A multi-model approach to understanding the role of Pacific sardine in the California Current food web

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Supplement 1: Structured Information for Ecopath, MICE, and Atlantis

Table S1. Model characteristics for the Ecopath, MICE, and Atlantis models testing the role of Pacific sardine in the California Current food web.

Model for California Current	Brief model description and intent	Domain	Defining features and key processes	Spatial and temporal scale and vertical resolution	Taxonomic scope	Key references
Ecopath	Static mass-balance food web model with high taxonomic resolution for forage fish and their predators. Accounts for diets and sources of mortality, including predation and fishing. Intent was to examine role of forage fish in ecosystem.	N. Vancouver Island, B.C. to Punta Eugenia, Baja California, Mexico and extending offshore to the 2000 m isobath	Snapshot representing average production, sources of mortality, and diets for 2000-2014, Monte Carlo handling of uncertainty in key parameters, including diets, leading to 500 balanced models.	Not spatially explicit. No temporal or vertical dimensions.	92 functional groups. Sardine, anchovy, herring, whitebait smelt, other smelt, and sandlance are represented at the species level. Predators include brown pelican and sea lions.	Koehn et al. (2016)
MICE	Dynamic simulation model linking forage fish abundance to predator survival and reproduction. Intent was to measure impacts of existing	Same as Ecopath but extending offshore to 200 nautical miles (370km)	Probabilistic outputs from 100 forward projections for 1,000 years. <u>One way</u> linking from prey abundance to California sea lion and brown	13 bins at 2° of latitude. No vertical dimension. Monthly steps for prey, annual steps for predators.	6 functional groups. Sardine, anchovy, 'other forage', 'other prey', brown pelicans, California sea lions	Punt et al. (2016)

	harvest policy on sardine and predator populations		pelican. 23 sensitivity tests reflecting alternate diets, predator responses, and recruitment			
Atlantis	Dynamic ecosystem simulation model linking forage fish abundance to ecosystem-level impacts. Intent was to measure effects of low sardine abundance on predators and ecosystem.	Same as MICE	50 year forward projections from 2013. <u>Two way linking between prey and predators.</u> Mortality added to sardine to explore six scenarios for sardine abundance. Scenarios added to explore high and low recruitment of sardine, anchovy	89 model polygons divided at isobaths and latitudinal breaks relevant to biogeography and management. Six depth layers. 12-hour timesteps.	78 functional groups. Sardine, anchovy, and herring are represented at the species level. Other groups include an aggregated group of "other forage" fish; California sea lions; and an aggregated pelagic feeding seabird group.	Kaplan et al. (2017)

Ecopath model

Model framework, domain, and taxonomic scope

Koehn et al. (2016) developed an Ecopath model for the California Current, applying the framework of Christensen and Walters (2004). A brief description of this model is listed in Table A1, including model intent, domain, key features, spatial and temporal scale, and taxonomic scope. The model extends to the 2,000m isobath (but not further offshore) to capture the bulk of habitat where commercially harvested forage fish interact with predators of interest in this study. The emphasis on predators meant that this Ecopath model has a very high taxonomic resolution, for instance including 18 seabird groups (14 at the individual species level, i.e. not aggregated into coarser functional groups) and 15 marine mammals (12 at the individual species level). Brown pelican are represented at the species level. The sea lion group aggregates California and Steller sea lions, but was heavily weighted to California Sea lions, which dominate biomass in this system.

US, Canadian, and Mexican fisheries and dynamics of sardine and harvest management

Fisheries catches are included for all harvested species, provided for the US (Pacific Fishery Management Council; Washington, Oregon, and California Department of Fish and Wildlife; PacFIN), Mexico (*Comisión Nacional de Acuacultura y Pesca*) and Canadian Fishery Operations System (DFO Canada). Fishery management rules are not included, since dynamic management rules are not relevant in this static model.

Diet information and predator-prey functional response

There is no explicit representation of time-varying predator-prey relationships since this is a static model, but Koehn et al. (2016) represented uncertainty in diets (primarily from Szoboszlai et al. (2015)), by resampling diets assuming that they follow a Dirichlet distribution to create 500 balanced Ecopath models.

Uncertainty and validation

Resampling of diets, biomasses, consumption, and production parameters to create 500 balanced Ecopath models followed explicit data quality ranking criteria that established coefficients of variation (CVs) for Monte Carlo draws, centered around original mass-balance parameterization, which yielded a final 500 balanced models. Model validation against historical time series is not possible (this is not a time-dynamic model), but model selection involves identifying 'balanced' models that have full accounting of biomass production and loss, without violating thermodynamic rules, from millions of potential model parameterizations.

MICE (Model of Intermediate Complexity for Ecosystem assessment)

Model framework, domain, and taxonomic scope

Punt et al. (2016) developed the MICE (Model of Intermediate Complexity for Ecosystem analysis), applying the philosophy of 'minimally complex' models (Plagányi et al. 2014). A brief description of this California Current MICE is listed in Table A1, including model intent, domain, key features, spatial and temporal scale, and taxonomic scope. This model (and the Atlantis model) extends quite far west (200 nautical miles or 370km) to cover the full US Exclusive Economic Zone. The emphasis on minimal complexity led to a very focused set of predators and prey (two main predators, two main forage fish prey, two 'other' prey groups).

US, Canadian, and Mexican fisheries and dynamics of sardine and harvest management

The model only includes catches of sardine (even though the other forage species are subject to fisheries). Future catches of sardine were governed by dynamic harvest control rules. The complexity of these rules was a key feature of this model. Simulated sardine harvest control rules for the US followed the actual harvest rules, including a cutoff below which targeted fishing ceases (150,000 mt of stock-wide 1+ biomass), and an exploitation fraction for biomass above 150,000 mt that varies from 0.05-0.2, depending upon temperature. Observation error was incorporated in both the measurement of temperature and the estimate of biomass used in the harvest rule. After calculation of the harvest guideline (catch limit), additional adjustments are made to decrease allowable catch to account for uncertainty and to avoid overfishing limits. Simulated catch was assigned to US areas (Figure 1) based on the average spatial distribution of actual catches during 2006-2010. Mexican sardine catch was simulated with a fishing mortality rate, rather than a dynamic harvest control rule, set to match average catches from the period 1999-2009. Mexican catch was apportioned to the three Mexican areas within the MICE domain (Figure 1), following recent spatial distribution of the catch. Canadian sardine catch followed a simple harvest control rule, again with a cutoff of 150,000 mt stock-wide 1+ biomass, and a 5% exploitation fraction for the biomass above that cutoff. Total catch was capped at 22,000 mt.

Diet information and predator-prey functional response

Diet information for sea lion and brown pelican (see Table 1 in main text) was taken directly from Koehn et al. (2016). Punt et al. (2016) also simulated alternate scenarios that double or halve the contribution of sardine to the diet of the predators, and proportionally reduce the proportion of anchovy, 'other forage', and 'other prey' in the diet. Those alternate scenarios

are not presented here, but the main result was that scenarios with higher reliance on sardine (which has very high variability) led to fewer brown pelicans and stronger effects of fishing. Note that this MICE does not include a typical predator-prey functional response that specifies consumption per predator as a function of prey abundance. Instead, the MICE was parameterized such that predator reproduction or survival varied as a function of availability of prey (the sum of sardine, anchovy, other forage fish, and other prey, weighted by predator preference for that diet item).

Uncertainty and validation

This model included both stochastic process error and structural uncertainty. The simulations included error terms for processes governing predator reproductive rate, fish recruitment, 'other forage' recruitment, sardine spatial distribution, stock assessment estimates of biomass, and measurements of temperature used within the harvest control rule. Structural uncertainty (i.e. alternate formulations for ecological relationships) was evaluated using 23 alternate model scenarios related to diets, recruitment, predator responses, natural mortality rates, and spatial distributions. Though here we focus on comparing only the base case MICE to Atlantis and Ecopath, these 23 alternate scenarios illustrate the key uncertainties in the model. Specifically, the strongest determinant of model behavior was the parameterization of predator response to prey abundance, and assumptions regarding diets. Parameterization of the forage species themselves, spatial distributions, and stock assessment performance were less important in terms of the long term behavior of predator populations. For the base case MICE we present here, and all alternate scenarios in Punt et al. (2016), uncertainty in long term behavior of the species was captured by summarizing the results of the 100 projections of 1000 years.

The MICE focused on long-term behavior of predators and forage fish under the current harvest control rule, thus the model was validated by comparing outputs to observed time series characteristics of these species. Specifically, simulated sardine and anchovy recreated the variability in abundance evidenced by scale deposition records; brown pelicans and California sea lions were extant (no extinctions even over very long simulations with periods of low sardine and anchovy abundance); and brown pelican showed periodic declines (consistent with MacCall 1984) stronger than those for California sea lions. Note that one of the advantages of this model is that fast run times allowed iterative evaluation of key parameters such as predator diet preferences, to ensure that long- term model behavior (in this case diets) matched expectations (in this case predator diets from Koehn et al. 2016).

Atlantis Model

Model framework, domain, and taxonomic scope

Kaplan et al. (2017) and Marshall et al. (2017) developed this ecosystem model for the California Current, applying the Atlantis framework (Fulton 2004, Fulton et al. 2011). A brief description of this California Current Atlantis model is listed in Table A1, including model intent, domain, key features, spatial and temporal scale, and taxonomic scope. The MICE model was built to match the Atlantis model spatial extent, but the emphasis of this Atlantis end-to-end ecosystem model is to quantify potential effects of low sardine abundance on the broader food web. Therefore taxonomic resolution in Atlantis includes almost 80 functional groups. Note however that this model has less taxonomic resolution of the predator species than the Ecopath model; this slightly more parsimonious approach was needed due to the very long simulation times of this dynamic, spatially explicit model, and a desire to represent additional lower trophic level species. Data for the Atlantis model and Ecopath model were collected jointly by authors of these two models during model development.

US, Canadian, and Mexican fisheries and dynamics of sardine and harvest management

Fishing mortality rates (in units of yr-1) were set such that catch for simulation year 1 matched observed catch for 2013, based on the same sources used in the Ecopath model. (Kaplan et al. 2017 Fig. 1). Simulations project 2013 initial conditions forward for 50 years, continuing fishing mortality rates at 2013 levels (for all species other than sardine). Sardine fishing mortality rates were scaled to 0, 0.5, 1, 2, 4, and 8 times the initial (2013) rates, for a total of six simulations. Fishing mortality for sardine was concentrated around six major fishing ports (Kaplan et al.2017 Figure 1). Fishing mortality rates for other species were uniform across the model domain. Fishery management rules (e.g. that dynamically adjust quotas) were not included in the scenarios presented here.

Diet information and predator-prey functional response

Diet information was collected jointly by the authors of the Atlantis and Ecopath model (and then passed to MICE). Key diet sources include syntheses by Szoboszlai et al. (2015) and Dufault et al. (2009). Differences in diets between models stem primarily from differing geographic scope and functional group structure as noted in **Table A1.** Predator-prey functional responses follow a modified Holling type II curve, meaning that consumption per predator increases with prey availability, then asymptotes at a level set by maximum consumption rates. In the context of our analysis, this means that predator diets adjust as relative abundance of various prey items fluctuates. Thus given sufficient spatial overlap of a predator with some subset of its preferred prey, predator consumption needs can be met. Note that the MICE model implicitly includes this (by summing over forage species, weighted by preferences), and the Ecopath model does not include dynamic prey switching (because the model itself is not dynamic).

Uncertainty and validation

The Atlantis simulations take ~3 days to run and therefore are not amenable to probabilistic handling of uncertainty, so instead in Kaplan et al. (2017) we applied a bounded parameterization approach (Fulton et al. 2011), taking advantage of output from MICE. Specifically, we asked how varying levels of added sardine mortality would affect predators and the food web if the simulations assumed levels of productivity (of sardine and anchovy) that were higher or lower than the base case. We forced low recruitment scenarios with sardine recruitment scaled by a constant 0.19 and anchovy recruitment by 0.46, and high recruitment scenarios with sardine recruitment scaled by a constant 9.64 and anchovy recruitment by 3.39. These scalars are taken from Year 1-25 and Year 201-225 of simulated annual recruitment deviations from the MICE. These scalars and scenarios were chosen as example levels of high and low productivity, to illustrate the effect of this key aspect of uncertainty. Results suggested that when productivity was high (high recruitment of sardine and anchovy), strong increases in fishing mortality caused larger ecosystem response (proportional changes in species abundance) than when productivity was low.

Model behavior for sardine was qualitatively compared to stock assessment results in Kaplan et al. (2017). Maximum yield in Atlantis was approximately 230,000 metric tons, across a broad range of F between 0.11 and $0.21yr^{-1}$. This estimate of F_{MSY} is consistent with recent stock assessments and allowable harvest rates under the harvest guideline. The projected level of Atlantis sardine biomass under 50 years of no fishing was 3.75 million metric tons, and biomass was 200,000 mt after 50 years of fishing at 0.38 yr^{-1} (which is approximately twice 2013 rates), consistent with the expected range of biomass. Validation for this Atlantis

model was also conducted in Marshall et al. (2017), where we compared model predictions of biomass trends of additional species to historical biomass trends from stock assessments.

Supplement 2: Alternate metrics of predator sensitivity

We explored other metrics of impacts of sardine abundance on predators in the MICE, but these metrics were less responsive or similar to the responses in predator abundance. For instance, average reproductive success of California sea lions declined by less than 1%, and reproductive success of pelicans declined by at most 5%, across investigated levels of sardine abundance (Figures B1, B2). The frequency of years with pelican reproductive failure (when offspring per adult fell below 10% of the level expected with no fishing) also increased at low sardine biomass. The maximum estimated impact on pelican reproductive success is more moderate than the estimated 29% decline in pelican abundance at the lowest sardine abundance. This is consistent with the detailed findings of Punt *et al*. (2016) that very low pelican reproductive rates are more related to the biomass of anchovy than that of sardine, as expected given that anchovy comprise the largest fraction of the diet of brown pelican. A second alternative method of measuring impacts on predators in the MICE was to only consider regimes of a certain level of sardine abundance, e.g., only consider predator abundance in years when sardine abundance has been at the lowest level for >= 10 years (Figure B3). Considering these longer regimes does not change the results for California sea lions and only slightly increases the projected decline in brown pelican abundance under the lowest sardine abundance level (from 29% to 32%).

Figure S1. Relative frequency of MICE-projected reproductive success of sea lion (top) and brown pelican (bottom) for six ranges of sardine biomass. Reproductive success is on an arbitrary scale, where 100 is the expectation of annual offspring per mature adult, with no fishing. MICE outcomes were binned into sardine biomass ranges that match Atlantis outputs. Frequencies of estimated predator reproductive success are relative to all years for which projected sardine biomass fell within that range. Note overlap of yellow and light orange lines.
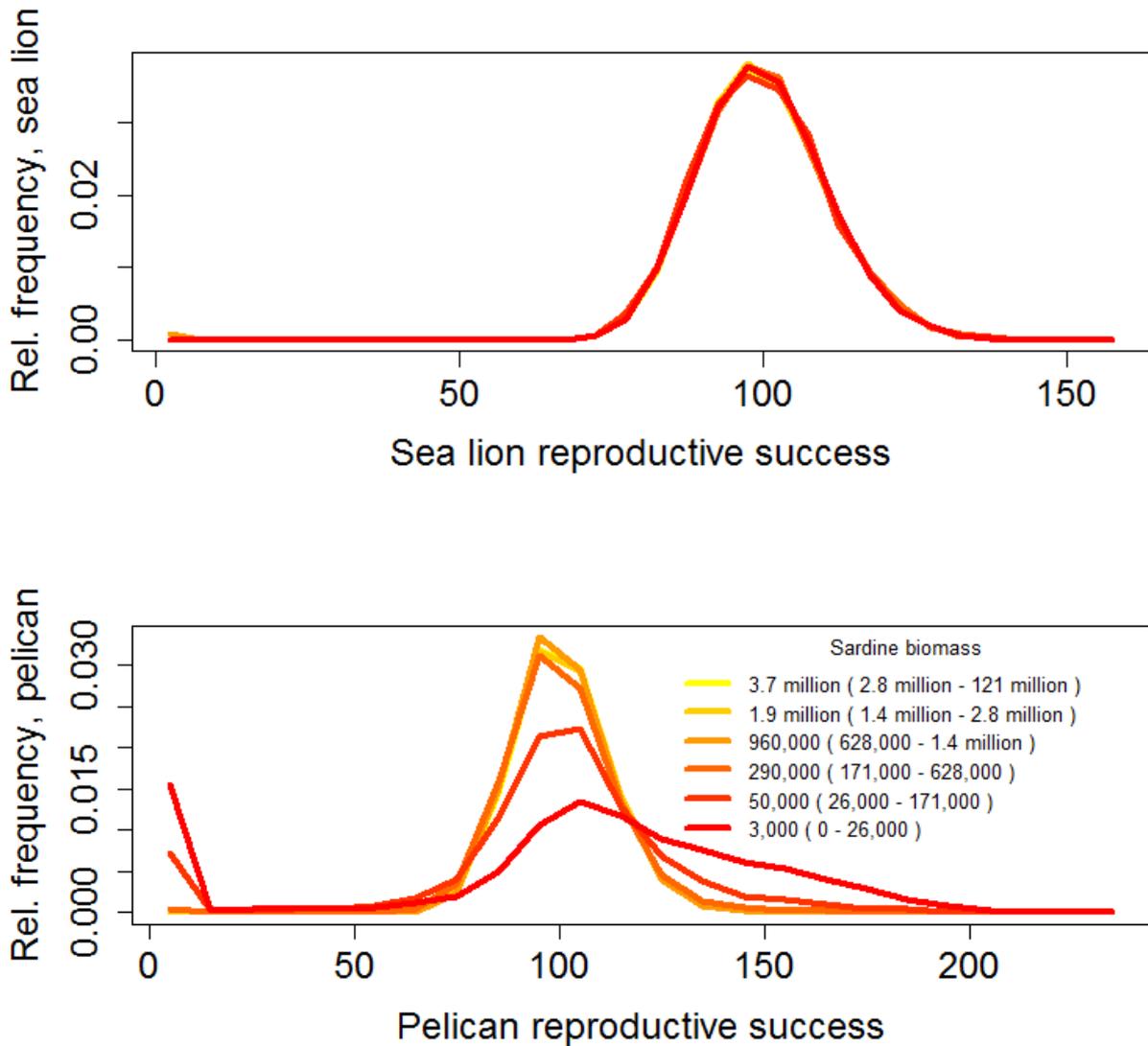
Figure S2. Identical to Figure 5, but the second and fourth rows are the <u>average relative change in reproductive success</u> projected by the MICE (California sea lions and brown pelicans only). All other results (all other rows) are from Atlantis.

3.7 million	1.9 million	960,000	290,000	50,000	3,000	
0.00	-0.50	-0.74	-0.92	-0.99	-1.00	Sardines
0.00	0.00	0.00	0.00	0.00	0.00	California sea lion MICE
0.00	-0.01	-0.02	-0.03	-0.03	-0.03	California.sea.lions
0.00	0.00	-0.01	-0.01	-0.05	0.00	Brown Pelican MICE
0.00	-0.03	-0.04	-0.04	-0.04	-0.04	Seabirds..pelagic.feeders.
0.00	-0.14	-0.20	-0.24	-0.25	-0.26	Large.piscivorous.flatfish
0.00	-0.06	-0.12	-0.19	-0.23	-0.24	Dolphins
0.00	-0.04	-0.06	-0.07	-0.08	-0.08	Seabirds..benthic.pelagic.feeders
0.00	-0.03	-0.05	-0.06	-0.07	-0.07	Migrating.birds
0.00	0.00	0.00	-0.01	-0.01	-0.01	Baleen.whales
0.00	0.07	0.08	0.07	0.07	0.07	Small.demersal.sharks
0.00	0.05	0.07	0.09	0.10	0.11	Myctophids
0.00	0.03	0.04	0.06	0.06	0.06	Small.planktivorous.fish
0.00	-0.03	-0.04	-0.06	-0.06	-0.06	Crangon.shrimp
0.00	0.07	0.11	0.14	0.15	0.16	Pteropods
0.00	0.04	0.06	0.08	0.09	0.09	Mesozooplankton
0.00	0.74	1.36	2.00	2.33	2.42	Microzooplankton
0.00	-0.09	-0.13	-0.16	-0.18	-0.18	Pelagic.bacteria
0.00	-0.04	-0.06	-0.07	-0.07	-0.07	Coccolithophore
0.00	-0.06	-0.09	-0.11	-0.11	-0.12	Small.phytoplankton
0.00	-0.03	-0.05	-0.06	-0.06	-0.06	Labile.detritus

Sardine biomass, tons

Figure S3. As for Figure 5, but considering individual years of MICE outputs only if sardine have been in that regime (i.e. that level of sardine abundance) for >= 10 years. Regimes defined by range of sardine abundance (x axis corresponding to bars in Figure 3).

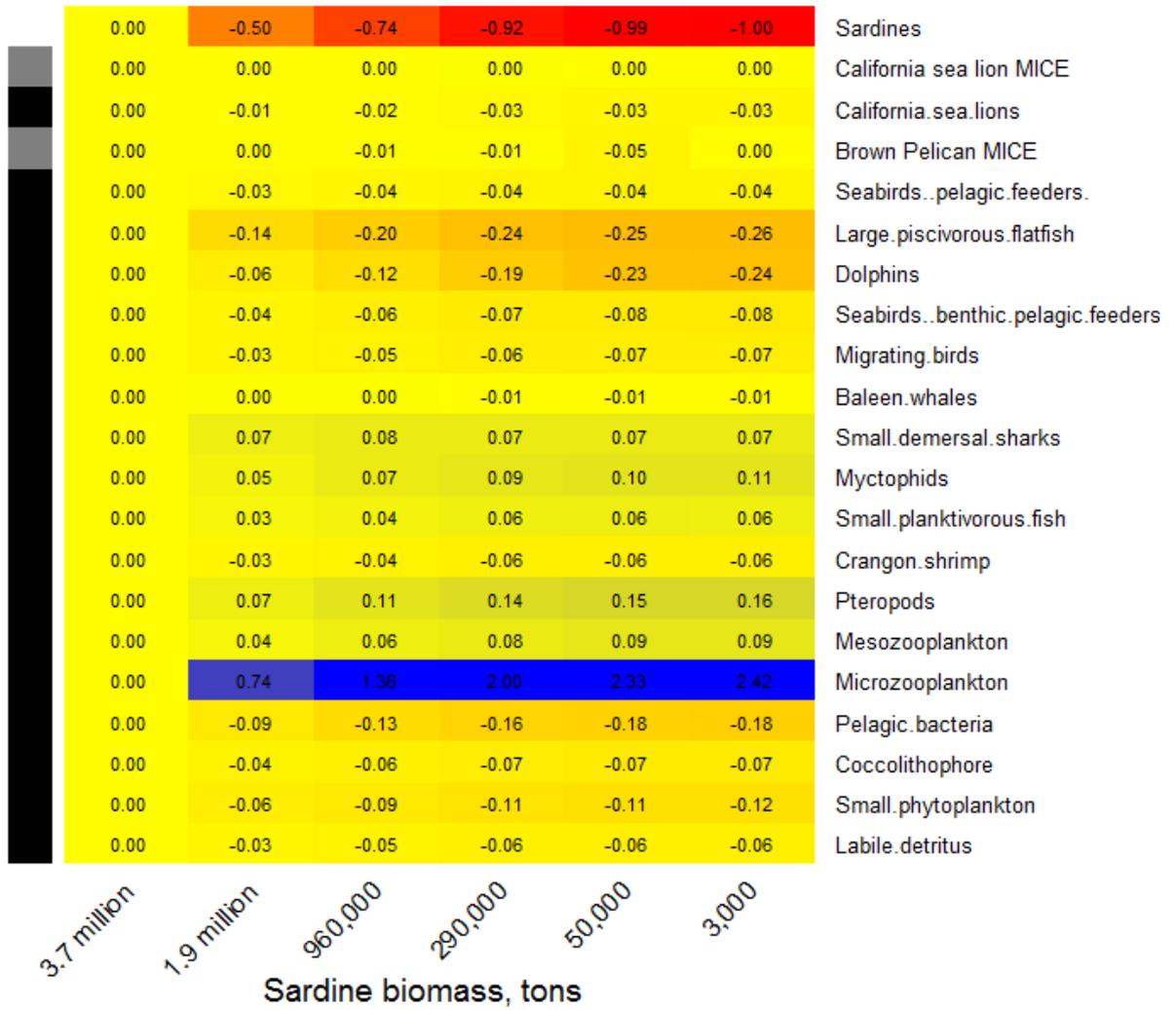| 3.7 million	1.9 million	960,000	290,000	50,000	3,000	
0.00	-0.50	-0.74	-0.92	-0.99	-1.00	Sardines
0.00	0.00	0.00	0.00	0.00	0.00	California sea lion MICE
0.00	-0.01	-0.02	-0.03	-0.03	-0.03	California.sea.lions
0.00	0.00	0.01	-0.02	-0.13	-0.32	Brown Pelican MICE
0.00	-0.03	-0.04	-0.04	-0.04	-0.04	Seabirds..pelagic.feeders.
0.00	-0.14	-0.20	-0.24	-0.25	-0.26	Large.piscivorous.flatfish
0.00	-0.06	-0.12	-0.19	-0.23	-0.24	Dolphins
0.00	-0.04	-0.06	-0.07	-0.08	-0.08	Seabirds..benthic.pelagic.feeders
0.00	-0.03	-0.05	-0.06	-0.07	-0.07	Migrating.birds
0.00	0.00	0.00	-0.01	-0.01	-0.01	Baleen.whales
0.00	0.07	0.08	0.07	0.07	0.07	Small.demersal.sharks
0.00	0.05	0.07	0.09	0.10	0.11	Myctophids
0.00	0.03	0.04	0.06	0.06	0.06	Small.planktivorous.fish
0.00	-0.03	-0.04	-0.06	-0.06	-0.06	Crangon.shrimp
0.00	0.07	0.11	0.14	0.15	0.16	Pteropods
0.00	0.04	0.06	0.08	0.09	0.09	Mesozooplankton
0.00	0.74	1.36	2.00	2.33	2.42	Microzooplankton
0.00	-0.09	-0.13	-0.16	-0.18	-0.18	Pelagic.bacteria
0.00	-0.04	-0.06	-0.07	-0.07	-0.07	Coccolithophore
0.00	-0.06	-0.09	-0.11	-0.11	-0.12	Small.phytoplankton
0.00	-0.03	-0.05	-0.06	-0.06	-0.06	Labile.detritus

Sardine biomass, tons