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Abstract

The carrying capacity of the French Frigate Shoals (FFS) region for the endangered Hawaiian monk seal was appraised using an updated version of the original FFS Ecopath model (Polovina 1984). Model parameters were updated using recent literature, and data from surveys of the seal population and its bottom-associated prey. Together they produced a static mass balance model for 1998 when the prey surveys began. The Ecopath-estimated monk seal biomass was 0.0045 t/km^2, which was in close agreement with the biomass calculated from monk seal field beach counts (0.0046 t/km^2). Model simulations through time were done in Ecosim using the

Ecopath balanced model and included fisheries data time series from 1998 to 2008. Monk seal biomass declined concurrently with decreases in benthic bottomfish biomass, which were influenced by large-scale changes in the environment of the North Pacific. This model scenario was extended from 2010, when the last permitted fishery in the Northwestern Hawaiian Islands was closed, through to 2040, assuming a constant environmental signal. Model results for this time period did not show a recovery of monk seals that exceeded the initial 1998 model biomass levels, highlighting the importance of including environmental variability in estimates of monk seals recovery at FFS.

Estimating the carrying capacity of the Northwestern Hawaiian Islands (NWHI) ecosystem for the endangered Hawaiian monk seal, *Monachus schauinslandi*, has been a priority since population recovery efforts were initiated in the early 1970s (Gilmartin *et al.* 1993, Gilmartin and Eberhardt 1995). The carrying capacity of a habitat for a species is a dynamic property with the point of equilibrium shifting in relation to the changing environment and structure of the biological community. Estimates of carrying capacity can improve the understanding of ecosystem effects and are an important consideration in the goal to recover the Hawaiian monk seal. The current recovery plan for the Hawaiian monk seal has identified a recovery target of 2,900 seals for the NWHI and 500 seals for the main Hawaiian Islands (MHI) (NMFS 2007). Despite recovery efforts, seal populations have exhibited an overall decline of ∼4% per year for the last two decades. Starting in the late 1980s, the number of seals in the French Frigate Shoals (FFS) beach counts rapidly declined by half, leveling somewhat in the mid-1990s, and then continued to decline annually from the year 2000 on. Because of this decline the monk seal is now the best studied component of the NWHI ecosystem, with annual mark and resight assessments and a wide range of supporting studies conducted by the National Marine Fisheries Service Pacific Islands Fisheries Science Center (PIFSC) (Craig and Ragen 1999, Antonelis *et al.* 2006, Baker and Thompson 2007). The poor survivorship of seals occurs throughout the NWHI, but is most obvious at FFS. Juvenile age classes (1–3 yr) in particular (Craig and Ragen 1999, Antonelis *et al.* 2003, Baker *et al.* 2007) have experienced mortality on the order of 80% (Baker *et al.* 2011). Surrounded by impoverished waters, seals reliant on the FFS food web are thought to be less nourished than those at northern sites (Polovina *et al.* 2008). The magnitude of decline in the FFS population contrasts its history as the largest of the six main breeding colonies in the NWHI (Kenyon and Rice 1959). A reduction in regional oceanic productivity, occurring on a decadal or longer scale, has been proposed as the primary factor recently affecting the trophic web of the FFS region (Polovina *et al*. 1994). The further the North Pacific productivity front (Polovina *et al.* 2001) oscillates to the south, the more it will change the environment and seed the production at the base of the trophic chain, enhancing the prey base of the monk seals.

The observed decline in the NWHI seal population has in recent years been mitigated by an increase in seals in the MHI. Assuming continual unrestrained growth in the MHI it has been estimated that within 15 yr there could be more seals in the MHI than the NWHI (Baker *et al*. 2011). These population trends raise many questions about the nature of energy flow in the region including concern that the seal carrying

capacity at FFS has declined. Recent progress in identifying the diet of seals, their foraging movements, and prey communities has provided the information needed to model the FFS region in relation to seal survivorship. To do this, we revised the original FFS Ecopath model (Polovina 1984) to estimate carrying capacity in 1998 when prey surveys were initiated in the region. The model was then run forward through 2009 to compare model estimates of monk seal biomass (B) over time with observed values of B calculated from field surveys during this period. Ecopath is a mass-balance model that tracks trophic energy through the food web of a defined ecological subsystem. Each component of the system includes information on diet, consumption, production, and estimates of B. Development of the Ecopath methodology (Christensen and Pauly 1992), including the software package "Ecopath with Ecosim" (EwE) versions 5 and 6 (Walters *et al.* 1997, 2000; Christensen *et al.* 2009*a*; available at http://www.ecopath.org) were essential to the revision of the model and subsequent analysis. A central tenet of Ecopath models is that the energy input and output of living systems is balanced. Biological information was obtained from field studies and the scientific literature. These values were then used as input for the mass balance routine of Ecopath to generate a possible energy flow pathway of the region. The more reliable the information the better the model will be able to constrain outcomes and identify the most probable scenarios. Ecopath models do not provide "the answer" but rather an understanding of the system's dynamics based on the available data.

Our approach was (1) to define the area that seals at FFS utilize, (2) construct the model from field data and published literature, (3) balance the model thermodynamically and run Ecosim simulations through time to attempt to understand the observed decrease in FFS monk seal B and project a possible ecosystem scenario for the future. Specifically, this article describes the static mass-balance model, and reports the success in (1) balancing the Ecopath model for 1998, (2) the resampling analysis to understand uncertainty in monk seal B estimates, (3) the time-dynamic simulation of the model accounting for known fishery removals in the ecosystem and changes in the environment from 1998 to 2009, and (4) the extension of this scenario holding the environment constant through 2040.

METHODS

The Ecopath Mass Balance Model

To construct an Ecopath model, one must first define the boundaries it will represent, and the time period of interest, as well as identify groups (ecological or taxonomic) that are key within the modeled ecosystem. Ecopath input parameters include B, production to biomass (P/B), consumption to biomass (Q/B), and ecotrophic efficiency (EE), which is the fraction of the production consumed within, or harvested from, the system. With three of these parameters, the Ecopath software can derive the fourth using its linear algorithms to solve for each of the food-web groups used in the model. EwE version 6 (Christensen *et al.* 2009*b*) was used for all analysis aside from the Ecoranger scenario, which was run in EwE version 5 as to date this module has not been included in EwE version 6.

Model Boundaries

Monk seals are "central place" foragers that rely on the isolated reef communities of the shallow peaks of the Hawaiian Ridge. The sand or basalt islets on these summits
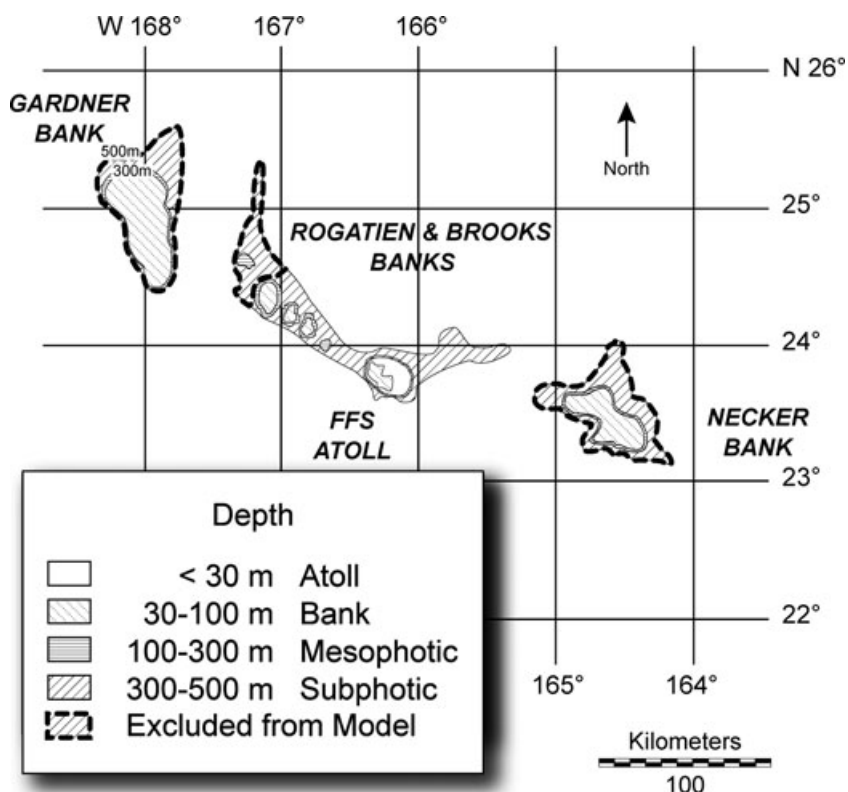
Figure 1. Map of the central portion of the Hawaiian Archipelago showing the foraging region of the French Frigate Shoals (FFS) seal population with the four depth-based ecological subsystems indicated. Dashed line indicates subphotic areas distant from the seal colony that were excluded from the model.

are the haul-out and breeding locations for the seals and serve as central points where seals forage from throughout the region. Members of the FFS seal colony routinely feed on bottom-associated fish (Goodman-Lowe 1998; Parrish *et al.* 2000, 2002, 2005; Longnecker *et al.* 2006; Iverson *et al.* 2011) at neighboring banks (Abernathy 1999, Stewart *et al.* 2006), as far south as Necker Bank (166 km SE) and north to Gardner Pinnacles (222 km) (Fig. 1). Diving as deep as 500 m foraging seals cross a number of different habitats terraced by a history of sea level change (Rooney *et al.* 2008), with each habitat type supporting its own prey community. These diverse forage grounds were represented in the model by four depth-based ecological subsystems, including atoll reefs, bank summits, and mesophotic and subphotic slope habitats (Parrish and Abernathy 2006) (Fig. 1). Actual movements determined from seals fitted with satellite tags (Abernathy 1999) showed that closer areas of moderate or lower foraging cost were the sites seals chose to visit. Sites of high cost (subphotic areas at the most distant locations) were not visited and were excluded (Fig. 1) putting the total model area at 11,850 km^2. Greater detail is available in the online supplemental materials.

Table 1. ECOPATH groups and vital parameters. Habitat is the fraction of area in the total model, Biomass is t/km^2 within the habitat area, P/B is the annual (per year) production/biomass ratio, Q/B is the annual (per year) consumption/biomass ratio and EE is the dimensionless ecotrophic efficiency (bold = field data, normal = literature source, *italics* = model derived).

No.	Group	Habitat	Biomass	P/B	Q/B	EE
1	Sea birds	0.08	*0.00247*	0.19	111	0.45
2	Tiger sharks	0.08	0.01	0.252	3	*0.179*
3	Monk seals	1	*0.00451*	**0.1**	**8**	**0.225**
4	Reef sharks	0.08	*0.0278*	0.2	2.2	0.9
5	Bank sharks	0.49	*0.00835*	0.2	2.2	0.9
6	Reef jacks	0.08	**0.25**	0.9	4.4	*0.02*
7	Bank jacks	0.49	**0.05**	0.9	4.4	*0.04*
8	Turtles	1	*0.128*	0.167	6.76	0.039
9	Benthic bottomfish	0.16	**0.16**	1.18	4	*0.702*
10	Demersal bottomfish	0.16	**0.13**	1.18	4	*0.134*
11	Small pelagic	1	*0.132*	0.55	6.5	0.8
12	Reef fish piscivores	0.08	**3.53**	1.303	7.02	*0.552*
13	Reef fish planktivores	0.08	**4.23**	3.235	15.15	0.6
14	Reef fish herbivores	0.08	**7.89**	1.5	23.34	*0.595*
15	Reef fish benthic carnivores	0.08	**5.11**	1.9	9.1	*0.741*
16	Bank piscivores	0.49	**0.09**	1.303	7	*0.854*
17	Bank planktivores	0.49	**1.5**	3.23	15.15	*0.107*
18	Bank herbivores	0.49	**1.32**	0.998	23.34	*0.284*
19	Bank benthic carnivores	0.49	**2.39**	1.856	9.1	*0.08*
20	Mesophotic piscivores	0.16	**0.05**	1.6	3.5	*0.278*
21	Mesophotic planktivores	0.16	**0.67**	3	7	*0.052*
22	Mesophotic benthic carnivores	0.16	**0.018**	2	4	*0.468*
23	Mesophotic forage fish	0.16	**0.59**	4	7	*0.514*
24	Subphotic piscivores	0.27	**0.014**	0.8	8.3	*0.566*
25	Subphotic benthic carnivores	0.27	**0.032**	1.7	3.42	*0.646*
26	Subphotic planktivores	0.27	**0.059**	1.75	4.5	*0.656*
27	Macroheterotrophs	1	*3.1*	3.4	9	0.936
28	Cephalopods	1	*0.587*	3.5	12	0.76
29	Heterotrophic benthos	1	*0.6*	97.767	200	0.92
30	Zooplankton	1	*0.398*	49.844	166	0.94
31	Phytoplankton	1	*1.046*	65.764		0.96
32	Benthic algae	0.57	*16.066*	13.682		0.69
33	Detritus	1	*1,000*			0.759

Ecosystem Functional Groups

The original FFS model (Polovina 1984) was revised to include greater spatial and trophic resolution of existing groups as well as new functional groups, including macroheterotrophic benthos (large crustaceans and echinoids), cephalopods, and detritus. The food web for this revised FFS model consisted of 33 groups, including monk seals, turtles, seabirds, three invertebrate groups, and 23 fish groups (Table 1, Fig. 2). Groups were largely defined by the ability of diet studies to distinguish them. For example, cephalopods could be distinguished from other diet items, and thus were separated from macroheterotrophs. Fish for each subsystem were divided into piscivores, benthic carnivores, planktivores, and herbivores (DeMartini *et al*. 2002,

FFS MONK SEAL
FOOD WEB
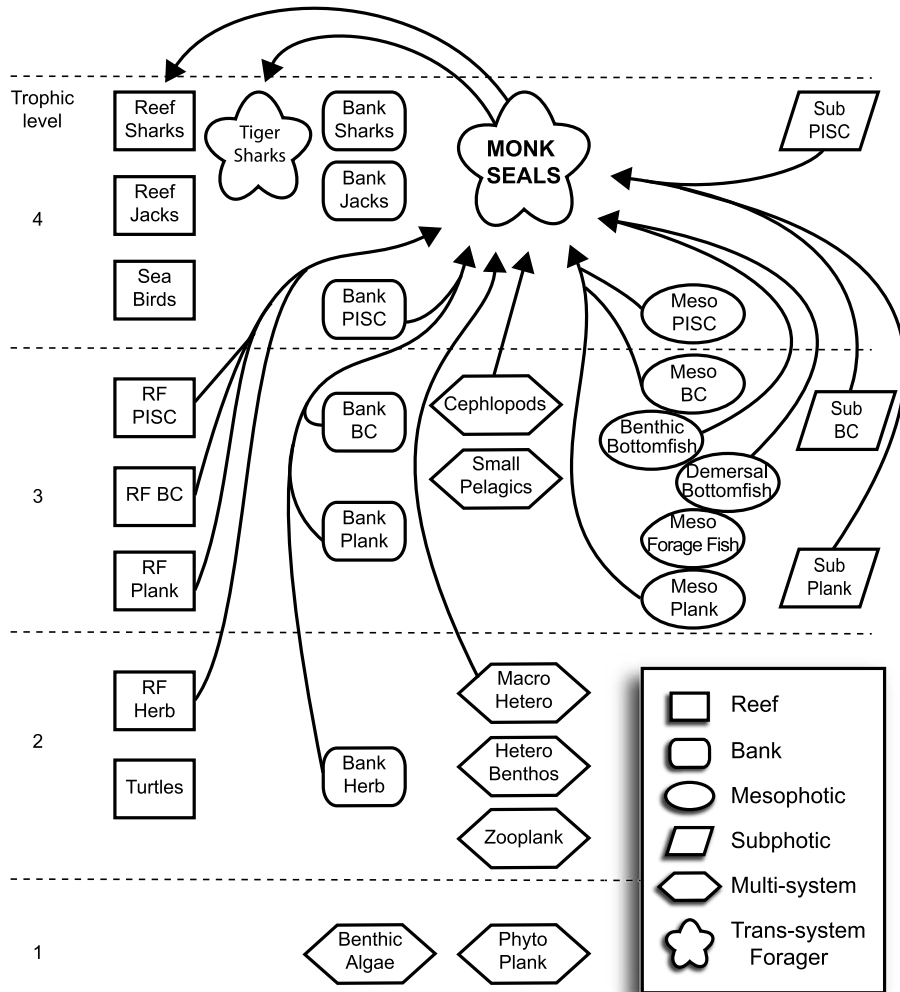
Figure 2. Diagram of the model food web for the monk seals FFS region. Model groups are plotted by trophic level and their box type indicates to what ecological subsystem they belong to. Energy flow through the food web is only shown for those groups that contribute to the monk seal and sharks that feed on the seals.

Parrish and Abernathy 2006). A "mesophotic forage fish" group was added to the mesophotic subsystem to deal with the large schools of tiny (*e.g.*, 2 cm) *Luzonichthys earli* that were found at this depth range. The bottomfish component was split into separate benthic and demersal bottomfish groups. Greater detail, including a list of

species that comprises the groups (Table S1), is available in the online supplemental materials.

Model B Estimates

To construct the Ecopath model, input parameters (Table 1) were calculated from the best available sources (Table S2). Surveys of the demersal/bottom-associated fish assemblages in each of the four ecological subsystems from 1998 to 2002 were used to calculate B for the Ecopath model. Within each subsystem, 35 area-based quantitative surveys of the fish community were conducted with sampling spread across the range of available habitat in the subsystem. For hard bottom habitats visual survey techniques were used (*e.g.*, divers and submersibles) while for soft bottom habitats bottom trawls were employed. Numbers and body lengths of the fish were converted to mass by using available length–weight regression coefficients for the taxa or proxy taxa that showed a similar body shape (Hawaii Cooperative Fishery Research Unit; PIFSC, unpublished data). The data from the surveys were extrapolated across the seals' available foraging grounds to get estimates of community B for all groups in the middle portion of the model's food web. B estimates for bottomfish groups were obtained using the region's latest stock assessment report (Brodziak *et al.* 2009). B values for nonprey groups such as sea birds or large jacks were similarly obtained from published studies conducted in the region. Monk seals and potentially tiger sharks were the only model groups known to forage across the four ecological subsystems. A conservative B estimate (derived from research fishing at FFS atoll, Dale *et al.* 2011) for the apex predator "tiger sharks" was used in the model. Counts and mean body weights from FFS seal population census data (Aguirre 2000) were used to calculate the 1998 B and derive the 1998–2009 time series. To convert between seal counts and the overall yearly B of the population (Craig and Ragen 1999), the average demography for FFS seals was used (1998–2009) (30% 0–2 yr at 60 kg; 5% 3–4 yr at 125 kg; 65% 5+ yr at 170 kg). For all groups, the ecosystem B is reported as a density value of metric tons per square kilometer (t/km^2). Effects of uncertainty and bias of B estimates were assessed as part of a resampling analysis presented later in the article.

Production, Consumption, and EE

P/B and Q/B parameters for 12 of the model groups were obtained from field studies conducted at FFS in the mid-1980s (Table 1 and S2). For the multispecies groups (piscivores, reef sharks, jacks, *etc.*), P/B and Q/B estimates were obtained from FishBase[1] (Froese and Pauly 2008). EE parameters were similarly selected from the literature (Christensen *et al.* 2009*a*) to enable the model in the EwE software to derive the B for model groups where there were gaps in field survey data (*i.e.*, algae, zooplankton, heterotrophic benthos, cephalopods, small pelagics, sharks). The EE for monk seals was derived based on the loss taken back up by the system (∼60% of juveniles or 22.5% of the total seal B (EE = 0.225) (Craig and Ragen 1999, Gobush 2010). Parameters were ranked by the level of uncertainty they potentially could introduce into the model with the greatest confidence being assigned to those obtained from the FFS region. These ranks or "pedigree" (Pauly *et al.* 2000) were used in the Ecoranger analysis.

[1] All FishBase data are available at http://www.fishbase.org.

Diet Information

Diet information for the reef fish assemblages were obtained from quantitative field studies conducted at FFS (Parrish *et al.* 1985, 1986; Norris and Parrish 1988). As the banks share many of the same species as the reefs, the same diets were applied to the bank groups. Except for the commercial bottomfish assemblage (Haight *et al.* 1993), little quantitative diet information was available for the mesophotic and subphotic groups. The initial diet proportion values for these unknown groups were entered based on the feeding guilds with known values to which they belonged (*e.g.*, reef fish planktivores diet values used as initial diet values for mesophotic planktivores). The diet of piscivores was set to reflect the relative proportion of their prey base of planktivores and benthic carnivores within their respective subsystems. Monk seal diet was based on the prey type and dominance identified in a quantitative fatty acid signature analysis (QFASA) (Iverson *et al.* 2004, 2006). A reference library of more than 100 fish taxa ($n = 2{,}190$) collected from all four ecological subsystems (Piche *et al.* 2010) was used to evaluate the signatures of monk seal blubber samples and indicated that the seals' diet was roughly made up of 12% reef fish, 67% mesophotic prey, and 21% subphotic prey (Iverson *et al.* 2011). Half of the seals diet in this updated model was represented by the benthic bottomfish group.

Fishery Removals

The annual B removed from the ecosystem by commercial fisheries was entered in the model using landing reports of sharks, jacks, bottomfish (benthic and demersal), and crustaceans (subset of macroheterotrophs group) (Hawaii, Division of Aquatic Resources commercial catch C-3 data for 1998–2008). Standardized spatial grid codes required for landing reports were used to apportion removals appropriately between reef and bank groups (*e.g.*, reef jacks *vs*. bank jacks). As the region has no resident human population, there was no other fishing (*e.g.*, recreational) that could impact the system.

Environmental Data

Environmental variability has been shown to affect the survivorship of both juvenile (Antonelis *et al.* 2003, Baker *et al.* 2007) and adult (Polovina *et al.* 1994) monk seals. Model results inferred that juvenile survivorship was closely linked to interannual variability (Baker *et al.* 2007), while the decline of the total population has been linked to environmental variability over longer time scales (Polovina *et al.* 1994). Environmental variability in the NWHI may change primary producer B over 50% (Polovina *et al.* 2008). As here we are concerned with the total monk seal population B, we used the Pacific Decadal Oscillation (PDO) index in the model to represent large-scale environmental trends in the North Pacific. Monthly values of the PDO from 1998 through 2009 were obtained from the index's data server.[2]

Ecosim Simulations with Time Series

Ecosim is the time-dynamic portion of the EwE framework and was used to compare model estimates of monk seal B to field data (1998–2009). Start year for simulations was set at 1998. Fishery landings obtained from the State of Hawaii

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[2]The PDO index is available in ASCII format at http://jisao.washington.edu/pdo/PDO.latest.

commercial catch report (C-3 data) were loaded as forced catch (Table S2). Ecosim scenarios were run for two time periods, 1998–2009 and 1998–2040. The year 2009 was chosen as the initial endpoint as this was the last complete year for which we had data for both the fisheries and environmental time series. The goal of the second simulation was to estimate monk seal B over time and determine if monk seals could return to 1998 levels after the 2010 fishery closures in the NWHI. For the first time period, Ecosim was run both with, and without the environmental forcing function applied to the two primary producer groups. For the extended 1998–2040 time period, the environmental forcing function was applied as a constant value of 1, which represented no environmental forcing effect on primary producers. This provided a unique opportunity to determine whether the future cessation of fishing alone could lead to improvement in the survivorship of NWHI monk seals. Randomized subsets of the historical PDO pattern were used to understand the effect of possible future environmental changes on monk seal biomass. Methodology for this step is available in the online supplemental material.

Addressing Model Uncertainty

We addressed model uncertainty by using the "Ecoranger" and "Monte Carlo" modules in Ecopath and Ecosim, respectively. Ecoranger within Ecopath enables the incorporation of variability around initial values for the basic input parameters: B, Q/B, P/B, EE, and diet composition for all groups (Coll *et al.* 2009). Ecoranger was programmed to perform a maximum of 10,000 runs randomly drawing input parameters from user-selected frequency distributions. Normal distributions were selected for all input parameters except diet, where a uniform distribution was used. Distributions were defined using the initial input parameter value as the mean, and a percentage value of the mean to approximate 95% confidence intervals. For normal distributions these percentage values corresponded to twice the standard deviation. Ecoranger selected percentage values based on the ranked uncertainty of the parameters, and ranged from 0% (low uncertainty) to 20% (high uncertainty). Ecoranger was then run with the randomized input parameters, stopping either after 10,000 runs, or when more than 3,000 runs resulted in a successfully balanced model. Ecoranger output provided a probability distribution of the estimated parameters (*e.g.*, $B_{\text{Monk seal}}$) in the model runs based on the randomized input parameters. A Monte Carlo scenario was run in Ecosim to understand the effect of Ecopath input parameter uncertainty on the 1998–2009 time-dynamic portion of the model that incorporated the PDO forcing function. The Ecosim Monte Carlo approach searches for possible Ecopath input parameter and vulnerability combinations that would improve the fit of the model to available time series data using the sum of squares reduction technique described above (Christensen *et al.* 2009*b*). The Monte Carlo scenario was set to randomly vary input parameters as in the Ecoranger scenario. There is currently no user interface to select a method to vary vulnerability estimates; therefore, these values were selected automatically by the program. The Monte Carlo scenario was run for 500 cycles following Christensen *et al.* (2009*b*).

<div align="center">RESULTS</div>

The Ecopath Mass Balance Model

A balanced Ecopath model was successfully achieved using the best available input data. Trophic parameters and diet matrix for the groups of the updated FFS model
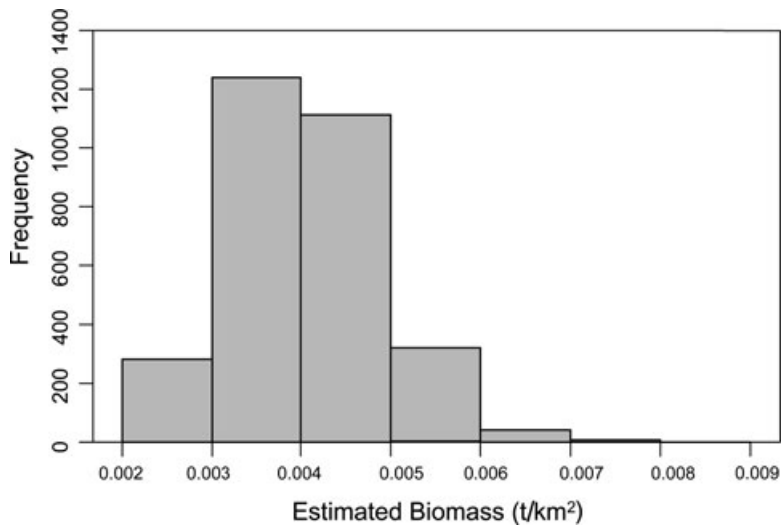
Figure 3. Results from Ecoranger resampling analysis exhibiting the probability distribution of monk seal biomass given the uncertainty in our input data.

are presented in Table 1 and 2. Energy flow through the trophic web to the monk seal group is represented in Figure 3. The model-estimated monk seal B at 0.0045 t/km^2 is in close agreement with estimates of 0.0046 t/km^2 calculated from field surveys. The Ecoranger resampling analysis provided a distribution of monk seal B estimates from 3,001 successfully balanced models using randomly varied input parameters (Fig. 3). This distribution showed that the seal B in the FFS region could theoretically range between 0.002 and 0.007 t/km^2 and still maintain thermodynamic balance in the model. Of the 3,001 successfully balanced runs in Ecoranger, 78.4% produced a monk seal B estimate between 0.003 and 0.005 t/km^2, and 37.1% produced an estimate in the 0.004–0.005 t/km^2 range that spanned the field survey B estimate.

Time Series Fitting

Fishing activity in the FFS region ranged from multiple trips conducted annually (*i.e.*, bottomfish) to a single year fishing event (*i.e.*, sharks) (Fig. 4). Fishing dropped off in 2006 with the implementation of take restrictions in the NWHI associated with the establishment of the Papahanamokuakea National Marine Monument. The PDO index shows that the environment underwent oscillating phases from 1998 through 2009, (Fig. 5A) and was generally negative from mid-1998 through mid-2002 and mid-2006 through 2009, and generally positive from mid-2002 through mid-2006. Results from the 1998–2009 Ecosim simulation that only incorporated fishing data showed a steady decline in the seal B over a decade (Fig. 5B). The modeled decline in monk seal B from this scenario was not a strong fit to the observed monk seal B time series, with B estimates higher than levels seen in the field census data (Fig. 5B). Incorporating the PDO index as a forcing function greatly improved the fit of the modeled to the observed monk seal B (Fig. 5B).
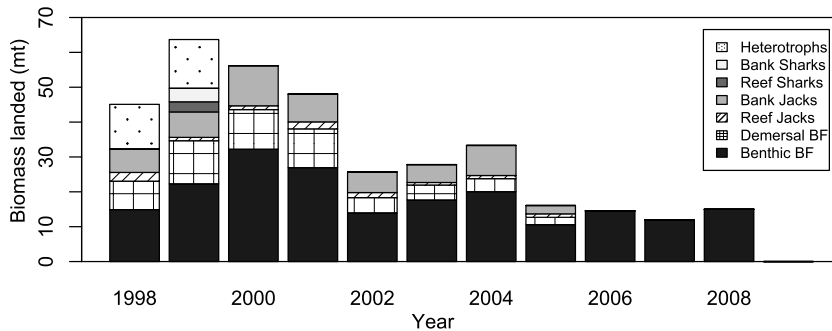
Table 2. Diet matrix used for the Ecopath model.

No.	Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	Sea birds		0.005																												
2	Tiger shark		0.015																												
3	Monk seals		0.030		0.006																										
4	Reef sharks		0.016		0.024																										
5	Bank sharks		0.043			0.034																									
6	Reef jacks		0.010		0.025																										
7	Bank jacks		0.040			0.025																									
8	Turtles		0.163																												
9	Benthic bottomfish			0.495	0.1	0.1	0.005	0.005																							
10	Demersal bottomfish			0.005	0.06	0.06	0.005	0.005																							
11	Small pelagics	0.259			0.006	0.006	0.205	0.300		0.02																					
12	Reef fish piscivores	0.158	0.008	0.137	0.07		0.066						0.092			0.003															
13	Reef fish planktivores	0.113	0.007	0.036	0.087		0.062			0.014			0.30			0.014															
14	Reef fish herbivores	0.126	0.009	0.025	0.15		0.249			0.001			0.25			0.011															
15	Reef fish benthic carnivores	0.344	0.037		0.120		0.348			0.001			0.262			0.001															
16	Bank piscivores		0.030			0.07		0.066									0.03			0.003											
17	Bank Planktivores		0.029			0.087		0.062		0.056							0.30			0.014											
18	Bank herbivores		0.034			0.152		0.079		0.004							0.174			0.011											
19	Bank benthic Carnivores		0.15			0.12		0.348		0.004							0.40			0.001											
20	Mesophotic piscivores			0.06																	0.05										
21	Mesophotic planktivores																				0.10										
22	Mesophotic benthic carnivores									0.036											0.05										
23	Mesophotic forage fish			0.005			0.01	0.03		0.35	0.005										0.75		0.30								
24	Subphotic piscivores			0.004																					0.05						
25	Subphotic benthic carnivores			0.002																					0.30						
26	Subphotic planktivores			0.04																					0.35						
27	Macroheterotrophs		0.173	0.04	0.065	0.065	0.02	0.030		0.014	0.255		0.04		0.111	0.1	0.04		0.111	0.1								0.10	1.0		
28	Cephalopds		0.201	0.10	0.286	0.281	0.025	0.025		0.01			0.056				0.056						0.20		0.2	0.30					
29	Heterotrophic benthos			0.003					0.1	0.49	0.23					0.871				0.871			0.50		0.1	0.7		0.50			
30	Zooplankton										0.50	0.85		0.889				0.889				1.0					1.0			0.20	
31	Phytoplankton													0.111				0.111													1
32	Benthic algae								0.9						0.889				0.889									0.40		0.40	
33	Detritus											0.15																		0.40	

Figure 4. Graph of commercial landings in the French Frigate Shoals region (1998–2008).

Results from the model run through 2040 assuming no fishing and a constant environmental forcing show a gradual increase in monk seal B post-2010, with a return to 1998 levels by 2040 (Fig. 5C). Results from model runs using 20 randomized PDO time series show that monk seal biomass estimates are variable, with the biomass estimates in 2040 ranging from 50%–125% of initial 1998 B values (Fig. 5C).

The Monte Carlo scenario was unable to find a base Ecopath model or vulnerability combination that resulted in a lower sum of squares residual than was obtained through the Ecosim "Fit to time series" procedure using the original model. The Monte Carlo routine produced sum of squares residuals in the range 0.45–223.5, compared to the sum of squares residual from our best fit model which was 0.07.

DISCUSSION

Model Structure and Uncertainty

We assume that any "noise" introduced to the model was less than the "signal" of ecosystem linkages derived from the model. Sources of uncertainty in the model included the temporal inconsistency in the collection of data, the quality of the derived parameters, the dispersion of foraging effort by seals within the model boundaries, and the connectivity of energy between model groups. To minimize the noise in the model, field surveys were conducted to collect habitat-specific B data, and production and consumption parameters were obtained where possible primarily from studies conducted in the Hawaiian Archipelago. For remaining gaps in information, values were left to be estimated by Ecopath. Overall, the quality of parameters or "pedigree index" for our model was moderate, but within the range reported for other ecosystem models (Morrissette 2007).

The model is uncertain for species that feed outside the FFS region. Turtles forage in the algal habitat of the MHI (Balazs 1976, Rice and Balazs 2008), albatross feed on the epipelagic fauna in the North Pacific (Ballance *et al*. 1997), and tiger sharks feed throughout the island chain and the open ocean visiting FFS to feed on chicks and turtle hatchlings during the annual nesting season (DeCrosta *et al*. 1984). Even though the flow of energy from turtles and albatross to tiger sharks intersects at FFS atoll, these groups are weakly connected to the benthic and demersal food web on which the monk seals feed and as a result this energy is not really imported or exported
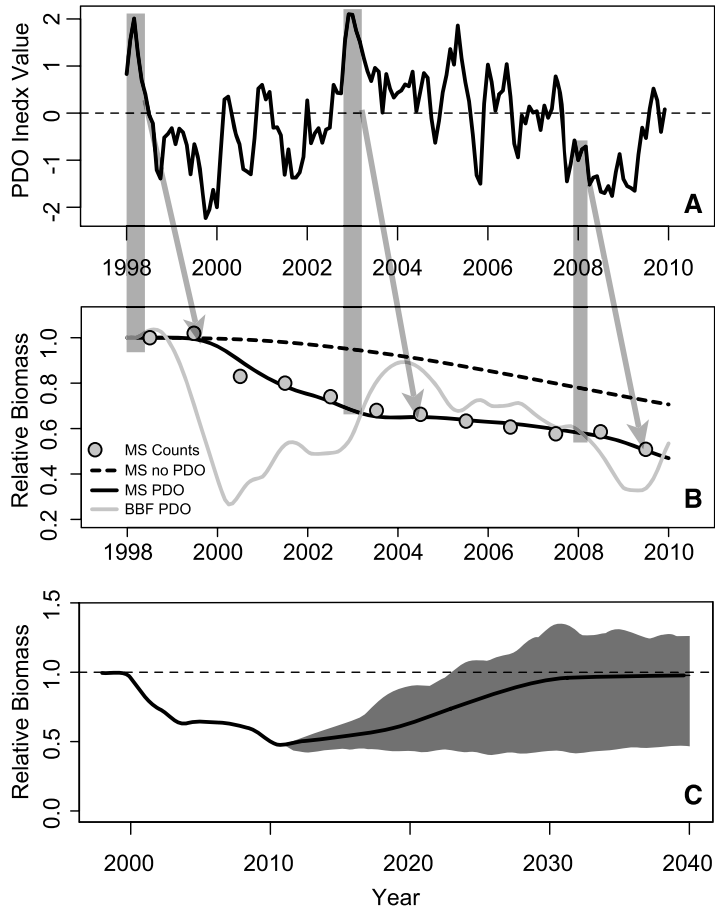
Figure 5. The time series of the PDO (A) used to improve the Ecosim fit of fishery removals (1998–2009), including the dominant seal prey benthic bottomfish (BBF), to the biomass data from monk seal (MS) counts (B). The simulation of the future in the lower panel (C) shows the gradual increase of monk seal biomass (Solid black line) to 1998 levels if there is no fishing and the PDO is assumed at a constant neutral signal. The grey area represents the 95% confidence intervals calculated using the randomized PDO time series.

from the system but rather transferred between visitors. This is reflected in the EEs for turtles, tiger sharks, and the albatross component of seabirds. Unlike the seal B, which is well documented from field surveys, the abundance of reef sharks and jacks is poorly known and can only be obtained from isolated fishing and diving surveys. Because the model is based on field data collected over a relatively short number of years, it is hard to appraise the degree of temporal change that may occur in the system. There has been annual monitoring of reef fish assemblages at FFS (DeMartini *et al.* 2002) and results suggest little interannual change in the prey base. But this is less certain in deeper mesophotic fish assemblages where the FFS seals most often feed. At this depth, schools of bottom associated planktivores closely linked to the seals prey base may quickly change in abundance with regional shifts in oceanic productivity.

Environmental Change

The PDO reflects large-scale patterns of climate variability over the North Pacific that vary on interannual to interdecadal time scales. Over these time scales, the North Pacific oscillates between two major phases, described in the literature as "warm" and "cool." For the central North Pacific (CNP) region, however, each of the phases result in a climate pattern that is the reverse from what the name would infer. A warm phase, when the PDO index is positive, represents a period when sea level pressure (SLP) is below average, and sea surface temperatures (SST) in the CNP are anomalously cool. This period of the PDO resembles El-Niño-like conditions, where large-scale oceanic features, such as the transition zone chlorophyll front (TZCF), are displaced further to the south (Bograd *et al.* 2004). This southern displacement of the TZCF has been hypothesized to raise primary productivity in the northern NWHI, which eventually propagates vertically through the food web to increase monk seal prey availability (Baker *et al.* 2007). Conversely, a cool phase, when the PDO index is negative, represents a period when seal level pressure (SLP) is above average, and SST in the CNP are anomalously warm. This period of the PDO resembles La Niña-like conditions, where the TZCF is displaced further north of the NWHI (Bograd *et al.* 2004). The PDO index was negative in our study period from mid-1998 to mid-2002 and 2007–2009. This would result in a northward displacement of the TZCF and infer a decrease in productive waters to the NWHI and FFS. The PDO index reversed sign to become positive during the mid-2002 to mid-2007 period, yet there is an observed downward trend during this time. Additionally, the PDO variability during this time is shown to change phases more frequently during the 12 yr of our study period, covarying with the El Niño Southern Oscillation indices.

Simulations with Fisheries and Environmental Data

The Ecosim scenarios indicated that changes in benthic bottomfish B had the most influence on seal B. This is due to the large fraction of benthic bottomfish (∼49%) in the seals' diet. Fishery removals of benthic bottomfish were able to partially explain the observed decrease in monk seals, yet model results indicate that environmental variability in the study region was important in explaining the changes in monk seal B over time. Other fishing, including removal of competitors (sharks and jacks) and potential prey (lobster portion of macroheterotrophs), had little influence on the seals' B. Fishing did effectively reduce the fraction of seal competitors in the model. However, because seals generally feed deeper than 100 m (Parrish *et al.* 2000, 2002; Stewart *et al.* 2006), where sharks and jacks are in low abundance (Parrish *et al.* 2008), their removal by fisheries does little to reduce the competition on the mesophotic prey base the seals currently use.

The addition of an environmental forcing function to the model scenario improved model estimates of monk seal B over time. The energy pathway in the model from primary producers to monk seal is relatively direct, and this is observed in the response of benthic bottomfish to changes in the environment. Plankton comprises half of the diet of benthic bottomfish and all of the diet of smaller planktivores that they feed on. This energy transfer may support the seals in a couple of ways. The number of prey may be less important than the fat that is added to their body during productive periods when water masses carry higher loads of plankton. Another possibility is that the seals are also eating the smaller planktivores that the benthic bottomfish

prey on. If the seals' dependence on benthic bottomfish was over represented by the QFASA modeling and seals are instead feeding mostly on the abundant, small-bodied, mesophotic planktivores then we would expect the bottomfish fishery to have removed competition for prey and improved the seals' forage base. Five decades of bottomfishing (WPRFM 2005) have not altered the continuous decline of the FFS seal population suggesting that bottomfish, and not their prey, is the more likely target of the seals. A final consideration is that the seals are probably most effective at capturing the smaller juvenile stages of the bottomfish community. Seal mounted video cameras show that seals feed on small-bodied fish (∼20 cm) that seek shelter in the bottom where the seals can easily corner and capture them (Parrish *et al*. 2000). The average length of an adult bottomfish (40–100 cm) exceeds the size targeted by seals, and in fact some adult snappers (*Aprion virescens*) are often seen on video from the seal mounted cameras attempting to capture stray prey flushed by the seals' searches of the bottom (Parrish *et al*. 2008). Juvenile bottomfish, like other small bodied prey, are dependent on plankton for survival and the seals' consumption of these provides another possible explanation why the PDO may have a direct, compounding effect on the FFS seal population.

Model Projections

The leading hypothesis for the continual decline of the FFS seal population since the 80s has been that the available prey base of seals is inadequate to support prior population levels in excess of 300 individuals. Observed declines in body weight across the population and loss of juveniles to starvation have supported this notion (Baker *et al.* 2011). The results from the Ecoranger analysis provide a probability distribution of monk seal B for the FFS region in 1998. While our model-estimated monk seal B (0.0045 t/km^2) falls near the median value in the Ecoranger distribution (0.004 t/km^2), the mode of the distribution (0.003–0.004 t/km^2) is slightly lower than the observed B of seals in 1998 (0.0046 t/km^2). This suggests that the forage B at FFS may be lower than what is required by the actual population (B) of seals. The result that 51% of the balanced Ecoranger runs resulted in a monk seal B lower than the observed field B is consistent with the notion that carrying capacity was in decline in 1998. Only 12% of the successful Ecoranger runs resulted in a seal B >0.005 t/km^2. This B value represents an abundance of seals not seen at FFS since the early 1990s, and represents a less likely scenario given current conditions.

The Monte Carlo routine in Ecosim allowed us to assess how the temporal dynamics of the model change based on variation in our input and vulnerability parameters. We were unable to find a better model fit than what was obtained through the time series module when using our base model and applying the PDO as an environmental forcing function. There was a large range in the sum of squares residuals based on the input parameters. This exercise was useful in validating that our base balanced Ecopath model and Ecosim-derived vulnerability estimates captured the observed trend of monk seals over time. The Monte Carlo method only retains model runs where a model was successfully balanced. Of the 500 balanced models produced by the routine, more than 50% of them resulted in a decrease of benthic bottomfish B to 0 during the time series, which resulted in a slight decrease in monk seals over time.

Ecosim only provides the parameter estimates from the "best fit" model, yet manual adjustment of parameters showed that bottomfish B trajectories were sensitive to

adjustments in their model vulnerability (not shown). As might be expected, a large increase in bottomfish vulnerability resulted in a quicker decrease in bottomfish B. As benthic bottomfish take refuge in the complexity of the seafloor, a fixed feature of the environment, we would not expect wide variations in vulnerabilities.

History of Seal Survivorship

Our model is based on prey surveys from the late 1990s and focuses on the anthropogenic activities of the last decade without accounting for the 8% annual decline of the seal population seen in the prior decade. Reduced oceanographic productivity at FFS in the late 1980s has been identified as a key environmental driver that impacted the NWHI ecosystem and the seal population. Impacts were evident with declining catches of lobster and bottomfish and poor survivorship of seabirds and seals (Polovina *et al.* 1994). The bottomfish stock B over the last two decades shows a ∼25% decline in the late 1980s coinciding with the oceanographic regime shift to a negative (cool) PDO phase, and then a tapered decline to two-thirds the starting B (Brodziak *et al.* 2009). Based on this 1998–2009 Ecosim scenario, oceanic productivity is the dominant effect with loss of prey to fisheries (*e.g.*, bottomfish) being a secondary impact.

Given the high diversity of prey in the seals' diet, the seals may be capable of switching between prey, and it is possible that in the past a preferred prey type became unavailable increasing their reliance on bottomfish. Such shifts between prey with changes in availability and preference have been documented in other top predators and ecosystems (Reid and Arnould 1996, Iverson *et al.* 2006, Springer *et al.* 2007). Prey switching may be evident in ongoing work in the MHI where seals in excellent body condition have successfully relied on forage grounds shallower than the bottomfish habitat.[3] Switching prey items due to their changing availability will alter carrying capacity and animals could incur loss of survivorship due to reduced caloric value of the new prey or increased energy cost of prey capture (Antonelis *et al.* 1984, Thompson *et al.* 1997, Iverson *et al.* 2011).

Finally, switching of foraging habitat can accompany prey switching, but it could also be the result of displacement from competition with other top predators. Competition for prey at the point of capture with large predatory fish (sharks and jacks) has been documented using seal-mounted cameras (Parrish *et al.* 2008), and avoiding competition by feeding deeper may be a factor in a seal's choice of where to forage. For reef fish, as a prey, there is an overlap in the diet of seals, sharks, and jacks. Jacks are the most effective in their ability to pursue and capture prey and easily out-compete monk seals, though the seals are better at probing and flushing prey from bottom cover. Jacks and sharks exploit the seals' bottom-searching ability by escorting and stealing prey from seals on their foraging runs. Juvenile seals, which suffer the highest mortality, are small and unskilled at competing for prey among the schools of large predatory fish in the shallows and have yet to gain the diving skills of an adult that permits them to make use of deeper foraging grounds (Horning and Trillmich 1997, Pitcher *et al.* 2005). If prey switching does occur or seals are subject to displacement from forage grounds by competitors, then the seals' carrying capacity could be very different from what we describe. Data are currently lacking to explore this hypothesis.

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[3] Personal observations by C. Littnan, 2010.

The Future

Based on our simulations, the present decline in monk seals will level out and slowly begin to increase in the coming decades. While the extended PDO time series used in this study may not capture future environmental dynamics, our results provide a range of estimated monk seal biomasses, including further decline, based on historical environmental events. Any increase of the seals by 2040 will likely be limited to something less than the 1998 levels unless there is marked improvement in the PDO. This is at odds with other monk seal forecasts that are based on the age structure and survival rates of the seals at FFS (Baker *et al.* 2007, Baker and Thompson 2007). Unlike those models, the Ecosim anticipates an increase in the availability of seal prey from the 2010 closure of all fishing by the Papahanamokuakea National Marine Monument. This effectively removes the bottomfish fishery as a competitor with the monk seal for prey. The extent of the seals' population growth will depend on the level of productivity we get in the FFS region from North Pacific oceanic conditions. With lower productivity we may see no recovery. Assuming the PDO remains constant at current levels, the abundance of bottomfish will exceed 1998 levels in a few short years and should augment the seals' available prey base and improve seal survivorship. Actually, witnessing this success is contingent on all significant ecosystem processes being accounted for by the model. Resilience is inherent to steady-state ecosystem models, but is uncertain in the wild.

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SUPPORTING INFORMATION

The following supporting information is available for this article online:

Table S1: Species and common names for the most frequently encountered taxa on the field surveys for the model groups.

Table S2: Source for parameters.