish are generally caught in November than December. While assessing model performance based on anomalies is standard practice in climate and weather forecasting, it is less common in species distribution modelling (Tommasi et al. 2017). However, examining anomalies is a critical analytical step when predicting climate change impacts, as the goal is to capture divergence from the climatological state. Here, examining catch anomalies was an effective way to quantitatively assess the added value of including low and high frequency environmental variability in swordfish catch models.

To calculate swordfish catch anomalies, we first predicted swordfish catch (number per 12 h set) in each model SDM for every day from 1998 to 2016. Predictions and observations were limited to the core fishing zone (Fig. 1) where 95% of drift gillnet swordfish catch was observed during that period. We then averaged observed and predicted swordfish catch in this core fishing zone for 1) each month in the fishing season (September–January), and 2) across four spatial resolutions (0.5°, 1°, 2°, and the entire core fishing zone). For both predicted and observed catch, catch anomalies were created by first calculating a climatology of monthly swordfish catch (1998–2016), then finding the catch difference between each month and its monthly climatological value.

Predicted and observed anomalies for each month were compared using two metrics. The first was Pearson correlation coefficients between predicted and observed anomalies, with significance assessed using the test statistic, *r*. The second was the probabilistic accuracy of the upper tercile (66%) of swordfish catch (Spillman and Hobday 2014). This metric calculates the proportion of a correct yes/no prediction of swordfish catch anomalies, where a 'correct yes' is when predicted and observed catch anomalies both lie within the upper tercile, and a 'correct no' is the opposite. Accuracy is

then calculated as the sum of ‘correct yes’ and ‘correct no’, divided by the total number of predictions (Spillman and Hobday 2014, Tommasi et al. 2017). Probabilistic accuracy ranges between 0 and 1, with values greater than 0.56 better than chance (Spillman and Hobday 2014).

Results

Decomposed environmental data

Decomposing environmental data into three temporal components (monthly climatology, low frequency and high frequency) highlighted both spatial and temporal trends in the structure of environmental variation. The monthly climatology revealed strong spatial gradients in ocean variables, including a cross-shore gradient in chlorophyll and a latitudinal gradient in SST, while the low frequency signal showed persistent and often widespread anomalies. In contrast, the high frequency signal isolated ephemeral features such as fronts and eddies (Fig. 1). Time-series of all environmental covariates (SST, ILD, Chl) showed that the marine heatwave from 2014 to 2016 was distinct from other years (Fig. 1,

Supporting information). Given the persistence of this event, its signal was most pronounced in the low-frequency time-series, which exhibited anomalously warm water, low chlorophyll and shallow isothermal layer depths (Fig. 1, Supporting information).

Species distribution models

Spatially-explicit predictions of swordfish catch in the core fishing zone varied substantially depending on which scales of decomposed environmental covariates were included. The SDM using daily values highlighted more fine-scale oceanographic features relative to the SDM that included only the monthly climatology (Fig. 2). The SDM that included both the monthly climatology and low frequency components highlighted some of the same features as the daily values model, with both of these models showing large differences in the distribution of swordfish catch between the two example years (2000 and 2015; Fig. 2). These differences amongst SDMs emerge partly as a result of different ranges of environmental data available for model fitting (Fig. 3, Supporting information). SDMs built from the daily values see a larger

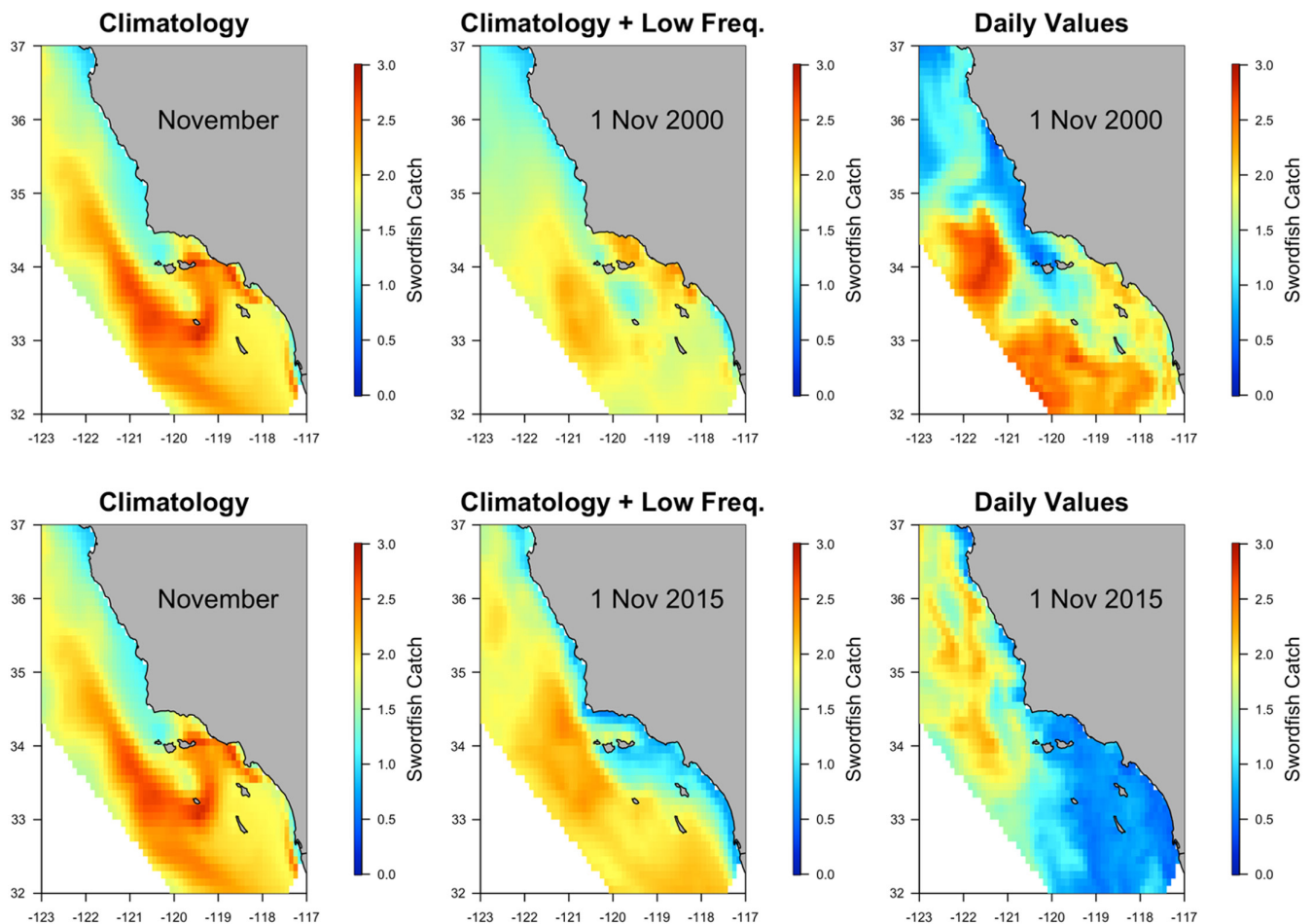


Figure 2. Predicted swordfish catch (number caught per 12 h set) from each species distribution model for two example days, 1 November 2000 (top row) and 2015 (bottom row).

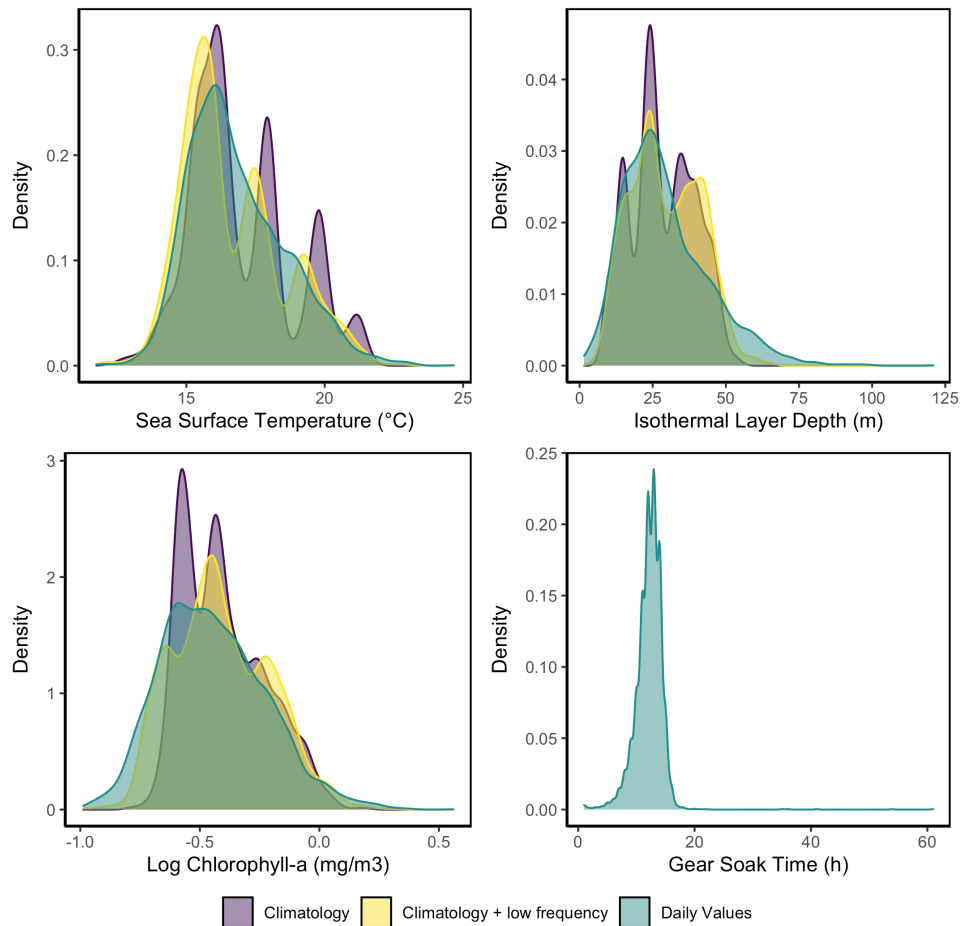


Figure 3. Frequency distribution of environmental covariates at swordfish catch locations temporally decomposed into their component parts (color). Covariates were used in species distribution modelling, with gear soak time consistent across all models so only one color is shown.

range of environmental data than the two other SDMs, for which temporal smoothing reduces extreme values of each predictor (e.g. deeper ILLD, warmer SST and higher chl) (Fig. 3, Supporting information).

Model evaluation: mean catch and distribution

We found only minor differences in model fit and performance among the three swordfish SDMs. Generally, there were incremental improvements in model fit, bias and performance as the temporal resolution of decomposed environmental predictors increased from the climatological SDM to the climatological plus low frequency SDM to the daily values SDM (Table 1). However, there were no meaningful differences among the SDMs for the four performance metrics (discrimination, accuracy, calibration and precision). This pattern generally held when cross-validating SDMs against marine heatwave years (2014–2016; Table 1). The minor differences among SDMs indicate that most of the predictive performance of the models is derived from the monthly climatology of environmental covariates.

Model evaluation: swordfish catch anomalies

Swordfish catch anomalies indicate whether more or less swordfish are caught relative to the long-term average for a given time and place (positive and negative anomalies, respectively). While the SDM built on environmental climatologies had no ability to predict anomalous swordfish catch, we found that the models including low and high frequency environmental variability were able to accurately predict swordfish catch anomalies over multiple spatial scales (Fig. 4, Supporting information). Differences in performance between the monthly climatology + low frequency SDM and the daily values SDM were minor, with variation in performance attributed to the month and spatial resolution of predictions (Fig. 4). The first performance metric, Pearson correlation coefficient, indicates the discriminatory power of predictions. That is, when a large anomaly is observed do we also predict a large anomaly? Our results show that the discriminatory power was highest in the daily values model, and peaked at a 2° spatial resolution. The second performance metric, probabilistic accuracy, indicates how well we can predict an anomaly regardless of the magnitude of that anomaly.

Table 1. Summary of species distribution model fit (AIC, % explained deviance and R^2), bias (gradient and intercept) and model performance (discrimination, accuracy, calibration, precision) metrics for each decomposed model (monthly climatology, monthly climatology and low frequency, and daily values). Colors indicate the best performing model (green), to the worst performing model (red) and in between (yellow). Model performance metrics were completed for models trained on all years (1998–2016) and cross-validated 10 times using a random 75%/25% split, with mean (\pm SE) shown. Metrics were also completed for models trained on a subset of years (1998–2013) and tested on marine heatwave years (2014–2016).

	Monthly climatology	Climatology + low frequency	Daily values
Trained on 1998–2016			
AIC	14 510	14 509	14 478
Explained deviance (%)	48.5	48.7	49.3
R^2	0.37	0.376	0.373
Slope	1.587	1.569	1.488
Intercept	−0.270	−0.200	−0.079
Discrimination: Mean correlation coefficient (SE)	0.352 (0.006)	0.336 (0.006)	0.334 (0.006)
Accuracy: Mean root mean square error (SE)	2.907 (0.05)	2.926 (0.05)	2.926 (0.05)
Calibration: proportion of predictions within 50% prediction interval	0.297 (0.034)	0.370 (0.035)	0.288 (0.024)
Precision: SD of predictions within 50% prediction interval	0.516 (0.02)	0.537 (0.02)	0.495 (0.01)
Trained on 1998–2013			
AIC	13 759	13 746	13 713
Explained deviance (%)	49	50	50
R^2	0.373	0.381	0.38
Gradient	1.629	1.592	1.508
Intercept	−0.293	−0.211	−0.085
Discrimination: Mean correlation coefficient (SE)	0.219	0.288	0.248
Accuracy: Mean root mean square error (SE)	3.122	3.043	3.014
Calibration: $ p < 0.05 $	0.366	0.382	0.140
Precision: SD of predictions within 50% prediction interval	0.325	0.463	0.524

Both the low and high frequency models had the same ability to differentiate the occurrence of an anomaly, and this was consistent across the four spatial resolutions that were tested (Fig. 4). These results indicate that swordfish SDMs were not only capable of predicting anomalous catch, but that most of the predictability of anomalous catch came from the low-frequency environmental component.

Discussion

The redistribution of biodiversity as a response to climate variability and change has driven the need for accurate and precise predictions of animal distributions, but has also exposed the challenges and complexities of using correlative models to represent multiple, multi-scale, responses of animals to their environment. Here, we temporally decomposed environmental information to better understand how component signals influence the distributions of swordfish, a highly mobile marine predator. We found that our ability to predict swordfish distribution and catch was driven predominantly by a combination of climatological and low frequency environmental signals. When focusing on deviations from historical mean swordfish catch due to anomalous environmental conditions, the low frequency component was the dominant source of predictive skill. This timescale is consistent with the target timescales of climate forecasts and projections, indicating a promising match between the

environmental and ecological scales of predictability. In contrast, higher frequency environmental variability (e.g. specific times and locations of oceanographic features such as eddies) is not predictable on climate timescales, but its relatively small contribution to SDM predictive performance in our study suggests this lack of predictability may not be a hindrance to predicting and projecting species distributions.

Decomposing the environmental drivers of animal distributions allowed us to incrementally assess each component's role in predicting swordfish catch and distribution. The environment will influence animal movements and behavior across multiple spatial and temporal scales, and thus an animal's observed location represents the integration of multiple scales of variation. Animal migrations and seasonal movements may be cued to the monthly climatology as it reflects long-term phenological patterns of resource availability (Bauer et al. 2011, Winkler et al. 2014), while finer-scale movements and behavior may be more closely linked to dynamic environmental cues that signal local prey enhancement (Scales et al. 2014, Abrahms et al. 2018). By partitioning temporal scales of environmental variability, our results contribute to understanding the mechanisms that structure species responses to the environment at multiple scales. Here, the monthly climatology of environmental covariates was likely a good predictor of swordfish distributions because swordfish exhibit seasonality and some degree of site fidelity in their movements (Sepulveda et al. 2020). The incremental improvement in model predictive

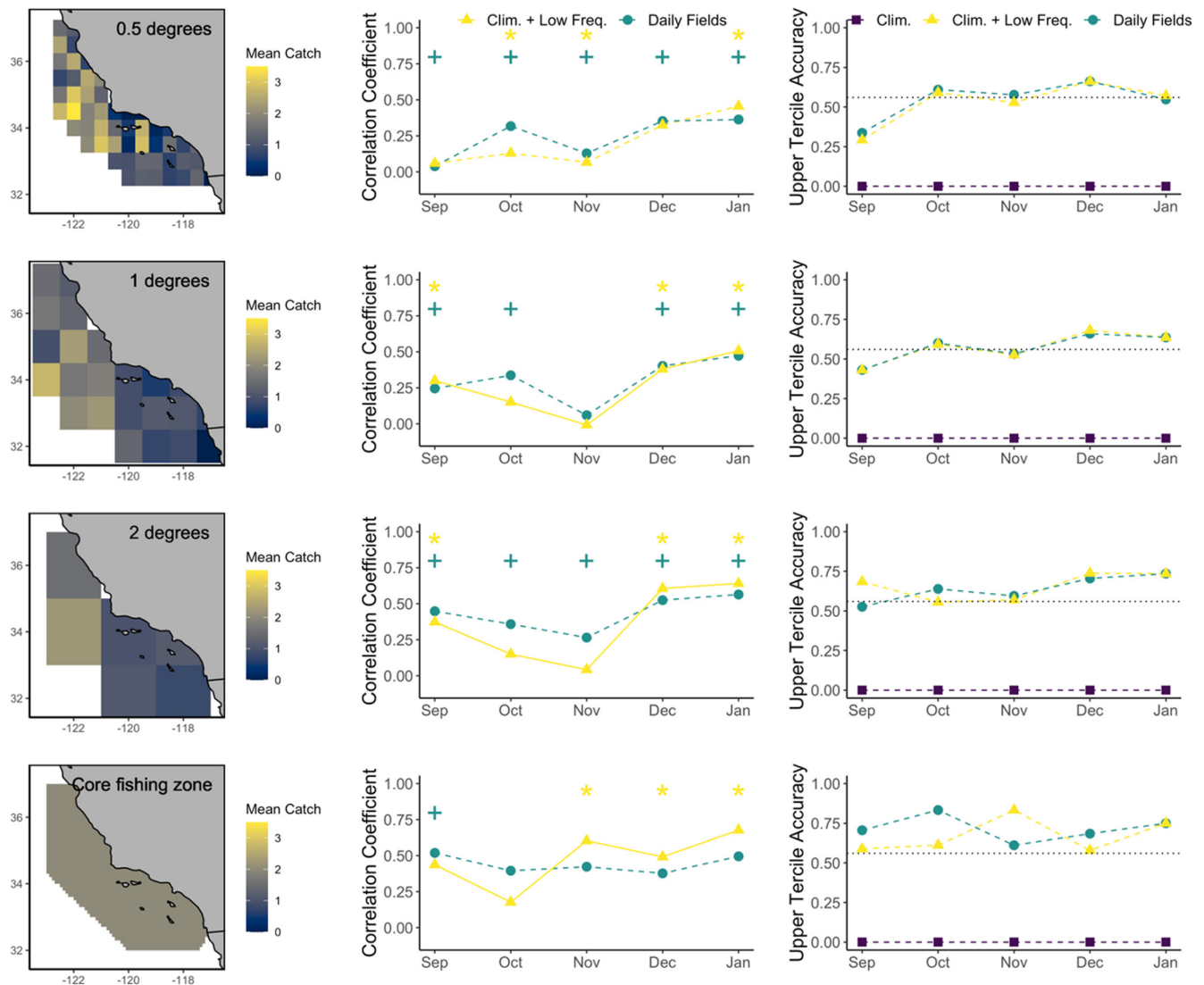


Figure 4. Average observed swordfish catch (maps) and predictive performance for modeled swordfish catch anomalies, with predictions averaged over four spatial resolutions (0.5°, 1°, 2° and the entire region). Anomaly correlation coefficients (middle column) and probabilistic accuracy (right column) are shown for each month for the daily values species distribution model (blue circles), the monthly climatology plus low frequency model (yellow triangles), and the monthly climatological model (purple squares). Blue crosses and yellow stars indicate significance of the correlation coefficients ($p < 0.05$). The horizontal black line at 0.56 indicates the minimum level of probabilistic accuracy, with values below this no better than random. Correlation coefficients for the monthly climatology are 0 and not shown.

performance with the addition of the low-frequency component reflects the high mobility of swordfish, which allows them to move in response to local and interannual variability. However, we found that the addition of high frequency environmental variability to these broader scale signals did not meaningfully improve predictability, although it did increase SDM explanatory power. This may be because fine-scale swordfish distributions are driven by prey distributions and foraging behavior at depth, and we therefore might not expect swordfish to respond to high frequency (e.g. ephemeral) environmental features in surface waters. In other words, our results suggest a swordfish was caught at a location not because of its immediate ‘here and now’ environment, but rather due predominantly to broader and

longer-term environmental conditions. The spatial scale of fisheries effort and ROMS data was ~10 km, so we were unable to resolve biological and environmental processes at finer scales at which swordfish respond to their immediate environment. Our decomposition approach systematically identified the temporal scales of swordfish predictability, but this approach would not be necessary if a swordfish SDMs purpose was to explain habitat use and historical distribution – as is the case in most SDM purposes (Araújo et al. 2019). Under such purposes, using the daily values of environmental covariates would likely maximize the explanatory power of models (Scales et al. 2017a).

Our analysis adds to a growing body of literature that indicates that the utility of climatological information is

becoming increasingly degraded given the accelerating pace of global change and non-stationarity in ecosystem responses (Zimmermann et al. 2009, Zurell et al. 2009, Scales et al. 2017a, Muhling et al. 2020). Indeed, much of the climate velocity literature argues that local environmental conditions drive species movements and population range shifts (Pinsky et al. 2013, Sunday et al. 2015, Brito-Morales et al. 2018). Here we show evidence that a combination of climatological and low-frequency environmental processes govern our ability to accurately predict the distribution and movements of a highly mobile predator species. We might expect this combination of inter-annual and long-term timescales of environmental variation to provide predictability of species distributions for many mobile marine and terrestrial species that exhibit spatial shifts in response to environmental change. However, the low-frequency component of predictability may be less important for species with high site fidelity, particularly terrestrial species that are able to exploit microclimates in response to adverse environmental conditions (e.g. thermal refugia; Pinsky et al. 2019). For species that can exploit microclimates, high frequency environmental variability (in addition to static variables, such as substrate type) may play a larger role in predicting species distribution than seen here for the pelagic swordfish. However, we should acknowledge that the spatial scale being examined will have a large influence on the relative importance of component signals. For example, on a global scale a species distribution might be best predicted by long-term mean conditions, but on a local scale (e.g. meters) the high frequency components should be more important in describing species distributions and habitat use. Testing our temporal decomposition approach on other species and on different spatial scales would further help to elucidate the spatiotemporal scales of predictability in species distributions.

The metrics of predictive performance that we used to compare across abundance-based SDMs are well known and frequently used (Norberg et al. 2019), yet showed inconsistent results and in certain cases indicated only minor differences across SDMs (Table 1). Such variability and minor improvement are consistent with similar studies that have compared SDMs built with climatological and extreme event data (e.g. heatwaves and droughts; Morán-Ordóñez et al. 2018), and local weather data (Zimmermann et al. 2009). Zimmermann et al. (2009) in particular noted that the primary impact of including local weather conditions in SDMs was a minimization of over- and underprediction, with only modest improvements in area under the receiver operating characteristic curve (AUC) (a standard evaluation metric of binomial SDMs). However, an important distinction should be made between the standard SDM performance metrics (Table 1) and assessment of skill for predicting anomalous species distributions. The climatological environmental data have by definition no ability to predict anomalous distributions. Since the goal of many prediction or projection analyses is to capture changes from the climatological state, it is critical in this context to assess model skill for predicting anomalies of species distribution and catch. While uncommon in

species distribution modelling, assessing skill based on anomalies is common practice in climate and weather studies: for example, a model is not assessed by whether it can predict if summer is on average warmer than winter, but whether a given summer is warmer or colder than the average summer. These skill metrics are becoming more common in ecological forecasting applications (Hobday et al. 2016). We suggest that in a prediction context, the suite of SDM performance metrics should distinguish skill in predicting distribution anomalies from skill in predicting climatological patterns.

Much of the explanatory power in our SDM of swordfish in the CCS came from the environmental monthly climatology, but the monthly climatology itself cannot be used to predict deviations from mean species distributions. Thus, the ability of low- and to a lesser degree high-frequency environmental variability to enable skillful predictions of anomalous species distributions is a key result of our study; indeed, it indicates the feasibility of forecasting species distribution changes on both short (seasonal) and long-term (climate change) timescales. For swordfish specifically, we might expect climate change to delay the arrival of cooler waters to the southern California Bight and subsequently shift the typical peak period of catch (Sep–Nov) to later in the winter season. The implications of such a shift for the fishery could be drastic without appropriate mitigation or adaptation. For example, temporal shifts in key swordfish fishing months may be impacted by poor weather (i.e. late winter and spring storms) and overlap with other seasonal fisheries (e.g. gear switching; Frawley et al. 2020) which would likely have an economic impact on this fishery (Smith et al. 2020). Application of a seasonal forecasting product to predict whether a swordfish fishing season will be typical or anomalous may help to improve the resilience and capacity of fishers in response to climate change. Our results show the potential for a skillful seasonal forecast for this swordfish fishery, as the low-frequency temperature variability that drives swordfish distribution anomalies in the CCS has been shown to be skillfully forecast by global climate prediction systems (Jacox et al. 2019). Additionally, we demonstrate a straightforward approach to decompose and evaluate the drivers of ecological predictability which could be applied in other study systems as a precursor to ecological forecasting.

Ecological forecasting requires identifying a particular metric that is accurately predictable and relevant to the forecast end-user (Jacox et al. 2020). Our results indicate that we could accurately predict swordfish catch anomalies during a historical testing period, but the two metrics used to assess predictive ability did not show consistent patterns across SDMs or spatial resolution of catch anomalies. This disparity is likely a function of how fisher behavior can influence fisheries data. For example, when environmental conditions become more favorable for positive catch anomalies, this doesn't necessarily mean that fishing effort or catch will increase. Other factors, like spatiotemporal management zones, historical fisher knowledge and weather can all impact where and when fishers fish (Frawley et al. 2020, Smith et al. 2020). In light of remaining uncertainties in swordfish

distribution predictions, along with relevant scales for management action, it may be more pragmatic to forecast species distributions probabilistically (e.g. with tercile classification; Fig. 4) than deterministically (e.g. with exact values of habitat suitability or catch). It is important to understand these limitations of predictability for ecological forecasting, and ongoing work could further explore predictability through retrospective skill testing (Hobday et al. 2016, Brodie et al. 2017).

Conclusion

Understanding the factors that promote accurate prediction of species distributions in response to environmental change is vital for informing climate-ready and proactive ecosystem management. Here, we identify the temporal scales of environmental variability that provide predictive skill for the distribution of a mobile marine predator, distinguishing their ability to explain historical mean distributions from their ability to predict distribution anomalies. In doing so, we highlight how both long-term and interannual environmental variability help to structure the distributions of a mobile marine predator. Understanding the scales that provide skill for predicting species responses to the environment gives confidence in our ability to accurately predict species redistributions, and to know which responses are likely unpredictable, under future climate change.

Data availability statement

NOAA fisheries observer data for the drift gillnet fishery is not publicly available. Contact authors directly to request access.

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Author contributions

Stephanie Brodie: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Briana Abrahms:** Writing – original draft (supporting); Writing – review and editing (supporting). **Steven J. Bograd:** Investigation (supporting); Writing – review and editing (supporting). **Gemma Carroll:** Investigation (supporting); Writing – review and editing (supporting). **Elliott L. Hazen:** Investigation (supporting); Writing – review and editing (supporting). **Barbara A. Muhling:** Writing – review and editing (supporting). **Mercedes Pozo Buil:** Writing – review and editing (supporting). **James A. Smith:** Methodology (supporting); Writing – review and editing

(supporting). **Heather Welch:** Data curation (supporting); Writing – review and editing (supporting). **Michael G. Jacox:** Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Writing – review and editing (supporting).

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