

# Using Hidden Markov Models to develop ecosystem indicators from non-stationary time series

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## Highlights (3-5 bullet points, 85 characters per bullet point)

- Hidden Markov models are a useful approach for developing ecological indicators
- They are flexible and allow for non-stationarity
- HMMs found shifts in ocean temperature regimes with increasing mean temperatures
- Regime shifts were reflected in both means and variances for seabird indicators

## 21    **Abstract**

22    Ecological indicators are an important mechanism for understanding ecosystem change and  
23    implementing Ecosystem Based Fishery Management, but developing useful indicators must  
24    account for ecosystem shifts that result in non-stationary processes over time. This necessitates  
25    the adoption of more adaptable statistical modeling approaches. Hidden Markov models  
26    (HMMs) provide a robust framework for distinguishing underlying ecosystem shifts from noisy  
27    time series data. In this paper, we illustrate the power of HMMs to develop model-based  
28    ecological indicators of non-stationary systems    , focusing on two case studies from the  
29    California Current Large Marine Ecosystem. In the first case study, we analyze four temperature  
30    time series from 1998-2022 which are used as indicators for environmental conditions  
31    experienced by juvenile salmon, using a three-state HMM incorporating temporal trends to  
32    account for non-stationarity in the means over time due to overall ocean warming. Output from  
33    this model reveals increasing temperatures for all four metrics in the California Current, with  
34    most years being assigned to the warmest estimated state. In our second case study, we analyze  
35    nine time series of seabird densities in the northern California Current from 2003-2022, to  
36    demonstrate how HMMs can be useful to identify sets of indicators that reflect different  
37    ecosystem processes and have different variances. We found the strongest support for the  
38    existence of two distinct temporal regimes in the seabird data, with an abrupt shift occurring after  
39    2010. While mean densities changed slightly for some species, this regime shift can be best  
40    characterized with a shift in variances: sooty shearwaters (*Ardenna grisea*) and Cassin's auklets  
41    (*Ptychoramphus aleuticus*) represented species with densities becoming more variable, while  
42    common murrelets (*Uria lomvia*) and gulls were estimated to have become less variable after 2010.  
43    Common murrelets, Cassin's auklets, sooty shearwaters, pink-footed shearwaters (

44 *creatopus*) and gulls all represent species that may be useful indicators of change in northern  
45 California Current, because of their differential responses to this regime change. Overall, our  
46 analysis provides a first step illustrating the potential applications of HMMs to developing  
47 ecosystem indicators in non-stationary systems and a framework that is widely useful for  
48 applications to ecosystems around the world.

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## 1. Introduction

A growing body of research over the last decade has demonstrated that many ecological processes are non-stationary and vary over time or space (Rollinson et al., 2021). Non-stationary processes can include longer term trends, seasonal variation or changes in phenology, extreme events, or additional random variation. While there are empirical examples of spatial non-stationarity (Ward et al., 2022), most research to date has focused on temporal aspects of non-stationarity (Litzow et al., 2018; Wainwright, 2021). These temporal applications can be coarsely grouped into whether temporal change is treated as a continuous or discrete process. Treating temporal change as a continuous process allows relationships to evolve over time, often in non-linear ways, such as with a random walk (Scheuerell and Williams, 2005). Alternatively, approaches that view temporal change as discrete assume that processes are constant for some period of time but may switch to new regimes where processes differ (Litzow et al., 2020).

Regardless of the mechanisms responsible for non-stationarity, or whether continuous or discrete processes provide a better approximation, it is critical for natural resource managers to understand patterns of ecosystem change. A widely used approach for synthesizing information for scientists, managers, stakeholders, and the public is the development of ecological indicators (Niemi and McDonald, 2004). Developing useful indicators can be challenging from both a data perspective and a management perspective. Datasets used for indicator development may be short, fragmented, redundant with one another, or subject to observation or sampling errors that otherwise corrupt the signal in the data. From a management lens, it is important to align indicators with management objectives (Kershner et al., 2011), and the utility of indicators may change when two or more time series are combined (Moriarty et al., 2018). Despite these hurdles, synthesizing information streams into a comprehensive indicator can aid in detecting

and understanding ecosystem changes, thereby facilitating informed decision-making and adaptive management strategies.

While most ecological applications of indicators have focused on changes in mean quantities of interest, there is increasing awareness that variability in ecological systems may also be changing, particularly in response to climate change and other anthropogenic impacts. Increasing variability in environmental conditions may impact the costs of physiological and behavioral mechanisms for adapting to these changes, decreasing the fitness of aquatic species and may also impact their ability to adapt to shifts in mean environmental conditions (Kroeker et al., 2020). In order to reflect both changes in the mean and variance of environmental conditions, flexible statistical modeling frameworks that allow for non-stationarity as well as changes in both the mean and variance of quantities of interest are needed. Dynamic factor analysis has previously been used in indicator development(Hunsicker et al., 2022) – this approach is useful if modeling changes in mean ecosystem state, however, these approaches have not evolved to include different kinds of non-stationarity (such as changing variances).

Another approach is Hidden Markov Models (HMMs) which represent a class of state-space models that discretize temporal change and offer a valuable framework for distinguishing coherent underlying state dynamics (regimes) from noisy time series data. HMMs achieve this by separating the observation process from the underlying state process (McClintock et al., 2020). Inputs to HMMs may include two or more time series, and data may be modeled with any response distribution that is available for generalized linear models. Outputs from fitted HMMs include estimates of the state trajectory (identifying the underlying regime at any point in time), estimates of the means and variances corresponding to each response in each state, and the transition probabilities between states. Covariates may be included as predictors of means and

variances, as well as transition probabilities. While HMMs have been applied widely beyond ecology, they have been utilized in freshwater (e.g., Gal and Anderson, 2010), terrestrial (e.g., Gennaretti et al., 2014), and marine ecosystems (e.g., Economou and Menary, 2019) to identify regime shifts.

One potential application of HMMs to ecological indicators for decision-making and ecosystem-based management is in integrated ecosystem assessments (IEA, (Levin et al., 2009). The use of IEAs has been primarily in marine ecosystems, but these have been developed in many regions around the world (Foley et al., 2013; Spooner et al., 2021; Walther and Möllmann, 2014). Focusing on the longest running IEA in North America, the California Current IEA (CCIEA) was initiated in 2010 and consists of several steps that may be informed by model-based indicators (Harvey et al., 2017), such as that generated from HMMs. HMMs may be useful for selecting and refining the suite of time series used for ecological indicator development and for describing non-stationarity as a time series of which regime or state an ecosystem is in.

Developing frameworks applicable to indicator development in non-stationary ecosystems has the potential to be broadly relevant to the CCIEA—which has attributed many management-relevant ecological processes to environmental forcing (e.g., Harvey et al., 2020; Samhouri et al., 2021; Santora et al., 2020; Tolimieri et al., 2018)—as well as similar efforts around the world. One general challenge is that as the relative importance of environmental drivers on biological responses changes over time (Litzow et al., 2020), the explanatory power of an indicator may change, which could undermine ecosystem indicator-based decision support. For the CCIEA, as in other IEAs, many of the time series initially included as indicators were selected based on expert knowledge, qualitative screening, and data availability (Levin et al., 2014; Levin and Schwing, 2011) and not externally validated. Model-based approaches offer the

ability to identify redundant sources of information (Moriarty et al., 2018) as well as time series that provide unique signals about the state of nature, which can greatly expand the explanatory power and management relevance of a suite of indicators. A second general challenge is that some marine ecosystems are experiencing rapid warming related to serial climate change and/or an increasing frequency of extreme events; these non-stationary trends necessitate the inclusion of trends in indicator development.

The primary objective of this paper is to explore and develop model-based ecological indicators of non-stationary systems that may be useful for stakeholders, managers, and other scientists. Using HMMs as a modeling framework, we focus on two case studies from the northern California Current Large Marine Ecosystem (CCLME), located on the west coast of North America. First, we demonstrate the applicability of HMMs to time series of physical drivers, which exhibit non-stationary trends across years. We contrast the results from HMMs to simpler descriptive approaches based on terciles—often the basis for “stoplight” depictions of indicators. . As a second application, we illustrate the use of HMMs for time series of seabird densities surveyed at sea, which exhibit non-stationary patterning with respect to variance over time. We demonstrate how our model-based approach using HMMs may be used to refine the list of indicator species by identifying which indicators are redundant and which may provide additional information not captured with the current suite of indicators. These biological time series are especially relevant for assessing the potential impacts of non-stationarity on indicator robustness, given the linkage of ecological dynamics to readily monitored physical oceanography variables and given evidence that seabirds are strong, integrative ecosystem indicators of ecological processes and disturbances across many spatial and temporal scales (Piatt and Sydeman, 2007; Sydeman et al., 2021).

## 2. Materials and Methods

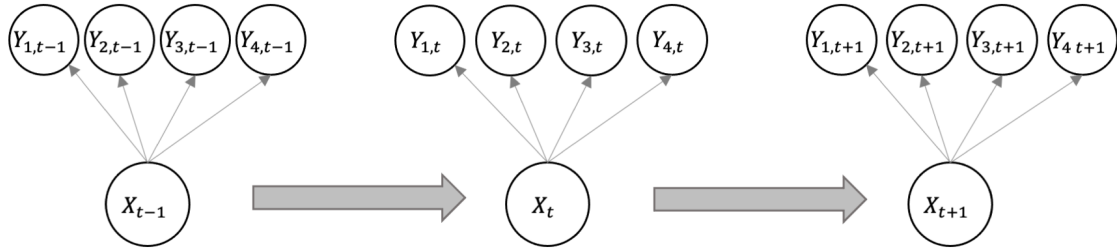
### 2.1 Case Study 1: physical data from the California Current

As a first case study, we focus on four time series of physical drivers that are used as indicators of the environment experienced by juvenile salmon, migrating from freshwater streams of origin to the Pacific Ocean. These time series are (1) sea surface temperature SST (averaged across seven NOAA NDBC buoys 46229, 46211, 46041, 46029, 46050, 46097, 46098 off the coast of Oregon and Washington states), (2) average ocean temperature at a depth of 20 m from station NH-5 off the coast of Newport, Oregon in summer months (May – September), (3) average ocean temperature at a depth of 20 m of the water column from station NH-5 in winter months (November – March), and (4) average ocean temperature at a depth of 50 m from station NH-5 in summer months (May – September). Past analyses have shown that these temperature data are among a suite of indicators that are correlated with juvenile-to-adult survival of Chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) in the region (Burke et al., 2013; Peterson et al., 2014). These data are updated annually and summarized for stakeholders by calculating anomalies from the historical mean, computing the tercile that each data point falls into, and visually summarizing these categorizations in a 'stoplight' chart with the value of each time series in each year qualitatively summarized with a red/yellow/green color scheme (e.g., Harvey et al., 2020; Peterson et al., 2014). These data are publicly available at <https://www.fisheries.noaa.gov/west-coast/science-data/ocean-conditions-indicators-trends> and in the repository for our paper <https://github.com/zoer27/HMM-indicators>.

While the tercile approach provides an informative visual summary, it does not account for non-stationary patterns in the mean or variance over time. Using data from 1998-2022, two of



the temperature time series in our dataset exhibit statistically significant positive trends (upper 20 m temperature in winter,  $p < 0.05$ ; 50 m temperature,  $p < 0.01$ ). Such trends may be accounted for by de-trending data prior to modeling (using regression or more complicated non-linear approaches), but these types of trends may also be accounted for within the HMM modeling framework. To demonstrate the power of HMMs to incorporate non-stationarity, we fit a three-state HMM to the suite of four physical drivers. HMMs separate the observation process for each physical indicator ( $i$ ) at each time step ( $t$ ),  $y_{i,t}$ , from an unobserved discrete state process,  $x_t$ . This assumes that each time series is an independent observation of the same latent state process (Figure 1). The number of discrete states must be chosen *a priori*. We fit a three-state model to allow comparisons with existing tercile summaries, and assumed all response variables were normally distributed (full model equations are in Appendix A). To facilitate easier model fitting with a multivariate model, each response variable was centered and standardized by subtracting the mean and dividing by the standard deviation so that all the response variables were on a similar scale. To account for non-stationarity in the mean of each response, we included a linear trend in each. HMMs are flexible in that trends may be unique to each state, or shared across states; for interpretability, we modeled the trend as shared across states. The model was fit using the package `hmmTMB` (Michelot and Glennie, 2023) in R v. 4.3.1 (R Core Team, 2023). The model was fit 500 times using different initial values to ensure convergence and the model fit with the lowest AIC was used. The underlying state in each year was calculated using the Viterbi algorithm. Model fit was assessed using simulation-based goodness of fit checks and residual checks.



**Figure 1.** Diagram of multivariate HMM where  $X_t$  represents the underlying (i.e. “hidden”) state process and  $Y_{i,t}$  the observations of a given indicator ( $i$ ) at time  $t$ .

## 2.2 Case Study 2: seabird density-anomalies in the northern California Current

As a second case study, we focus on density-anomaly time series from 2003-2022 for nine taxa of seabirds in the northern California Current. Data from this study are collected on the Juvenile Salmon Ocean Ecosystem Survey (JSOES), a long term, multi-trophic level research program examining factors affecting early marine growth and survival of Pacific salmon, including densities of upper-trophic level consumers. Seabirds were counted along eight east-to-west survey lines from Cape Flattery, WA (48.2 °N) to Newport, OR (44.7 °N; (Zamon et al., 2014) using standard 300 m strip-transect methods (Heinemann, 1981; Tasker et al., 1984). Density-at-sea values were log-transformed ( $\ln(x+1)$ ) and expressed as anomalies by subtracting the long-term mean.

Density anomalies for three of these species, common murres (*Uria aalge*), Cassin's auklets (*Ptychoramphus aleuticus*), and sooty shearwaters (*Ardenna grisea*) are currently used as seabird indicators in the annual California Current Ecosystem Status Report, which has been produced for the Pacific Fishery Management Council by the CCIEA team since 2014 (e.g., Harvey et al., 2023). Experts on the CCIEA team initially chose these three species as indicators of the seabird trophic group because they (1) represent three of the most abundant seabird species using shelf and shelf-slope break waters throughout the California Current Ecosystem, (2) include resident breeding species (common murre, Cassin's auklet) and non-breeding summer migrants (sooty shearwater), (3) encompass birds with a planktivorous diet (Cassin's auklet) and a diet of pelagic fish and krill (common murre, sooty shearwater), (4) cover shallow (Cassin's auklet, 0–30 m), moderate (sooty shearwater, 0–70 m), and deep (common murre, 0–180 m) diving species, and (5) utilize soaring (sooty shearwater) and flapping (Cassin's auklet, common murre) flight in the air. Applying HMMs to these data can be seen as a model-based alternative to the expert elicitation described above. Rather than restrict HMMs to the three species currently used as indicators, we fit a multivariate HMM to an expanded set of nine seabird taxa (Table 1) by selecting the most variable time series across all species using an arbitrary standard deviation threshold of 0.2. We fit both a two-state and three-state model to the log density anomalies and chose the best-fitting model based on AIC. Each model was fit 200 times with different initial values to ensure convergence. All time series were assumed to be normally distributed; we assumed that the observations had a constant mean in each state (no time effect) and allowed for separate estimates of variance for each state. The model was fit using the package hmmTMB (Michelot and Glennie, 2023) in R v. 4.3.1 (R Core Team, 2023). The underlying state in each year was calculated using the Viterbi algorithm. Model fit was

224 assessed using simulation-based goodness of fit checks and residual checks.

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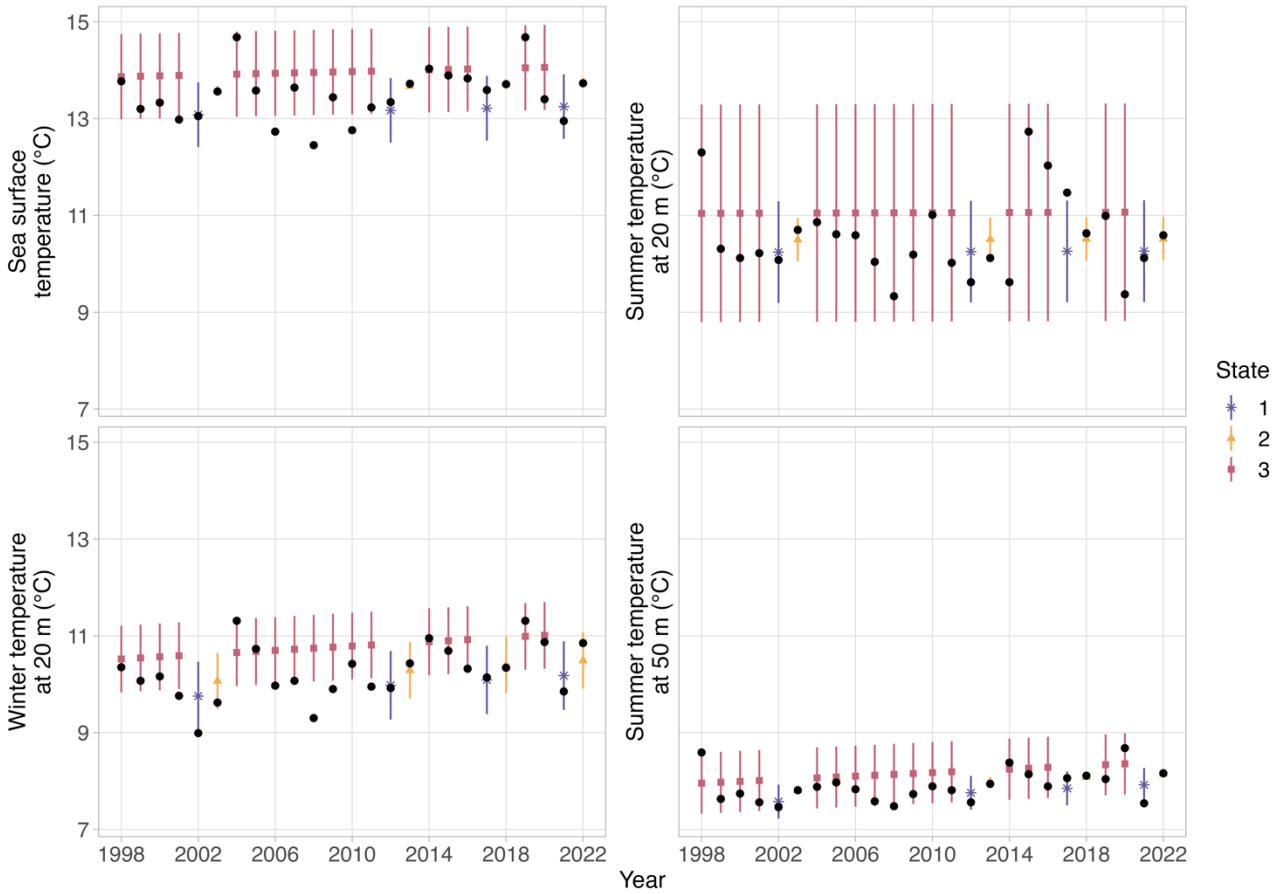
226 **Table 1.** Seabird taxa used to fit multivariate HMM.

| Common name                         | Scientific name                         |
|-------------------------------------|---|
| Black-footed albatross              | <i>Phoebastria nigripes</i>             |
| Caspian tern                        | <i>Hydroprogne caspia</i>               |
| Cassin's auklet                     | <i>Ptychoramphus aleuticus</i>          |
| Common murre                        | <i>Uria aalge</i>                       |
| Northern fulmar                     | <i>Fulmarus glacialis</i>               |
| Pink-footed shearwater              | <i>Puffinus creatopus</i>               |
| Sooty shearwater                    | <i>Ardenna grisea</i>                   |
| Western gull                        | <i>Larus occidentalis</i>               |
| Western*Glaucous-winged hybrid gull | <i>Larus occidentalis x glaucescens</i> |

227 **3. Results**

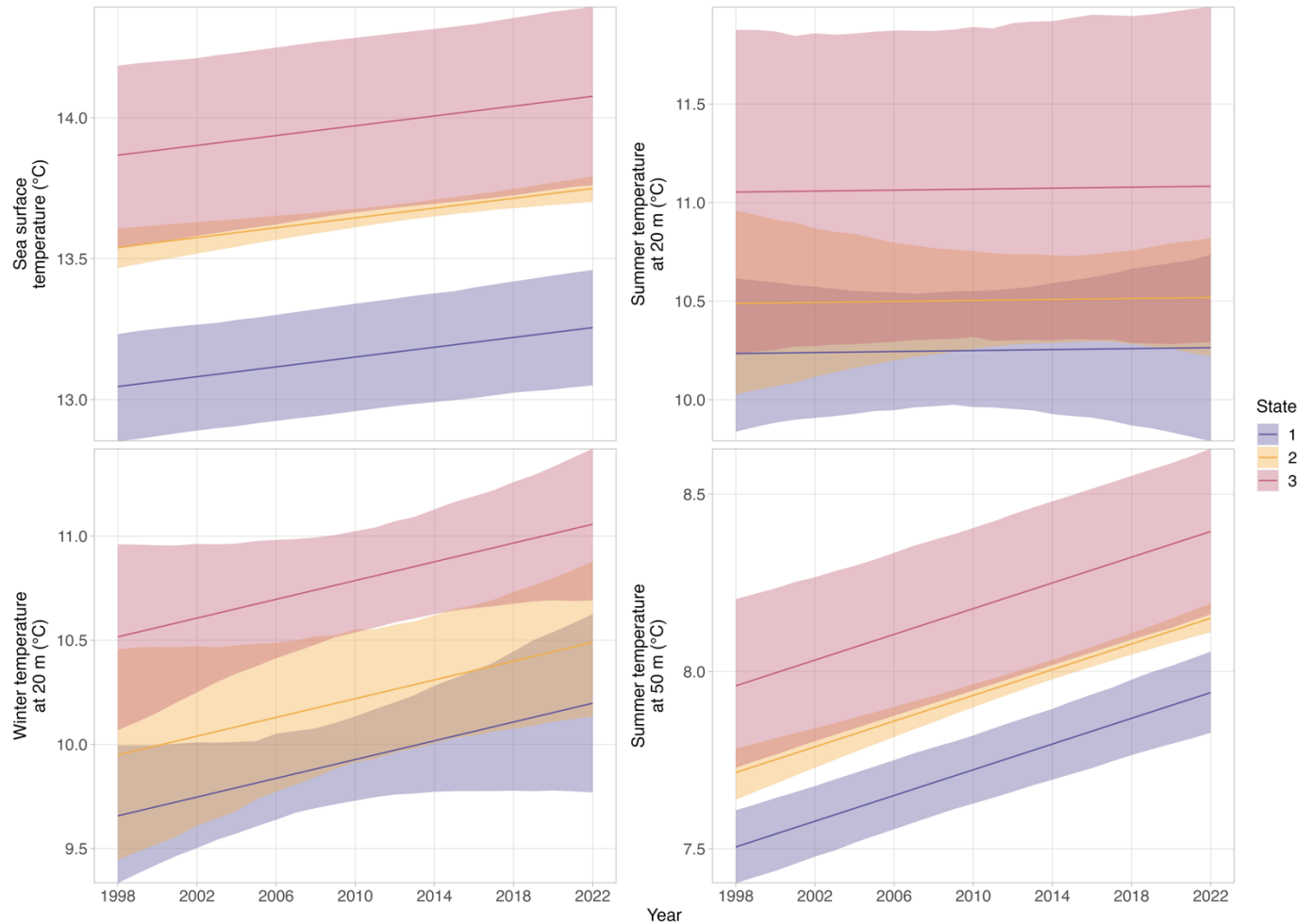
228 *3.1 Case Study 1*

Our HMM of non-stationary physical responses in the California Current indicated a high degree of similarity among the four temperature metrics (increasing temperatures from states 1 – 3, Fig. 2). Output from the Viterbi algorithm, providing the most probable sequence of states, showed that state transitions moved from the warmest regime (State 3) to the coldest (State 1), and then to the middle state (State 2) before returning to the warmest regime. The probability of moving from State 1 to State 2 and from State 2 to State 3 was estimated to be approximately 1.0, indicating deterministic transitions in a single direction. The probability of moving from State 3 to State 1 was estimated to be 0.33, with the probability of remaining in State 3 estimated as 0.67, suggesting that the transition from State 3 to State 1 is stochastic though less likely than remaining in State 3 (Appendix A). Our HMM results can also be contrasted with existing tercile indicators of these same drivers (<https://www.fisheries.noaa.gov/west-coast/science-data/ocean-conditions-indicators-trends>, Appendix B), which provides a summary of the data without imposing a Markov process. Both approaches highlight the same general periods as being warmer than average (1998, 2004–2005, 2014–2020), however because the HMM accounts for increasing temperatures over time, the model assigns all years between 2004–2011 to the warm regime, even though temperatures in the following warm regimes (2014–2016 and 2019–2020) are higher. Additionally, this also allows the model to detect a cold regime in 2017 that is missed in a tercile approach.



**Figure 2.** Model-estimated means (colored symbols) and 95% prediction intervals (lines) in each year for physical indicators on the real scale, developed from a three-state Hidden Markov Model (HMM). Indicator values are represented by black circles.

We found an increase in temperature over time for all four temperature metrics. This increase was strongest for summer temperature at 50 m, and weakest for summer temperature at 20 m. Although we assumed three states in order to compare to the tercile approach, the values of summer temperature at 20 m were essentially indistinguishable among the three states (Figure 3).

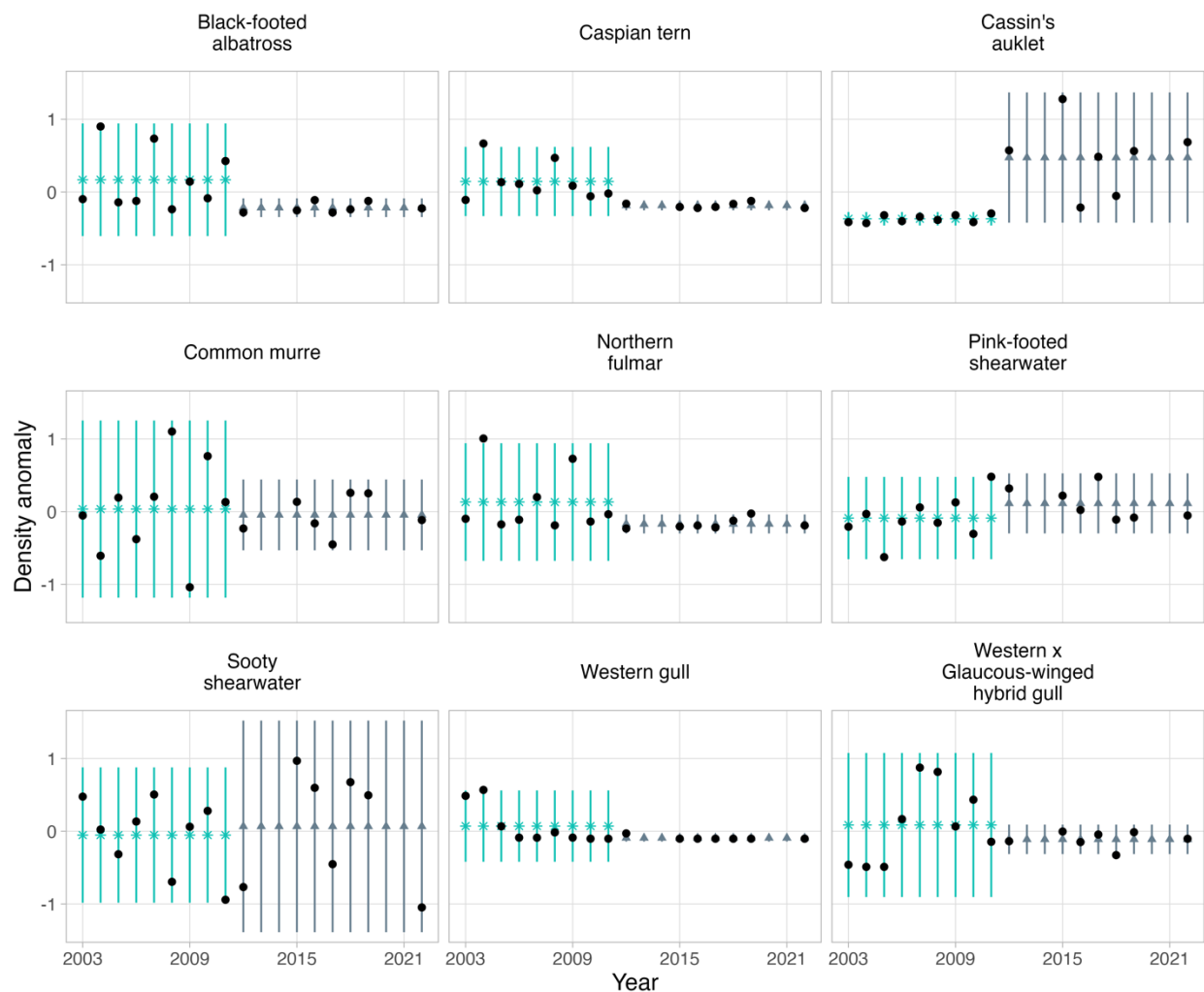


**Figure 3.** Effect of time (in years) on the estimated mean indicator value in each state. Shading represents 95% confidence intervals. The slopes of each trend are constrained by our model to be the same across states.

### 3.2 Case Study 2

The best-fitting HMM for the seabird density-anomaly time series was a two-state model, with a shift between the first state and the second state occurring between 2010 and 2011. The estimated means between the two states were very similar for many species with the notable exception of Cassin's auklets, which increased in density after 2010. Unlike the means, the

265 estimated variances differed greatly between states. Black-footed albatross, Caspian tern,  
 266 common murre, northern fulmar, western gull, and western x glaucous-winged hybrid gull all  
 267 had higher estimated variances prior to 2010. Conversely, Cassin's auklet and sooty shearwater  
 268 had higher estimated variances after 2010. Pink-footed shearwater variance was similar across  
 269 the two states (Figure 4). The model estimated a 0.11 probability of switching from state 1 to  
 270 state 2 (Table A.4).





**Figure 4.** Model-estimated means (colored symbols) and 95% prediction intervals (lines) for nine seabird taxa used in our two-state Hidden Markov Model. Density anomaly values for each taxon are indicated by black circles.

#### 4. Discussion

In this study, we explore two distinct applications of Hidden Markov Models (HMMs) in addressing non-stationary time series, utilizing datasets that encompass both physical drivers and biological responses within the California Current ecosystem. For the physical drivers that are relevant to adult returns of Pacific salmon, we found that a three-state model successfully discriminated among warm, transitional, and cold regimes, though these regimes were more clearly differentiated in sea surface temperature and temperature at 50 m in the summer than in the 20 m temperatures in winter or summer. All three regimes demonstrate an overall warming trend, with the strongest trend for winter temperature at 20 m and summer temperature at 50 m (Figure 3). The predicted states in each year suggest that most years are spent in the warm regime, with random transitions to the cold regime that are followed by the transitional regime in the next year and then a return to the warm state (Figure 2). This “flipping” between warm and cold regimes is not as clearly detected in a tercile approach and is obscured by the overall warming over the course of the time series. For example, in the tercile method, 1999-2001, 2007-2009, generally appear to be “cooler” years (Figure B.1), however, this is partly due to the influence of higher temperatures at the end of the time series because of overall warming. Flipping behavior may be important for the viability of species that do better in colder water and may be more strongly impacted by the overall warming trend. However, while our results

demonstrate the utility of HMMs in reflecting non-stationarity when compared to the tercile methods, additional model formulations and potentially the inclusion of additional covariates should be considered before making substantial ecological conclusions about these results.

For the biological responses of seabird densities, we saw a case where variance clearly was changing between states (Figure 4). This is not something that a traditional quantile approach would be able to detect since the estimated means in each state were quite similar. This suggests that Hidden Markov models can be a more useful approach for identifying ecological indicators when regime shifts primarily affect the variance rather than the mean.

#### *4.1 Moving toward model-based approaches*

The adoption of a model-based approach, such as HMMs, presents multiple advantages in non-stationary systems over traditional summaries, such as those using quantile statistics. Output from our application of HMMs to time series of temperature in the California Current can be contrasted with the tercile approach that has been used to generate visual summaries of the data (“stoplight” charts). Most importantly, our model-based approach was able to account for non-stationarity in the mean over time by incorporating time as a covariate. This allowed the model to detect shifts in ecosystem states while still accounting for increasing temperatures over time (and estimating the magnitude of the trend for each response dataset). Because HMMs separate the latent state process from the observation process and model sequential time steps as autocorrelated, we found fewer transitions between low, middle, and high temperature states compared to the tercile approach. While we restricted our analysis to only include HMMs with

three states, this approach is flexible and could be extended to include models with alternative states; similarly, covariates could be included to evaluate hypotheses responsible for the trends.

Our application of HMMs to seabird density anomalies illustrates how model-based approaches may be used to select or refine ecosystem indicators by highlighting taxa that respond differently to regime shifts. Species currently used as indicators by the CCIEA (common murre, Cassin's auklet, and sooty shearwater) were selected using expert elicitation, and our model-based approach supported their inclusion as indicators, because all three species had different responses to the regime shift we identified in 2011. Common murres had similar mean density anomalies between the two states, but the variance decreased after 2010. In contrast, Cassin's auklets and sooty shearwaters both had higher variance after 2010. The mean density anomaly for sooty shearwaters was similar between the two states, while the mean density anomaly of Cassin's auklets increased after 2010 (Figure 4). This suggests that these species are responding to different ecosystem processes which supports their use as ecosystem indicators.

Our model-based approach can also be useful in identifying indicators that may be redundant or potentially useful. All four temperature metrics had similar estimated intercept, slope, and variance parameters (Figure 3, Appendix A), which suggests that only a subset of these may be needed in order to detect ecosystem shifts. Additionally, Caspian terns, northern fulmars, western gulls, and western x glaucous-winged hybrid gulls responded similarly to our estimated regime shift, with a decrease in variance after 2010, therefore adding all these species as indicators may not provide additional information about ecosystem shifts. However, as these species demonstrated a stronger decrease in variance than for common murres, they are likely responding to an additional ecosystem process not currently represented by the current suite of indicators. For Caspian terns, the decline in at-sea densities is likely related to active wildlife

management that reduced their large breeding colony in the Columbia River estuary starting in 2008 (Roby et al., 2021). Moreover, the density anomaly of pink-footed shearwaters did not change significantly between the two states, suggesting they are not responding to the same processes as the other species. These results suggest that other species could be added to the indicator portfolio to provide additional information about ecosystem states, particularly if the species also represents unique life history, foraging, or migration traits; northern fulmar, as a migrant from more arctic areas, might be one such addition.

While our model identified a shift in seabird density anomalies between 2010 and 2011, we did not detect a shift during or after the multi-year marine heatwave from 2014-2015 in the Northeast Pacific, known as the “warm blob” (Bond et al., 2015; Di Lorenzo and Mantua, 2016). Seabird densities in the northern California current were likely affected by this heatwave, and coastwide die-offs during this time were reported for both common murre (Piatt et al., 2020) and Cassin’s auklet (Jones et al., 2018). Additionally, marine heatwaves cause significant and sudden shifts in primary productivity (Wyatt et al., 2022) and have been shown to influence seabird productivity by limiting the availability of forage fish and their nutritional value (von Biela et al., 2019). Reduced foraging can also result in decreased juvenile and adult survival (Warzybok et al., 2018), which may be reflected in observed at-sea densities of seabirds. However, our model may not have detected a regime shift after this heatwave because its effects may have been obscured by longer-term regime change that has been occurring since 2011 such as the gradual warming reflected in the temperature metrics in Case Study #1. As longer-lived organisms exposed to naturally-occurring ocean warming events like El Niño events, seabirds may also be fairly resilient to short-term perturbations in food webs by changing where they forage (Avalos et al., 2017) or engaging in diet-switching behavior (Warzybok et al., 2018;

Wells et al., 2017). Additionally, the lack of observations in 2013-2014 and 2020-2021 could affect the ability of the time series to detect state changes after 2011.

Both of our cases studies are meant to be illustrative of potential applications of model based approaches for identifying ecosystem states (and transitions) and contrasts with traditional approaches; as such, the 3-state HMM applied to each may not necessarily represent the best statistical model that could be constructed for these datasets. A general challenge for both case studies is that our time series are relatively short (< 30 years). As such, the complexity of potential models is limited – simpler approaches, such as 2-state HMMs or breakpoint regression analyses may also be worth exploring for these case studies. Adding additional indicator time series or including more years of data may help reduce uncertainty for these HMMs, particularly if new information is consistent with existing indicators and estimates of underlying states.

#### *4.2 Future work*

Our analysis provides a first step illustrating the potential applications of HMM to developing ecosystem indicators in non-stationary systems and motivates the need for additional research. One area of future research for ecosystem state applications would be to extend our HMMs to include covariates . While our approaches allowed means and variances to vary by regime (state), we did not introduce models with non-stationary effects of covariates in the transition probabilities between states; increasing or decreasing transition probabilities may result in systems becoming less or more stable over time. Another area of future research would be to include data from multiple trophic levels or states, such as seabirds alongside physical drivers. These types of analyses introduce additional challenges, such as identifying appropriate time lags between datasets, but have the potential to help understand non-stationary change

between different types of responses. Third, additional work could be used to generate different types of model uncertainty – one example unique to HMMs may be estimates of uncertainty in state assignments.

The estimated transition probabilities from Hidden Markov models also offer a valuable opportunity for managers to forecast the possibility of a regime shift. Estimated transition probabilities from these models can be used to forecast the probability of moving from one state to another in a future year, as well as the probability of any state in future years. While this is similar to approaches using dynamic factor analysis to forecast the probability of extreme events (Hunsicker et al., 2022), HMMs provide estimates of discrete underlying states rather than the continuous estimates generated from dynamic factor analysis. Forecasts of the timing of climate-driven shifts in the marine environment could lead to earlier detection of these shifts, and therefore more effective responses from scientists, managers, and other stakeholders.

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## Appendix A. Model equations, numerical results and model diagnostics

### Case Study 1

Hidden Markov models (HMMs) are a form of state-space model, with a process model that has discrete latent states which follow a Markov process, so the probability of being in each state ( $x$ ) at timestep  $t$ , given the states at all previous time steps ( $X^{(t-1)}$ ) depends only on the state at the previous timestep ( $t-1$ ; Eqn. 1).

$$Pr Pr (X_t | X^{(t-1)}) = Pr Pr (X_{t-1}), t = 2, 3, etc. \quad (1)$$

We assumed that the probability of transitioning between states was constant over time.

The observation model depends only on the state at the given timestep ( $t$ ). In this case study, the observation process was multivariate, which assumes that each temperature time series ( $i$ ) represents independent observations of the same underlying state process. The mean value ( $\mu$ ) in each state ( $j$ ) was assumed to be time dependent, with an estimated intercept ( $\alpha$ ) representing the value of the indicator at  $t = 0$ , and a slope ( $\beta$ ) for the effect of time, which was assumed to be the same for each indicator across all states (Eqn 2.)

$$\mu_{i,j,t} = \alpha_{i,j} + \beta_i * t \quad (2)$$

We assumed that all observations ( $Y_{i,t}$ ) were normally distributed, conditioned on the underlying state (Eqn 3.)

$$Y_{i,t} | \{X_t = j\} \sim N(\mu_{i,j,t}, \sigma_{i,j}) \quad (3)$$

The results from this model include estimates of the probability of transitioning between states (Table A.1) as well as the parameter estimates for the observation model (Table A.2).

**Table A.1.** Transition probability matrix for 3-state HMM fit to four time series of ocean temperature. Probabilities are read as moving from the state on the row (time  $t$ ) to the state on the column (time  $t+1$ ).

|         | $t+1$   |         |         |
|---------|---------|---------|---------|
| $t$     | State 1 | State 2 | State 3 |
| State 1 | 0.00    | 1.00    | 0.00    |
| State 2 | 0.00    | 0.00    | 1.00    |
| State 3 | 0.33    | 0       | 0.67    |

**Table A.2.** Model estimates for the observation model from 3-state HMM fit to four time series of ocean temperature with a time effect on the mean temperature. The model was constrained so that the slope was the same across states.

| Indicator   | <i>State 1</i> |      | <i>State 2</i> |       | <i>State 3</i> |      | Slope |
|-------------|----------------|------|----------------|-------|----------------|------|-------|
|             | Intercept      | SD   | Intercept      | SD    | Intercept      | SD   |       |
| SST         | -0.85          | 0.64 | 0.08           | 0.054 | 0.69           | 0.84 | 0.016 |
| Summer 20m  | -0.36          | 0.63 | -0.06          | 0.27  | 0.58           | 1.34 | 0.001 |
| Winter 20 m | -1.07          | 0.64 | -0.56          | 0.52  | 0.44           | 0.62 | 0.039 |

|             |       |      |       |      |      |      |       |
|-------------|-------|------|-------|------|------|------|-------|
| Summer 50 m | -1.28 | 0.55 | -0.62 | 0.09 | 0.12 | 0.99 | 0.056 |
|-------------|-------|------|-------|------|------|------|-------|

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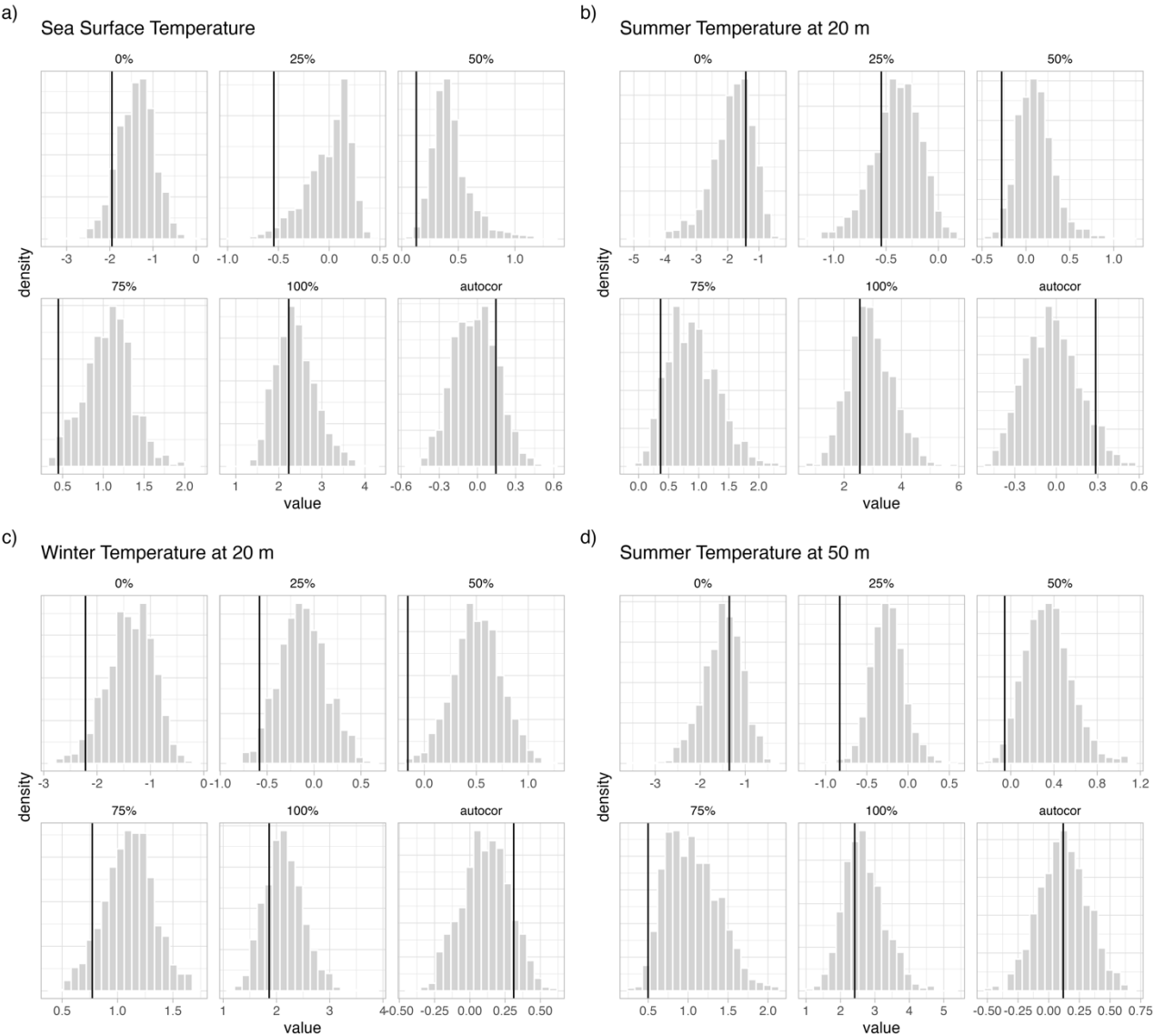
Simulations from the fitted model were used to evaluate goodness of fit. In general, observed

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values of tested summary statistics fell within the ranges of simulated data, suggesting that the

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model fit the data well (Figure A.1)



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**Figure A.1** Results from simulation-based goodness of fit tests for each response variable. Density plots

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indicate the minimum (0%), 25% quantile, median (50%), 75% quantile, and maximum (100%) as well as

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the autocorrelation from the observation process from 1000 simulated datasets based on the model result.

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The observed values of these statistics are indicated by the vertical line.

## Case Study 2

The HMM for this case study was similar to the one described above, however we assumed that the mean value in each state was constant over time (Eqn 4).

$$Y_{i,t} | \{X_t = j\} \sim N(\mu_{i,j}, \sigma_{i,j}) \quad (4)$$

Based on AIC, the best-fitting model had two underlying states (Table A.3). The results from this model include the transition probabilities between each state (Table A.4) and the estimates of the observation model parameters (Table A.5).

**Table A.3.** AIC results from multivariate HMMs fitted to time series of density anomalies of nine seabird species. Compared models were identical except for the assumed number of underlying states (2, or 3 states). The best-fitting model is indicated by (\*).

| Model    | AIC   | DeltaAIC |
|----------|-------|----------|
| 2-State* | 35.24 | 0.00     |
| 3-state  | 81.24 | 46.0     |

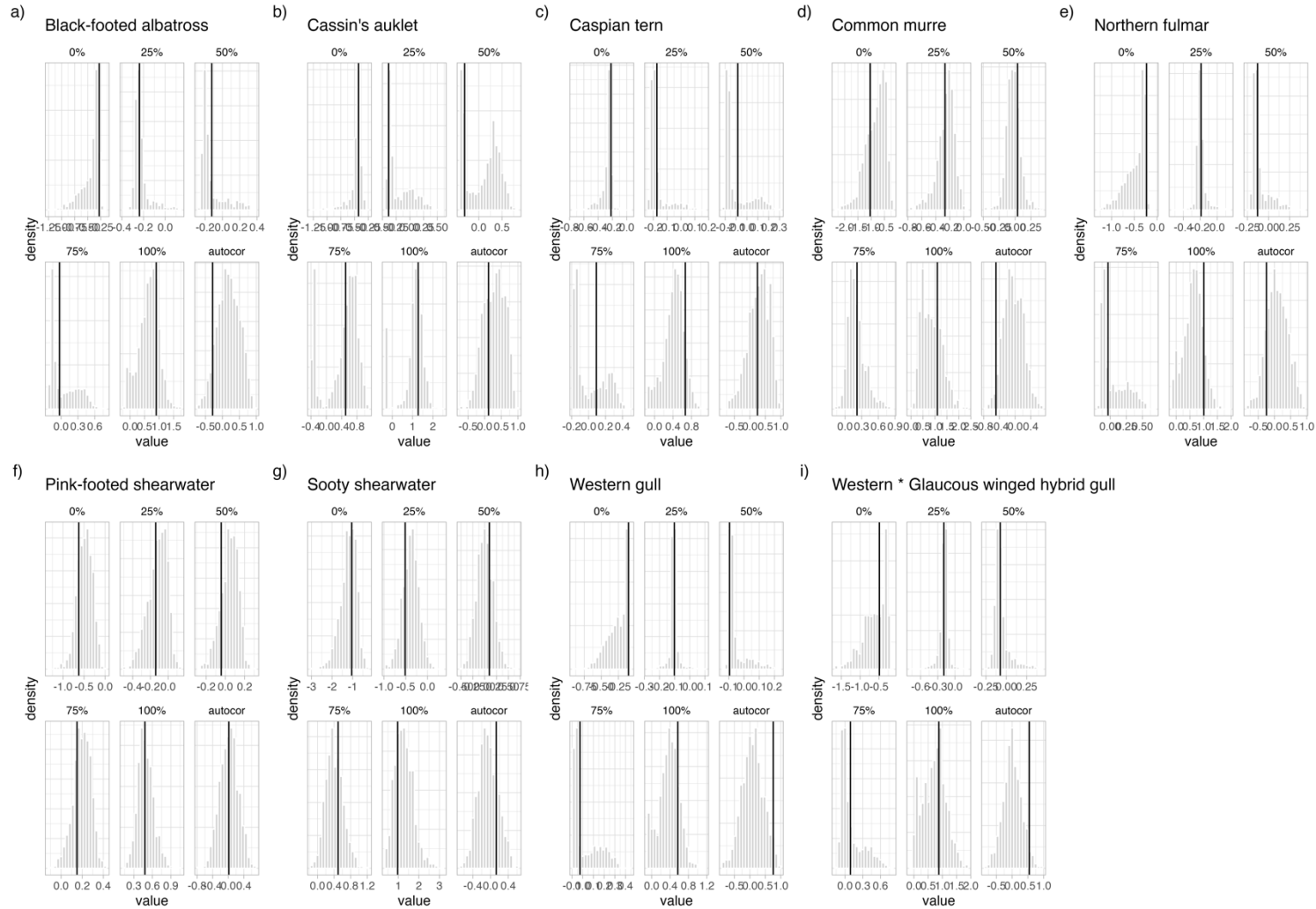
**Table A.4.** Transition probability matrix from the 2-state multivariate HMM fit to seabird density anomalies. Probabilities are read as moving from the state on the row (time  $t$ ) to the state on the column (time  $t+1$ )

| $t$     | $t+1$   |         |
|---------|---------|---------|
|         | State 1 | State 2 |
| State 1 | 0.89    | 0.11    |
| State 2 | 0.00    | 1.00    |

**Table A.5.** Estimates from the observation model for a two-state HMM fit to nine timeseries of seabird density anomalies.

| Species                                 | <i>State 1</i> |       | <i>State 2</i> |       |
|---|----------------|-------|----------------|-------|
|   | Intercept      | SD    | Intercept      | SD    |
| Black-footed albatross                  | 0.168          | 0.395 | -0.216         | 0.066 |
| Cassin's auklet                         | -0.368         | 0.047 | 0.473          | 0.457 |
| Caspian tern                            | 0.144          | 0.243 | -0.185         | 0.034 |
| Common murre                            | 0.035          | 0.621 | -0.045         | 0.248 |
| Northern fulmar                         | 0.132          | 0.412 | -0.169         | 0.066 |
| Pink-footed shearwater                  | -0.088         | 0.289 | 0.113          | 0.210 |
| Sooty shearwater                        | -0.052         | 0.475 | 0.067          | 0.742 |
| Western gull                            | 0.071          | 0.250 | -0.092         | 0.025 |
| Western and Glaucous-winged hybrid gull | 0.086          | 0.505 | -0.111         | 0.103 |

Simulations from the fitted model were used to evaluate goodness of fit. In general, observed values of tested summary statistics fell within the ranges of simulated data, suggesting that the model fit the data well (Figure A.2)



**Figure A.2** Results from simulation-based goodness of fit tests for each response variable for case study 2. Density plots indicate the minimum (0%), 25% quantile, median (50%), 75% quantile, and maximum (100%) as well as the autocorrelation from the observation

625 process from 1000 simulated datasets based on the model result. The observed values of these statistics are indicated by the vertical  
626 line.

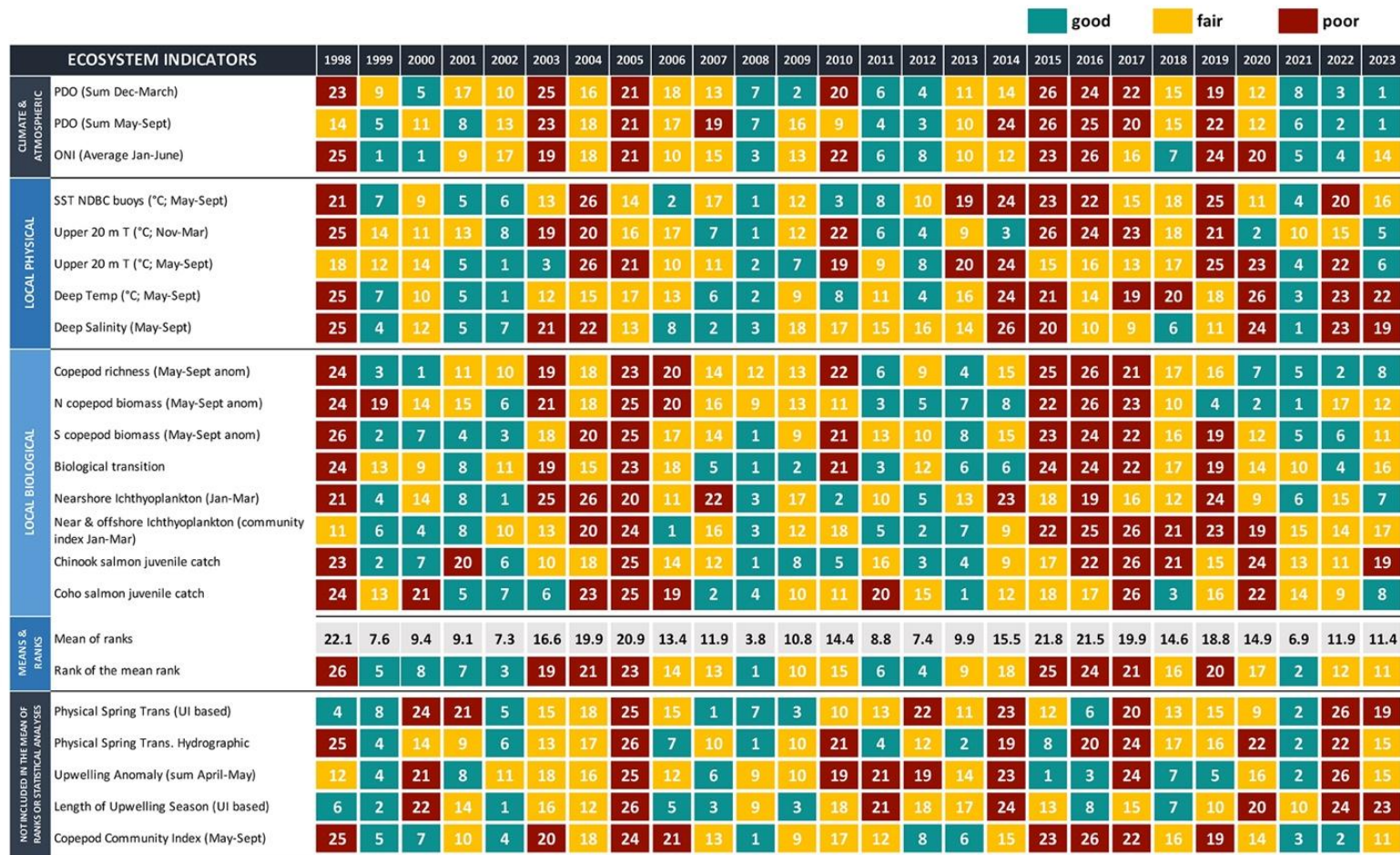
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## 2023 OCEAN CONDITION INDICATORS TREND



**Figure B.1.** “Stoplight” chart for ocean conditions that affect the growth and survival of juvenile salmon in the northern California Current. Numbers indicate ranking from low (favorable) to high (unfavorable) for juvenile salmon survival. This chart and raw data can be accessed here: <https://www.fisheries.noaa.gov/west-coast/science-data/ocean-conditions-indicators-trends>