

Research



Cite this article: Fennie HW *et al.* 2022 An anchovy ecosystem indicator of marine predator foraging and reproduction. *Proc. R. Soc. B* **290**: 20222326.
<https://doi.org/10.1098/rspb.2022.2326>

Received: 17 November 2022

Accepted: 13 January 2023

Subject Category:

Ecology

Subject Areas:

ecology, ecosystems

Keywords:

ecosystem-based management, ecosystem indicator, predator–prey dynamics, forage fish

Author for correspondence:

H. William Fennie

e-mail: will.fennie@noaa.gov

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6406074>.

An anchovy ecosystem indicator of marine predator foraging and reproduction

H. William Fennie^{1,2}, Rachel Seary^{1,3}, Barbara A. Muhling^{1,2}, Steven J. Bograd³, Stephanie Brodie^{1,3}, Megan A. Cimino^{1,3}, Elliott L. Hazen³, Michael G. Jacox^{3,4}, Elizabeth A. McHuron⁵, Sharon Melin⁶, Jarrod A. Santora^{7,8}, Justin J. Suca^{1,3}, Julie A. Thayer^{1,9}, Andrew R. Thompson², Pete Warzybok¹⁰ and Desiree Tommasi^{1,2}

¹Institute of Marine Sciences, University of California-Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA

²Fisheries Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037-1508, USA

³Environmental Research Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 99 Pacific Street, Suite 255A, Monterey, CA 93940-7200, USA

⁴Physical Sciences Division, Earth System Research Laboratory, National Oceanic and Atmospheric Administration, 325 Broadway, Boulder, CO 80305, USA

⁵Cooperative Institute for Climate, Ocean and Ecosystem Studies, University of Washington, 3737 Brooklyn Avenue NE, Seattle, WA 98105, USA

⁶California Current Ecosystems Program, Alaska Fisheries Science Center, National Marine Mammal Laboratory, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA

⁷Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, CA 95060, USA

⁸Department of Applied Math, University of California-Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA

⁹Farallon Institute for Advanced Ecosystem Research, 101 H Street, Suite Q, Petaluma, CA 94952, USA

¹⁰Point Blue Conservation Science, 3820 Cypress Drive Suite 11, Petaluma, CA 94954, USA

id HWF, 0000-0002-5610-455X; RS, 0000-0001-7496-8792; BAM, 0000-0002-4555-6382; SJB, 0000-0003-3872-9932; SB, 0000-0003-0869-9939; MAC, 0000-0002-1715-2903; ELH, 0000-0002-0412-7178; MGJ, 0000-0003-3684-0717; EAM, 0000-0003-3147-2628; JAS, 0000-0002-5991-4283; JJS, 0000-0001-5532-4780; ART, 0000-0002-1384-2229; PW, 0000-0003-1076-8745; DT, 0000-0003-4027-6047

Forage fishes are key energy conduits that transfer primary and secondary productivity to higher trophic levels. As novel environmental conditions caused by climate change alter ecosystems and predator–prey dynamics, there is a critical need to understand how forage fish control bottom-up forcing of food web dynamics. In the northeast Pacific, northern anchovy (*Engraulis mordax*) is an important forage species with high interannual variability in population size that subsequently impacts the foraging and reproductive ecology of marine predators. Anchovy habitat suitability from a species distribution model (SDM) was assessed as an indicator of the diet, distribution and reproduction of four predator species. Across 22 years (1998–2019), this anchovy ecosystem indicator (AEI) was significantly positively correlated with diet composition of all species and the distribution of common murre (*Uria aalge*), Brandt's cormorants (*Phalacrocorax penicillatus*) and California sea lions (*Zalophus californianus*), but not rhinoceros auklets (*Cerorhinca monocerata*). The capacity for the AEI to explain variability in predator reproduction varied by species but was strongest with cormorants and sea lions. The AEI demonstrates the utility of forage SDMs in creating ecosystem indicators to guide ecosystem-based management.

1. Introduction

Forage species are critical components of many marine ecosystems as they translate primary productivity into energy available to predators [1,2]. They also support commercially important fisheries, with catches contributing more than 30% of total global marine fisheries landings [3]. Forage species experience large and unpredictable population fluctuations, which have been associated

with variability in fisheries landings [3] and predator reproduction in a variety of ecosystems [4]. For example, in the Southern Ocean, fluctuations in Antarctic krill (*Euphausia superba*) biomass precipitate seabird and marine mammal population booms and busts [5]. Similarly, in both Norway and Alaska, seabird reproductive success is driven by forage fish abundance [6,7]. Additionally, commercial forage fish removals, combined with environmental variability, affect forage abundance, distribution and population dynamics of predators in the northern Humboldt and Benguela Current Systems [8,9]. Because of their role in fisheries, strong responses to environmental variability, and their capacity to drive population dynamics of higher trophic levels, elucidating the connectivity between forage species and their predators is paramount for effective ecosystem-based management.

There is growing interest in assessing how management actions on forage species affect the conservation of protected forage fish predators. Multiple ecosystems have shown increased variability in forage populations when fisheries exist [10]. However, it is difficult to determine whether forage fish removals affect predator population dynamics at broad scales because forage species are highly sensitive to environmental changes, causing large natural fluctuations and highly variable localized abundance [11,12]. Importantly, environmental variability coupled with forage removals may decrease forage abundance or availability within predator foraging ranges, directly impacting local predator population dynamics [9]. Developing forage-based ecosystem indicators that guide the management of overlapping uses in marine ecosystems requires techniques that capture oceanographic variability and forage distribution at appropriate scales.

Ecological modelling can align spatial scales of forage fish distribution and predator foraging, facilitating the creation of indicators at scales relevant to management objectives [13,14]. Species distribution models (SDMs) quantify relationships between environmental variables and species habitat-use to create predictions of species distributions [15]. These predictions can be tailored to specific regions to provide spatially resolved estimates and fill gaps in species distribution data [16]. Indeed, SDMs have been used to develop dynamic and spatially explicit bycatch-reduction measures [17,18]. The need for forage indicators is apparent when considering ecosystem-based management in ecosystems like the California Current System (CCS) where environmentally driven changes in the spatial availability of forage species have been associated with shifts in predator distribution, increased predation pressure on endangered fish stocks [19] and increased marine mammal entanglements with fishing gear [14].

Here, we create a northern anchovy (*Engraulis mordax*) ecosystem indicator, a key forage species in the CCS, and use predator data to assess its utility in indicating predator foraging and reproductive ecology. Over the last 70 years northern anchovy abundance has fluctuated by orders of magnitude, acting as a barometer of ecosystem productivity in the CCS [20]. Although the mechanisms regulating anchovy population fluctuations are not well understood [21], SDMs can accurately describe the distribution of anchovy adults (i.e. habitat suitability) in relation to ocean conditions (e.g. temperature, chlorophyll *a*). We generated an SDM-based [22] anchovy ecosystem indicator (AEI) to capture the mean anchovy habitat suitability during the reproductive season in the foraging range of seabird colonies in the Gulf of the Farallones (GOF) and for a California sea lion (*Zalophus californianus*) rookery at

San Miguel Island (SMI). We then used long-term observations of predator diet during the reproductive season, predator at-sea distribution data from visual surveys [23], and metrics of predator reproduction [24–27] to evaluate the capacity of the AEI to explain variability in predator foraging and reproduction. The predators included California sea lions and three seabird species with different foraging and reproductive strategies: common murre (*Uria aalge*), rhinoceros auklets (*Cerorhinca monocerata*) and Brandt's cormorants (*Phalacrocorax penicillatus*). Previous work in the GOF suggests that common murre and rhinoceros auklet consume anchovy when available, but their reproductive success is not strongly tied to anchovy availability [25,28]. We, therefore, hypothesize that for these species, the AEI would capture trends in their diet and distribution but would not capture variability in reproductive success. Comparatively, the reproductive success of Brandt's cormorants and California sea lions has been linked to anchovy consumption [24,29] and thus we hypothesize that the AEI should provide an effective indicator of the foraging and reproductive ecology of these two species. We compared the variance explained between the fine-scale AEI in the two predator regions with a coastwide estimate of anchovy spawning stock biomass and a regional spring anchovy abundance index to determine if our indicator improved our ability to explain variability in predator foraging and reproductive ecology. Our analyses used a 22-year time-series encompassing high oceanographic variability, including multiple El Niño events and an unprecedentedly large marine heatwave in 2014–2016 [30] to understand predator responses under highly variable forage and ecosystem states and to inform ecosystem management.

2. Methods

(a) Anchovy species distribution model

The AEI was built upon the SDM described by Muhling *et al.* [22,31]. Briefly, we trained and validated a generalized additive model (GAM) using fishery-independent presence/absence data for adult anchovy caught in Coastal Pelagic Species trawl surveys conducted by the NOAA Southwest Fisheries Science Center. Sampling was conducted in surface waters at night using a Nordic 264 trawl [32]. Environmental covariates used to describe anchovy habitat suitability included sea surface temperature (°C), sea surface height (m), mixed layer depth (m), surface currents and winds (northward and eastward wind stress (N m^{-2}), northward and eastward surface current velocities (m s^{-1}), wind stress curl (N m^{-3})) and an estimate of water column stratification (buoyancy frequency (s^{-1}) averaged over the top 200 m) available at daily 0.1° resolution from a data assimilative configuration of the Regional Ocean Modeling System (oceanmodeling.ucsc.edu) [33], and monthly surface chlorophyll *a* (mg m^{-3}) from a satellite reanalysis [34]. An annual index of anchovy spawning stock biomass (metric tons) [21,35,36] was also included as a covariate to account for higher probabilities of occurrence within environmentally suitable habitat at larger stock sizes [22]. Predicted anchovy habitat suitability was generated for every day from 1998 to 2020 at 0.1° spatial resolution for the CCS domain (30°–48°N and inshore of 134°W). In this study, these daily predictions were averaged monthly for each grid cell. For a detailed description of the SDM used here and the key ways it was modified from Muhling *et al.* [22,31], see the electronic supplementary material.

(b) Predator data sources

To evaluate the utility of an SDM-based forage fish indicator of predator ecology, we selected four central place foragers:

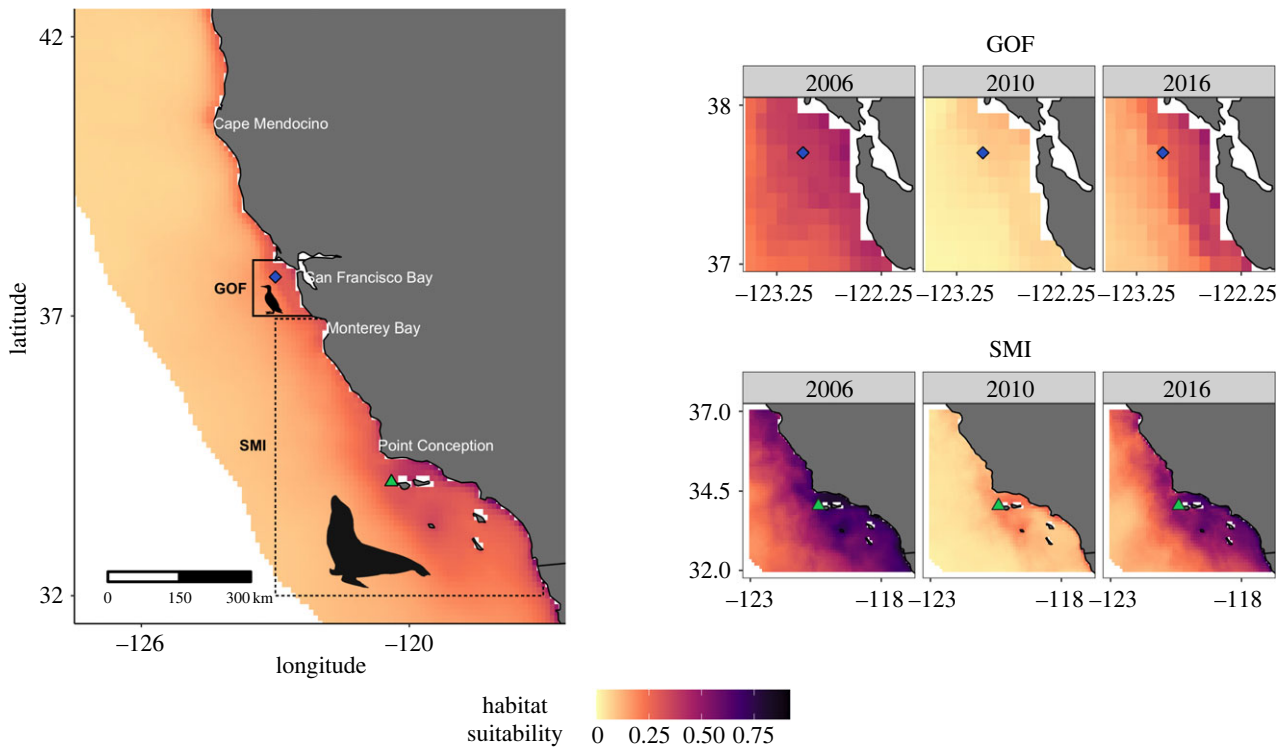


Figure 1. Study location in the California Current System (CCS) demonstrating the average anchovy habitat suitability from 1998 to 2020 throughout the CCS (left). The blue diamond marks the seabird colony on the southeast Farallon Island in the Gulf of the Farallones (GOF). The green triangle marks the sea lion rookery on San Miguel Island (SMI). Solid black line represents the area the anchovy ecosystem indicator (AEI) was calculated for the seabirds, and the dashed line is the AEI for the sea lions. The figures on the right demonstrate how the AEI captures fine-scale spatial variability in anchovy habitat during the reproductive season of each predator in example years of high and low anchovy occurrence in the GOF (top) and SMI (bottom).

common murre, rhinoceros auklet, Brandt's cormorant and California sea lion. We examined the relationships between the AEI and predator diet, distribution and reproduction. The predators chosen in this study are largely piscivorous and mainly consume forage species [25,37]. Common murre diet data were obtained from visual surveys of adults returning to their nests with fish in their bills [25,38]. Rhinoceros auklets were captured in mist nets, when they returned to the nests in the evening, to identify and quantify prey carried in their bills [25,39]. Brandt's cormorant diet information was obtained from examining regurgitated pellets and identifying prey by hard parts (i.e. fish bones and otoliths [25,40]). We used the annual percentage by number of anchovy for our analyses of murre and auklet chick diets and percentage occurrence of anchovy in cormorant diets. Sea lion diet data were collected from June to September, from long-term monitoring of a rookery at SMI ([37,41]; figure 1; electronic supplementary material, table S1) and were reported as percentage occurrence of anchovy in scats.

Seabird and sea lion at-sea distribution data were obtained from the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) [23] (electronic supplementary material table S1; figures S1–S4). This annual survey measures a variety of aspects of the CCS including the abundance and distribution of seabirds and marine mammals from late April to early June [42]. Observations of seabirds and sea lions were collected during daylight hours by observers on the flying bridge in a 300 m (seabirds) semicircle from either side and in front of the vessel centred at the bow or to the horizon (sea lions). Sightings of seabirds and sea lions were aggregated at 0.9 km² and at 3 km² respectively. We treated any sightings within a 0.1° × 0.1° ROMS grid cell within one spring survey period as presences and no sightings on transects within a grid cell as absences.

Reproductive success data for seabirds in the GOF was measured as the number of chicks that survived to fledging per breeding pair in each year. These data were reported as annual

fledging anomalies derived from the annual mean number of chicks fledged per breeding pair minus the long-term fledging mean (1971–2019) [25,26] (electronic supplementary material, table S1). Sea lion reproductive dynamics were assessed using pup weight and pup count data [26,43]. To determine sea lion reproduction, accounting for interannual differences in population size, we divided sea lion pup count data by the number of reproductively mature females (estimated from [43]; electronic supplementary material, table S1). We also examined pup weight data as a measure of pup condition.

(c) Anchovy ecosystem indicator development

To create the AEI, we used the adult anchovy SDM to create estimates of anchovy habitat suitability (probability of adult anchovy occurrence) at different spatial and temporal scales tailored to match predator foraging ranges during their reproductive season (figure 1; electronic supplementary material, figure S5). The AEI was generated at two spatial scales: one was an annual average adult anchovy habitat suitability value during predator reproductive season in each predator foraging area, the other was at each 0.1° grid cell within a predator foraging region during the reproductive season. Specifically, to encompass seabird foraging habitat [24,39], we constrained the SDM output region to the GOF region—37°N to 38°N and inshore of 123.5° W (figures 1 and 2). We first averaged SDM daily anchovy habitat suitability in each 0.1° grid cell within the GOF region to the monthly scale. When examining seabird diet and reproductive success, we then calculated the annual average habitat suitability across all grid cells within the GOF region over April–July (seabird hatching–fledging season [44]), to get an annual reproductive season mean anchovy habitat suitability in the GOF (electronic supplementary material, figure S5). For our analyses of seabird distribution, we computed the mean habitat suitability from April to June (the months the RREAS seabird and mammal survey data were collected) in each

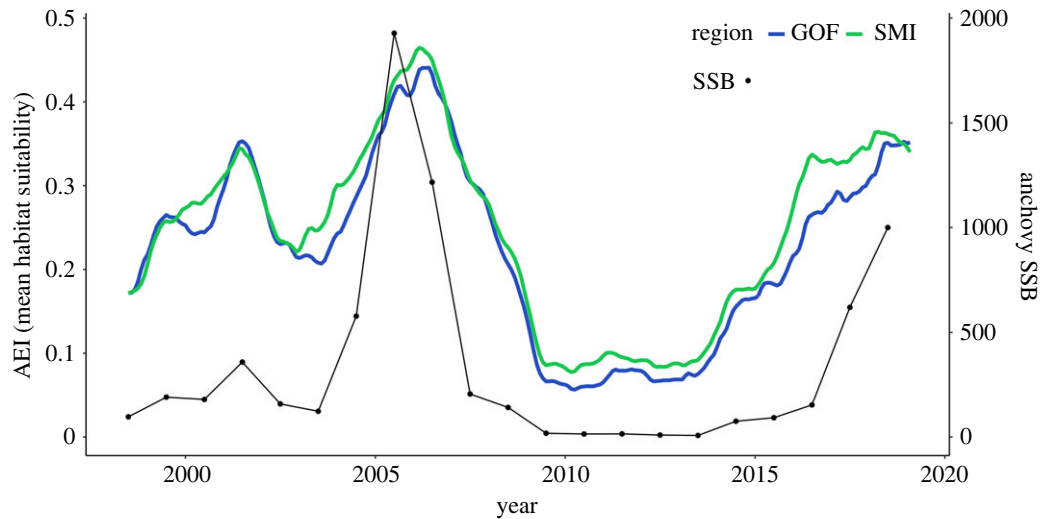


Figure 2. Time series of the AEI averaged monthly for seabirds in the GOF region (blue), for sea lions in the SMI region (green) and annual estimates of anchovy spawning stock biomass (SSB, metric tons) from Thayer *et al.* [35] (black circles).

grid cell to align spatially and temporally with gridded seabird observations from the RREAS. We examined the distribution of seabirds within this GOF region at the scale of 0.1° grid cells.

Our analyses of sea lion diet, distribution and reproduction were bound at 32°N to 37°N and inshore of 123°W based on the observed foraging range of lactating female sea lions from SMI [45] (figure 1). California sea lions at SMI begin giving birth in May, pups are counted in July and weighed in October [43]. To capture the influence of anchovy habitat on sea lion diet and reproduction, we averaged monthly anchovy habitat suitability from May to October across all grid cells in the SMI region (figures 1 and 2). For the sealion distribution analysis, we took the April–June average of anchovy habitat suitability in 0.1° grid cells in the SMI region to compare with sea lion distribution from RREAS observations at the scale of 0.1° grid cells. There are multiple sea lion rookeries in the study area, so the distribution analysis is not solely based on individuals from SMI. We used Spearman’s rank correlation to examine the correlation between the AEI in the GOF during the seabird reproductive season and in SMI during the sea lion reproductive season.

(d) Evaluation of the anchovy ecosystem indicator

To evaluate the capacity of the AEI to explain variability in the diet, distribution and reproduction of predators, we ran four statistical tests. First, we used beta regression to compare the annual proportion of anchovy found in each predator’s diet with the AEI (annual average of probability of adult anchovy occurrence across predator region). Second, we applied GAMs to assess whether the AEI (annual average at 0.1° resolution within the predator region) explained the distribution (presence or absence) of predators at sea. Distribution GAMs were built using a binomial family and logit link function in the *mgcv* package [46,47]. We included a tensor product smooth containing latitude, longitude and year to reduce autocorrelation in the model residuals. We used the area under the receiver operating characteristic curve (AUC) to evaluate the performance of these distribution GAMs. Third, we used GAMs to examine the correlation between the AEI (annual average across predator region) and predator reproduction. Reproduction GAMs were constructed with a Gaussian distribution and identity link function. Finally, we explored the value of the AEI to understanding predator foraging and reproduction by comparing the AEI with anchovy spawning stock biomass and the regional spring anchovy abundance index. Anchovy spawning stock biomass provides a coastwide annual estimate of adult anchovy abundance, is derived from geospatially weighted anchovy egg and larval abundances, and was used in the

development of the AEI [35,36]. The regional spring anchovy abundance index is derived from a delta-GLM of adult anchovy catch-per-unit-effort in spring from the RREAS survey core region that includes the GOF, but does not cover SMI and could not be used to evaluate sea lions [48]. We compared the number of significant relationships ($p < 0.05$) and the variance explained between each anchovy indicator and predator diet and reproduction metrics. In all our analyses, the AEI (or other anchovy metrics) was the independent variable used to explain variability in predator diet, distribution and reproduction.

3. Results

(a) Anchovy ecosystem indicator spatio-temporal dynamics in the California Current System

The AEI varied through space and time and was consistent between the two predator regions (Spearman’s $\rho = 0.98$; figures 1 and 2). The AEI was consistently high from 1998 to 2007, peaking in 2006, before declining rapidly to a minimum in 2010. Thereafter it remained low until the system experienced a marine heatwave from 2014 to 2016. The heatwave coincided with a sharp increase in the AEI (figures 1 and 2) that persisted through 2020. These patterns tracked estimates of anchovy spawning stock biomass (figure 2).

(b) Anchovy ecosystem indicator and predator diet

The AEI was a strong indicator of anchovy in predator diets. The AEI was significantly positively correlated with the proportion of anchovy by number in chick diets of common murre ($\beta_{\text{AEI}} = 7.7$, $p < 0.0001$; table 1, figure 3), rhinoceros auklet ($\beta_{\text{AEI}} = 6.7$, $p = 0.001$; table 1, figure 3), with the percentage of Brandt’s cormorant pellets containing anchovy hard parts ($\beta_{\text{AEI}} = 9.1$, $p < 0.0001$; table 1, figure 3) and the percentage of sea lion scats containing anchovy hard parts ($\beta_{\text{AEI}} = 10.4$, $p < 0.0001$; table 1, figure 3).

(c) Anchovy ecosystem indicator and predator distribution

GAMs including the AEI and a spatio-temporal tensor product smooth captured variability in predator distribution

Table 1. Summary of beta regression results for predator diet. Significant *p*-values are in italics.

diet	parameter	coefficient	s.e.	<i>p</i> -value	log likelihood	pseudo- <i>R</i> ²
common murre	intercept	−2.205	0.488	<0.001	8.912	0.5628
	AEI	7.701	1.723	<0.001		
	phi	4.139	1.175	<0.001		
rhinoceros auklet	intercept	−2.247	0.594	<0.001	11.66	0.4458
	AEI	6.7	2.064	<0.001		
	phi	1.838	0.504	<0.001		
Brandt's cormorant	intercept	−3.383	0.578	<0.001	14.15	0.7139
	AEI	9.078	1.925	<0.001		
	phi	5.749	2.273	0.011		
California sea lion	intercept	−2.674	0.558	<0.001	10.69	0.691
	AEI	10.43	2.032	<0.001		
	phi	4.332	1.361	0.0015		

(table 2). However, the AEI covariate was not significantly related to observed rhinoceros auklet presence (table 2). Probability of common murre presence increased with increasing AEI then levelled off above an AEI of approximately 0.1 probability of adult anchovy occurrence (table 2, figure 3). The AEI was positively related to Brandt's cormorant and California sea lion at-sea distribution (table 2, figure 3).

(d) Anchovy ecosystem indicator and predator reproduction

The strength of the relationship between the AEI and predator reproduction varied by predator. The AEI was not significantly correlated with common murre or rhinoceros auklet reproductive success (figure 3; table 3). However, the AEI was significantly positively correlated with Brandt's cormorant reproductive success and with sea lion pup counts per female (table 3; figure 3). Additionally, the AEI was positively correlated with sea lion pup weight (table 3; electronic supplementary material, figure S6), a metric of pup condition.

(e) Comparison of anchovy ecosystem indicator to annual and regional estimates of anchovy abundance

The AEI outperformed the non-spatial anchovy spawning stock biomass estimate and was comparable to the regional spring anchovy abundance index in explaining variability in predator diet and reproduction. Anchovy spawning stock biomass was significantly positively related to the diets of all four predators; however, the AEI explained considerably more of the variability in predator diets (table 1; electronic supplementary material, table S2; figure S7). The regional spring anchovy abundance index and the AEI explained similar predator diet variability (table 1; electronic supplementary material, table S2 and figure S8). Neither the AEI, anchovy spawning stock biomass, nor the regional spring anchovy abundance index explained significant variability in common murre or rhinoceros auklet reproductive success; however, spawning stock biomass was also unrelated to Brandt's cormorant and sea lion reproduction (table 3;

electronic supplementary material, table S3, and figures S7 and S8). The AEI outperformed the regional spring anchovy abundance index in explaining cormorant reproductive success (table 3; electronic supplementary material, table S3 and figure S8). Anchovy spawning stock biomass did explain a significant portion of variability in sea lion pup weight, but the AEI explained approximately 40% more variability than spawning stock biomass alone (table 3; electronic supplementary material, table S3). Finally, because neither spawning stock biomass or regional spring anchovy abundance index are available at 0.1° resolution, they could not be used to understand the distribution of seabirds or sea lions. These findings reiterate the value of spatio-temporally explicit predictions of anchovy occurrence compared to broad-scale metrics of abundance for explaining variability in the ecology of CCS predators. While the AEI and anchovy spawning stock biomass are not independent (the anchovy SDM incorporated anchovy spawning stock biomass as a predictor), the addition of spatially explicit environmental variables enhanced the ability of the AEI to predict anchovy availability at relevant spatio-temporal scales. The regional spring anchovy abundance index is spatially and temporally explicit and was not incorporated in the construction of the AEI, making it a valuable independent comparison supporting the utility of the AEI.

4. Discussion

Effective ecosystem-based management benefits from an in-depth understanding of predator–prey dynamics in variable environments. Forage species are important ecosystem indicators for predator population dynamics because they link primary and secondary productivity to higher trophic levels. Here, we developed an ecosystem indicator for the CCS using anchovy SDM output that was spatially and temporally matched to the life histories of specific predators. The AEI was highly correlated with predator diet for all species, the distribution of two seabirds and one marine mammal, and reproduction of one seabird and marine mammal. The strong relationships between the AEI and predator foraging and reproduction allows for assessments of how predators

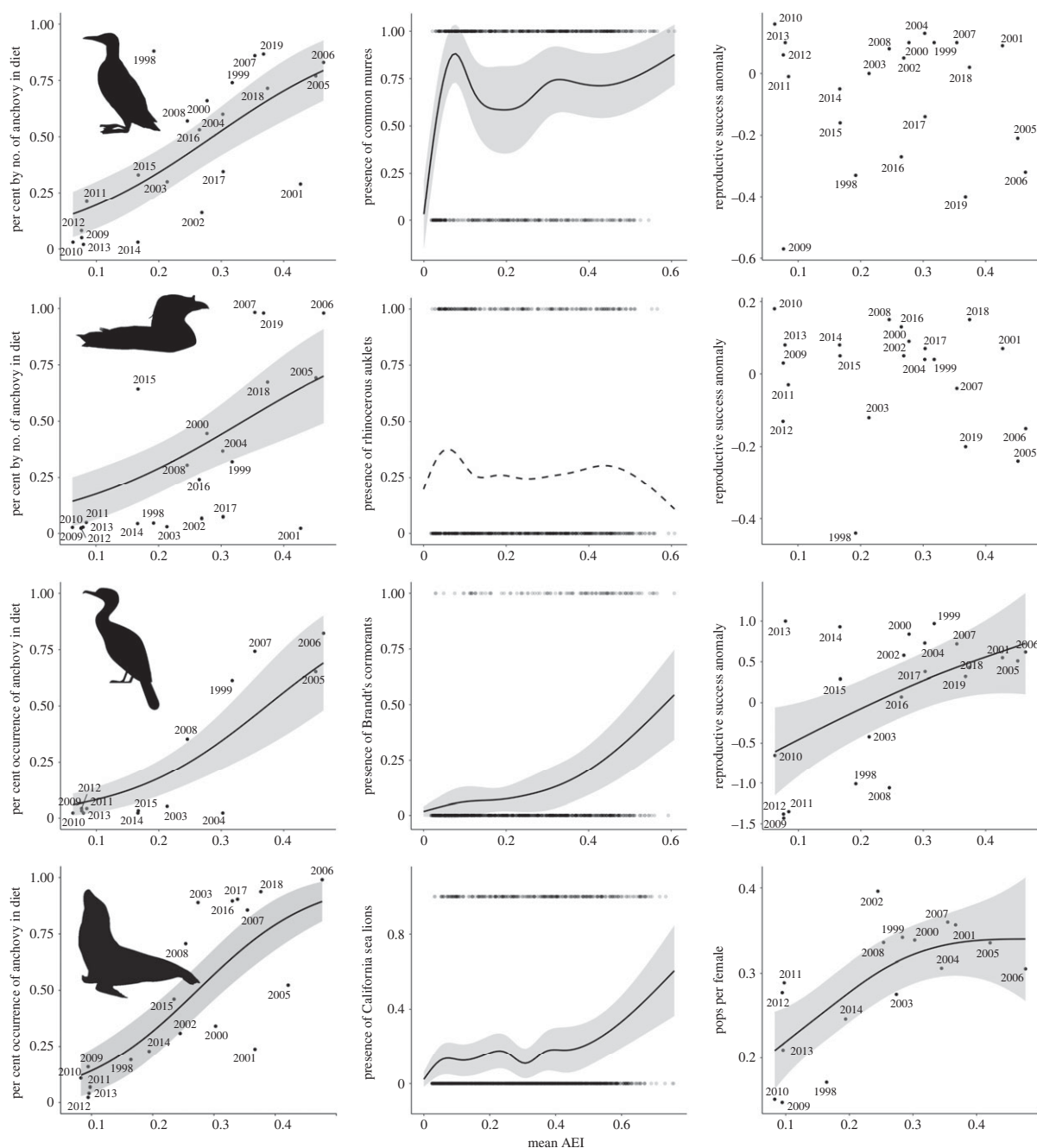


Figure 3. Response of common murre (top), rhinoceros auklet (second from top), Brandt's cormorant (third from top), and California sea lion (bottom) diet (left), distribution (middle) and reproduction (right) to the AEI (i.e. mean anchovy habitat suitability). Grey ribbons represent 95% CI. Comparisons of the AEI with predator diet are beta regressions with points labelled by year, the response curves for at sea distribution are derived from GAMs, and reproduction analyses are linear regressions with points labelled by year. See electronic supplementary material, figures S7 and S8 for spawning stock biomass and regional anchovy abundance index, respectively.

Table 2. Estimated regression parameters for binomial logit GAM models of predator presence/absence. Significant *p*-values are in italics.

response predator	smooth term	edf	Ref.df	Chisq	<i>p</i> -value	AUC
common murre	s(mean AEI)	6.772	7.863	23.71	<i>0.0028</i>	0.932
	te(lon,lat,year)	80.829	89.226	171.73	<i><0.001</i>	
Brandt's cormorant	s(mean AEI)	1.001	1.001	13.8	<i><0.001</i>	0.936
	te(lon,lat,year)	27.360	36.020	127.8	<i><0.001</i>	
rhinoceros auklet	s(mean AEI)	1.342	1.591	0.993	0.634	0.736
	te(lon,lat,year)	31.837	43.067	85.822	<i><0.001</i>	
California sea lion	s(mean AEI)	5.431	6.588	18.38	<i>0.009</i>	0.795
	te(lon,lat,year)	38.190	46.055	189.85	<i><0.001</i>	

Table 3. Summary of GAM results for the relationship between the AEI and predator reproduction. Significant *p*-values are in italics.

predator		smooth term	<i>n</i>	Edf	Ref.df	<i>F</i>	deviance explained (%)	<i>p</i> -value
common murre	reproduction	s(mean AEI)	22	1	1	0.12	0.59	0.74
rhinoceros auklet	reproduction	s(mean AEI)	22	1	1	0.61	2.97	0.44
Brandt's cormorant	reproduction	s(mean AEI)	22	1	1	10.04	33.4	<i>0.005</i>
California sea lion	reproduction	s(mean AEI)	17	1.99	2.4	7.25	57.9	<i>0.005</i>
	pup weight	s(mean AEI)	17	3.23	3.95	6.82	61.7	<i>0.002</i>

will respond to fluctuations in the forage base and could be developed further to provide an indicator of unusual mortality events [24,29]. The common responses of marine predators to variability in forage fish abundance [4] suggest this approach has the potential to be applied to ecosystem-based management in other marine ecosystems with similar trophic dynamics.

(a) Anchovy ecosystem indicator as an indicator of predator ecology

The strength of the relationships between the AEI and predators is related to each predator's life-history strategy. Each seabird species demonstrated strong linkages between the AEI and anchovy consumption, reflecting their capacity to prey on anchovy when readily available [24,25]. However, the foraging and reproductive strategies of each species may ultimately explain the variable importance of AEI to their distribution and reproduction. Rhinoceros auklets have flexible diets [25] and, during daylight hours, forage along the continental shelf break where anchovy are less abundant [28,49]; however, rhinoceros auklets forage at dusk to feed chicks and this nocturnal foraging distribution is not captured by daytime observations, potentially explaining why their distribution and reproduction are not tied to the AEI. Common murres largely feed between the Farallon Islands and the mainland of California [49] consuming anchovy when abundant but will switch to other prey (mainly juvenile rockfishes) to maintain reproduction in the absence of anchovy [25]. The rapid increase in common murre presence at low AEI values that persists with increasing AEI is indicative of shared habitat associations between common murres and anchovy. Both species are rare offshore and abundant on the continental shelf. By comparison, the positive relationship between AEI and Brandt's cormorant presence is likely to be due to cormorants feeding coastally where anchovy tend to be more abundant. Common murres and rhinoceros auklets lay one egg per pair and, by switching prey, maintain relatively consistent reproduction across variable ecosystem states [25]. Because of their flexible diets, distributions and breeding strategies, common murre and rhinoceros auklet reproduction may be more sensitive to changes in collective forage abundance (e.g. rockfish and anchovy) and less sensitive to the AEI [19,28]. By contrast, Brandt's cormorants typically feed near the coast where anchovy are more abundant, experience more variable reproduction, and can produce up to five eggs per breeding season allowing for increased chick survival when forage availability is high, especially when anchovy are abundant [24,40].

California sea lion diet, distribution, reproduction and pup condition follow changes in the AEI. Sea lions at SMI forage in

both shallow coastal and offshore waters depending on prey distributions [41,45], but consume more anchovy when anchovy are abundant [29,37]. During our study, the strong relationship between sea lion metrics and the AEI may be due to the often high anchovy habitat suitability surrounding the sea lion rookery on SMI (figure 2); however, the strong link between forage prey fat content and pup condition may drive the strong linkage between sea lion reproduction and anchovy habitat suitability [25,29]. These findings demonstrate that the AEI provides a reliable indicator of the foraging and reproductive ecology of SMI California sea lions.

(b) Management implications

In the future, oceans are projected to become warmer, more acidic and more hypoxic. Extreme events occurring in combination with these long-term trends will increasingly produce unprecedented ocean conditions [50], with concurrent impacts on ecosystems [51]. Thus, there is a pressing need for science-based tools to improve management responsiveness to such climate-driven shifts in species abundance and distribution. Here, we identify an ecosystem indicator that provides dynamic, spatio-temporally resolved information on the forage base that is relevant to the management of threatened or protected species in a highly variable environment.

As the AEI is spatially resolved, it has potential as a tool for spatial management practices, such as the setting of seasonal closures or the use of in-season dynamic management tools to minimize protected species–fisheries interactions (e.g. [17]). For example, anomalous conditions in the central CCS during the 2014–2016 marine heatwave were related to decreases in offshore krill abundance and aggregated anchovy close to shore. These changes resulted in high overlap between humpback whales foraging on anchovy and the central California crab fishery leading to a 10-fold increase in whale entanglements [14,52]. In the future, the AEI could be applied to understand where and when protected species are likely to co-occur with their prey and commercial activity, allowing for the development of early warnings to minimize human–wildlife conflict during periods of high overlap.

The AEI could be particularly valuable for the management of species that suffer high offspring mortality when overall forage is low and lacking high quality species. Here, we demonstrate that anchovy availability is correlated with sea lion reproduction and confirm known associations between anchovy consumption and sea lion pup condition [29] as well as the reproductive success of Brandt's cormorants [24]. As such, there is potential for further development and testing of indicators based on forage SDMs to provide advanced warning of unusual mortality events in regions where the environment and anchovy spawning stock biomass can be

forecasted with adequate skill. Combining the AEI with indicators of additional forage species (e.g. Pacific sardine, market squid or juvenile rockfish) would improve the application of a SDM forage indicator beyond species with strong ties to anchovy.

In ecosystems where forage species are heavily exploited, indicators such as the AEI could be used to quantify the impact of harvest policies at scales relevant to forage fish predators [9]. Because the AEI was a better indicator of predator state than coastwide estimates of anchovy spawning stock biomass alone, the performance of targeted spatial closures compared to broad catch limits for meeting conservation and economic management objectives should be examined. However, on the US west coast, where anchovy catches remain low despite increasing biomass, recent shifts in anchovy dynamics were largely driven by climate variability rather than fishing pressure [36]. Thus, reductions in anchovy harvest in this region may only affect predator productivity when anchovy abundance is low and highly concentrated near predator colonies, but more quantitative studies are needed. The AEI could also be integrated into marine mammal stock assessments to consider the impact of climate-driven shifts in forage availability on population growth rate (e.g. [21]).

(c) Species distribution model approach to creating ecosystem indicators

Our approach to creating an SDM-based ecosystem indicator proved to be highly effective and overcame challenges faced with more traditional approaches to developing indicators. Previous efforts to create forage indicators were less effective because they were based solely on shipboard observations, which are limited in space and time, and cannot be applied coastwide due to regional differences in sampling techniques [53]. While the AEI is correlative rather than a mechanistic model, we have demonstrated its use for understanding predator–prey dynamics in the CCS over multiple decades. Here, the use of an SDM informed by both observations of anchovy and environmental covariates allowed us to develop a spatio-temporally resolved indicator of anchovy habitat that helps understand the diet, distribution and reproduction of key predators in the central and southern CCS. The relationships between the AEI and predator ecology were mostly equivalent to the regional spring anchovy abundance index and better than the coastwide estimate of spawning stock

biomass. Our results suggest that SDMs are important tools for future use in modelling forage species [54] and could be developed to provide forage-based indicators of predators in other systems. The dynamic nature of our ecosystem indicator shows promise for supporting managers and decision-makers under future climate variability and change.

Data accessibility. Data and code are available from the Dryad Digital Repository [55].

Additional information is provided in the electronic supplementary material [56].

Authors' contributions. H.W.F.: formal analysis, investigation, methodology, visualization, writing—original draft; R.S.: formal analysis, investigation, methodology, visualization, writing—original draft; B.A.M.: conceptualization, data curation, investigation, methodology, supervision, validation, writing—review and editing; S.J.B.: conceptualization, funding acquisition, investigation, methodology, supervision, writing—review and editing; S.B.: conceptualization, investigation, supervision, writing—review and editing; M.A.C.: conceptualization, investigation, methodology, writing—review and editing; E.L.H.: investigation, methodology, supervision, writing—review and editing; M.G.J.: investigation, methodology, writing—review and editing; E.A.M.: investigation, methodology, writing—review and editing; S.M.: investigation, methodology, writing—review and editing; J.A.S.: conceptualization, funding acquisition, investigation, methodology, supervision, writing—review and editing; J.J.S.: investigation, methodology, writing—review and editing; J.A.T.: data curation, investigation, methodology, writing—review and editing; A.R.T.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—review and editing; P.W.: data curation, investigation, methodology, writing—review and editing; D.T.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. Funding was provided by FATE/SAIP/CESC, CCIEA, Future Seas (NOAA Climate and Fisheries Adaptation Program grant number NA20OAR4310507); US Marine Biodiversity Observation Network jointly funded by NOAA, NASA and the National Oceanographic Partnership Program (80NSSC20M0001).

Acknowledgements. We thank the vessels, scientists and crews involved in collecting the biological observations central to the development of the SDM as well as Y. Gu, W. Watson, J. Zwolinski and B. Macewicz for data provision and guidance. We thank the University of Santa Cruz Ocean Modeling and Data Assimilation research group for the provision of environmental fields from the UCSC ROMS. We thank the Farallon Institute for anchovy spawning stock biomass data, and both Point Blue and USFWS Farallon Islands National Wildlife Refuge for collecting and supporting seabird diet and reproduction monitoring. This manuscript was improved by helpful comments from C. Petrik and W. Watson.

References

- Chavez FP, Ryan J, Lluch-Cota SE, Niquen CM. 2003 From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* **299**, 217–221. (doi:10.1126/science.1075880)
- Pikitch EK *et al.* 2014 The global contribution of forage fish to marine fisheries and ecosystems. *Fish Fish.* **15**, 43–64. (doi:10.1111/faf.12004)
- Alder J, Campbell B, Karpouzi V, Kaschner K, Pauly D. 2008 Forage fish: from ecosystems to markets. *Annu. Rev. Environ. Resour.* **33**, 153–166. (doi:10.1146/annurev.enviro.33.020807.143204)
- Cury PM *et al.* 2011 Global seabird response to forage fish depletion: one-third for the birds. *Science* **334**, 1703–1707.
- Boyd IL, Murray AWA. 2001 Monitoring a marine ecosystem using responses of upper trophic level predators. *J. Anim. Ecol.* **70**, 747–760. (doi:10.1046/j.0021-8790.2001.00534.x)
- Durant JM, Anker-Nilssen T, Stenseth NC. 2003 Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proc. R. Soc. B* **270**, 1461–1466. (doi:10.1098/rspb.2003.2397)
- Piatt JF, Harding AMA, Shultz M, Speckman SG, Van Pelt TI, Drew GS, Kettle AB. 2007 Seabirds as indicators of marine food supplies: Cairns revisited. *Mar. Ecol. Prog. Ser.* **352**, 221–234. (doi:10.3354/meps07078)
- Barbraud C *et al.* 2018 Density dependence, prey accessibility and prey depletion by fisheries drive Peruvian seabird population dynamics. *Ecography* **41**, 1092–1102. (doi:10.1111/ecog.02485)
- Durant JM, Crawford RJM, Wolfaardt AC, Agenbag K, Visagie J, Upfold L, Stenseth NC. 2010 Influence of feeding conditions on breeding of African penguins: importance of adequate local food supplies. *Mar. Ecol. Prog. Ser.* **420**, 263–271. (doi:10.3354/meps08857)

10. Essington TE, Moriarty PE, Froehlich HE, Hodgson EE, Koehn LE, Oken KL, Siple MC, Stawitz CC. 2015 Fishing amplifies forage fish population collapses. *Proc. Natl Acad. Sci. USA* **112**, 6648–6652. (doi:10.1073/pnas.1422020112)
11. Hilborn R, Amoroso RO, Bogazzi E, Jensen OP, Parma AM, Szuwalski C, Walters CJ. 2017 When does fishing forage species affect their predators? *Fish. Res.* **191**, 211–221. (doi:10.1016/j.fishres.2017.01.008)
12. Free CM, Jensen OP, Hilborn R. 2021 Evaluating impacts of forage fish abundance on marine predators. *Conserv. Biol.* **35**, 1540–1551. (doi:10.1111/cobi.13709)
13. Samhuri JF, Stier AC, Hennessey SM, Novak M, Halpern BS, Levin PS. 2017 Rapid and direct recoveries of predators and prey through synchronized ecosystem management. *Nat. Ecol. Evol.* **1**, 1–6. (doi:10.1038/s41559-016-0068)
14. Santora JA *et al.* 2020 Habitat compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. *Nat. Commun.* **11**, 1–12. (doi:10.1038/s41467-019-14215-w)
15. Elith J, Leathwick JR. 2009 Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* **40**, 677–697. (doi:10.1146/annurev.ecolsys.110308.120159)
16. Hazen EL *et al.* 2018 A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Sci. Adv.* **4**, 1–8. (doi:10.1126/sciadv.aar3001)
17. Hobday AJ, Hartog JR, Spillman CM, Alves O. 2011 Seasonal forecasting of tuna habitat for dynamic spatial management. *Can. J. Fish. Aquat. Sci.* **68**, 898–911. (doi:10.1139/f2011-031)
18. Howell EA, Kobayashi DR, Parker DM, Balazs GH, Polovina JJ. 2008 TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endanger. Species Res.* **5**, 267–278. (doi:10.3354/esr00096)
19. Wells BK *et al.* 2017 Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. *J. Mar. Syst.* **174**, 54–63. (doi:10.1016/j.jmarsys.2017.05.008)
20. Harvey CJ, Garfield NT, Williams GD, Tolimieri N. 2021 *Ecosystem status report of the California Current for 2020–21: a summary of ecosystem indicators compiled by the California Current Integrated Ecosystem Assessment Team (CCIEA)*, NOAA Technical Memorandum NMFS-NWFSC-170. Washington, DC: US Department of Commerce.
21. Sydeman WJ, Dedman S, García-Reyes M, Thompson SA, Thayer JA, Bakun A, MacCall AD. 2020 Sixty-five years of northern anchovy population studies in the southern California Current: a review and suggestion for sensible management. *ICES J. Mar. Sci.* **77**, 486–499. (doi:10.1093/icesjms/fsaa004)
22. Muhling BA, Brodie S, Smith JA, Tommasi D, Gaitan CF, Hazen EL, Jacox MG, Auth TD, Brodeur RD. 2020 Predictability of species distributions deteriorates under novel environmental conditions in the California Current System. *Front. Mar. Sci.* **7**, 1–22. (doi:10.3389/fmars.2020.00589)
23. Santora JA *et al.* 2021 Pelagic biodiversity, ecosystem function, and services an integrated observing and modeling approach. *Oceanography* **34**, 16–37. (doi:10.5670/oceanog.2021.212)
24. Ainley DG *et al.* 2018 Ecosystem-based management affecting Brandt's Cormorant resources and populations in the central California Current region. *Biol. Conserv.* **217**, 407–418. (doi:10.1016/j.biocon.2017.11.021)
25. Warzybok P *et al.* 2018 Prey switching and consumption by seabirds in the central California Current upwelling ecosystem: implications for forage fish management. *J. Mar. Syst.* **185**, 25–39. (doi:10.1016/j.jmarsys.2018.04.009)
26. Weber ED *et al.* 2021 State of the California Current 2019–2020: back to the future with marine heatwaves? *Front. Mar. Sci.* **8**, 1–23. (doi:10.3389/fmars.2021.709454)
27. Melin SR, Orr AJ, Harris JD, Laake JL, DeLong RL. 2012 California sea lions: an indicator for integrated ecosystem assessment of the California Current System. *Calif. Coop. Ocean. Fish. Investig. Rep.* **53**, 140–152.
28. Santora JA, Schroeder ID, Field JC, Wells BK, Sydeman WJ. 2014 Spatio-temporal dynamics of ocean conditions and forage taxa reveal regional structuring of seabird-prey relationships. *Ecol. Appl.* **24**, 1730–1747. (doi:10.1890/13-1605.1)
29. McClatchie S, Field J, Thompson AR, Gerrodette T, Lowry M, Fiedler PC, Watson W, Nieto KM, Vetter RD. 2016 Food limitation of sea lion pups and the decline of forage off central and southern California. *R. Soc. Open Sci.* **3**, 150628. (doi:10.1098/rsos.150628)
30. Di Lorenzo E, Mantua N. 2016 Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nat. Clim. Chang.* **6**, 1042–1047. (doi:10.1038/nclimate3082)
31. Muhling B *et al.* 2019 Dynamic habitat use of albacore and their primary prey species in the California Current System. *CalCOFI Rep.* **60**, 1–15.
32. Zwolinski JP, Demer DA. 2012 A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. *Proc. Natl Acad. Sci. USA* **109**, 4175–4180. (doi:10.1073/pnas.1113806109)
33. Neveu E, Moore AM, Edwards CA, Fiechter J, Drake P, Crawford WJ, Jacox MG, Nuss E. 2016 An historical analysis of the California Current circulation using ROMS 4D-Var: system configuration and diagnostics. *Ocean Model.* **99**, 133–151. (doi:10.1016/j.ocemod.2015.11.012)
34. Sathyendranath S *et al.* 2019 An ocean-colour time series for use in climate studies: the experience of the ocean-colour climate change initiative (OC-CCI). *Sensors* **19**, 4285.
35. Thayer JA, MacCall AD, Sydeman WJ, Davison PC. 2017 California anchovy population remains low, 2012–16. *Calif. Coop. Ocean. Fish. Investig. Rep.* **58**, 1–8.
36. MacCall AD, Sydeman WJ, Davison PC, Thayer JA. 2016 Recent collapse of northern anchovy biomass off California. *Fish. Res.* **175**, 87–94. (doi:10.1016/j.fishres.2015.11.013)
37. Lowry MS, Stewart BS, Heath CB, Yochem PK, Francis JM. 1991 Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981–86. *Fish. Bull.* **89**, 331–336.
38. Ainley DG, Spear LB, Allen SG, Ribic CA. 1996 Temporal and spatial Patterns in the diet of the common murre in California waters. *Condor* **98**, 691–705.
39. Thayer JA, Sydeman WJ. 2007 Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. *Mar. Ecol. Prog. Ser.* **329**, 253–265. (doi:10.3354/meps329253)
40. Elliott ML, Schmidt AE, Acosta S, Bradley R, Warzybok P, Sakuma KM, Field JC, Jahncke J. 2016 Brandt's cormorant diet (1994–2012) indicates the importance of fall ocean conditions for northern anchovy in central California. *Fish. Oceanogr.* **25**, 515–528. (doi:10.1111/fog.12169)
41. Melin SR, DeLong RL, Siniff DB. 2008 The effects of El Niño on the foraging behavior of lactating California sea lions (*Zalophus californianus californianus*) during the nonbreeding season. *Can. J. Zool.* **86**, 192–206. (doi:10.1139/Z07-132)
42. Ainley DG, David Hyrenbach K. 2010 Top-down and bottom-up factors affecting seabird population trends in the California current system (1985–2006). *Prog. Oceanogr.* **84**, 242–254. (doi:10.1016/j.pocean.2009.10.001)
43. Laake JL, Lowry MS, DeLong RL, Melin SR, Carretta JV. 2018 Population growth and status of California sea lions. *J. Wildl. Manag.* **82**, 583–595. (doi:10.1002/jwmg.21405)
44. Ainley DG, Boekelheide RJ, eds. 1990 *Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community*. Stanford, CA: Stanford University Press.
45. Briscoe DK *et al.* 2018 Characterizing habitat suitability for a central-place forager in a dynamic marine environment. *Ecol. Evol.* **8**, 2788–2801. (doi:10.1002/ece3.3827)
46. Wood S. 2022 mgcv: mixed GAM computation vehicle with automatic smoothness estimation. See <https://cran.r-project.org/web/packages/mgcv/index.html>.
47. R Core Team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
48. Santora JA, Rogers TL, Cimino MA, Sakuma KM, Hanson KD, Dick EJ, Jahncke J, Warzybok P, Field JC. 2021 Diverse integrated ecosystem approach overcomes pandemic-related fisheries monitoring challenges. *Nat. Commun.* **12**, 1–10. (doi:10.1038/s41467-021-26484-5)

49. McGowan J, Hines E, Elliott M, Howar J, Dransfield A, Nur N, Jahncke J. 2013 Using seabird habitat modeling to inform marine spatial planning in Central California's National Marine Sanctuaries. *PLoS ONE* **8**, 1–15. (doi:10.1371/journal.pone.0071406)
50. Fox-Kemper B *et al.* 2021 Ocean, cryosphere and sea level change. In *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change* (ed. V Masson-Delmotte *et al.*), pp. 1211–1361. Cambridge, UK: Cambridge University Press.
51. Pinsky ML, Mantua NJ. 2014 Emerging adaptation approaches for climate-ready fisheries management. *Oceanography* **27**, 146–159.
52. Feist BE, Samhoury JF, Forney KA, Saez LE. 2021 Footprints of fixed-gear fisheries in relation to rising whale entanglements on the US West Coast. *Fish. Manag. Ecol.* **28**, 283–294. (doi:10.1111/fme.12478)
53. Thompson AR *et al.* 2019 Indicators of pelagic forage community shifts in the California Current Large Marine Ecosystem, 1998–2016. *Ecol. Indic.* **105**, 215–228. (doi:10.1016/j.ecolind.2019.05.057)
54. Santora JA, Sydeman WJ, Messié M, Chai F, Chao Y, Thompson SA, Wells BK, Chavez FP. 2013 Triple check: observations verify structural realism of an ocean ecosystem model. *Geophys. Res. Lett.* **40**, 1367–1372. (doi:10.1002/grl.50312)
55. Fennie H *et al.* 2023 Data from: An anchovy ecosystem indicator of marine predator foraging and reproduction. Dryad Digital Repository. (doi:10.7291/D1V96R)
56. Fennie H *et al.* 2023 An anchovy ecosystem indicator of marine predator foraging and reproduction. Figshare. (doi:10.6084/m9.figshare.c.6406074)