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Comparative application of trophic ecosystem models to evaluate drivers of endangered Hawaiian monk seal populations

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ABSTRACT: The Northwestern Hawaiian Islands share comparable biological community structures and have similar histories of fishing pressure, yet monk seal subpopulations show different trends of decline between locations. Using trophic models, we compared ecosystem structure and energy flows supporting 2 subpopulations (on Laysan Island and French Frigate Shoals (FFS) atoll), each with varied rates of decline (1998–2015). Through simulated perturbations, we showed that the Laysan community had much higher productivity and was mainly forced by bottom-up processes, but prey and predator abundance also controlled the energy flow and community structure. The FFS ecosystem was less productive and strongly influenced by a change in primary productivity. Although the FFS system responded to a change in predator and prey abundance, the monk seals were more influenced by benthic bottomfish biomass than by a change in predator abundance. We clarified the role of external drivers (Pacific Decadal Oscillation [PDO] and benthic bottomfish fishery): while the PDO did show correlation with monk seal population trends, the best models were driven by prey biomass as impacted by bottomfish removals. However, monk seal predator and prey trophic dynamics were not sufficient to explain the observed decline in monk seal biomass. We suggest that other factors amplifying mortality played a role; for example, shark predation on monk seal pups at FFS. Because of the uncertainties inherent in a complex ecosystem model, the results cannot be used for tactical management but they can help direct management or future research efforts in the recovery of the endangered monk seal population.

KEY WORDS: Endangered species · System understanding · Drivers · Conservation · Trophic model · Recovery · Hawaiian monk seals · Northwestern Hawaiian Islands

INTRODUCTION

Endangered species are impacted by complex interactions of environmental and ecological factors. Endangered species conservation can benefit from understanding ecosystem-level processes. Hawaiian monk seals *Neomonachus schauinslandi* provide an excellent example of a species imperiled by complex factors (National Marine Fisheries Service 2007, Lowry et al. 2011). This species is endemic to the Hawaiian archipelago and was listed as endangered under the US Endangered Species Act and as a depleted stock under the Marine Mammal Protection Act of 1976. Direct interventions have been successful in mitigating some threats to the species (for example, disentanglement from marine debris, treatment of abscessed infections, translocation to higher-survival areas; Harting et al. 2014), yet the population continued to decline until recently. Between 2013 and 2016, this downward trend seems to have stopped and reversed (National Marine Fisheries Service 2017). Ecological drivers, such as variable ocean productivity, food limitation, interspecific competition, and predation are thought to influence monk seal populations.

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Although Hawaiian monk seals have generally declined since at least the late 1950s, there are temporal and spatial variations in individual survival and population dynamics across their range (Baker & Thompson 2007). This variability is driven by processes at multiple scales. Broad-scale oceanographic factors have the potential to exert bottom-up forcing by changing the primary productivity of the system. Monk seal populations have responded to changes in primary productivity associated with oceanographic regime shifts, such as the Pacific Decadal Oscillation (PDO) (Baker et al. 2007, Polovina et al. 1994, Polovina et al. 2017). Increases in oceanic productivity may boost recruitment and settlement of prey, which directly influences juvenile monk seal survival (Antonelis et al. 2003, Baker et al. 2007), a key factor in monk seal population growth (Parrish et al. 2005). Previous work has shown variable influence of the PDO, depending on geographical location (Baker et al. 2012, Parrish et al. 2012). We will investigate the role of the PDO in driving productivity at southern monk seal breeding sites in the NWHI.

In addition to oceanographic drivers, regional shifts in prey availability have the potential to impact wildlife populations. The decline in at least 1 monk seal population coincided with a region-wide decrease in bottomfish abundance (Parrish et al. 2012). Over time, changes in fishing pressure may have altered the availability of, or competition for, bottomfish as a food resource. With the relatively recent cessation of all commercial fishing in the NWHI (in 2011) as part of the region's new status as the Papahānaumokuākea Marine National Monument, there is now an opportunity to assess whether the rebuilding of this prey resource has influenced recovery in the predator (monk seal) population.

Highly localized factors and site-specific threats also have the potential to drive monk seal dynamics, which vary widely across the Hawaiian archipelago. Most (~75%) of the remaining approximately 1400 Hawaiian monk seals inhabit 8 breeding sites in the remote NWHI (Fig. 1). This portion of the population declined at a rate of 2.8% annually over the past decade (2005–2014, National Marine Fisheries Service 2017) though this trend has appeared to reverse since 2013, with a 3% annual increase between 2013 and 2016 (Pacific Islands Fisheries Science Center [PIFSC], unpubl. data). Meanwhile, seal populations in the 8 main Hawaiian Islands increased by 5.2% over this same time period (National Marine Fisheries Service 2017). Poor juvenile survival, driven by food limitation, is suspected to be one of the key factors in decline of NWHI populations (Craig & Ragen 1999, Antonelis et al. 2003, Antonelis et al. 2006), but additional threats vary from site to site. For example, monk seals have one of the highest entanglement rates among pinnipeds, and entanglement rates vary across the NWHI chain (Donohue et al. 2001, Henderson 2001, Howell et al. 2012). Shark predation is a particular risk at French Frigate Shoals (FFS), where Galapagos sharks target young pups, removing upwards of 20% of pups produced at this site each year (Harting 2010). This highly targeted predation is not observed at any other NWHI site.

The complex interplay of factors, from the local to oceanographic scale, creates unique challenges in monk seal recovery. To add the context of inter-site variability, we expand on previous ecosystem modeling efforts focused on FFS (Parrish et al. 2012) to include another breeding site with divergent characteristics, Laysan Island. FFS, which historically supported the largest breeding colony (Kenyon & Rice 1959), has experienced the most dramatic reduction of any of the Hawaiian monk seal breeding sites. Over the course of the study period (1998–2015), the FFS seal population declined from 412 to 188, at a relatively consistent rate of 4.3% annually (PIFSC unpubl. data). Meanwhile, 700 km to the northwest, Laysan has hosted one of the most stable monk seal populations in recent decades. During the same period, the Laysan population declined from 291 to 244 individuals, with a decline of 2.4% to 2006, followed by relative stability for the past decade (PIFSC unpubl. data).

The main objective of this study was to understand the difference in ecosystem dynamics that could explain the observed decrease in monk seal biomass at FFS and the more stable biomass at Laysan. We built on the foundation of an Ecopath with Ecosim (EwE) model of FFS by Parrish et al. (2012), extending the time series from 1998 to 2015, and adding Laysan as a second site. We took a 3-fold approach to evaluate ecosystem structure and drivers. We first developed a Laysan EwE model and updated the FFS model and compared ecosystem structure and productivity between the 2 models. We then evaluated 4 perturbation scenarios: baseline, altered predator abundance, altered monk seal prey abundance, and altered primary productivity to better understand the driver of trophic structure and energy flow (e.g. bottom up or top down). Finally, we evaluated competing hypotheses regarding the relative influence of (1) productivity (PDO), (2) fishery impacts on benthic bottomfish (important prey source of monk seals), and (3) sources of extra mortality to monk seals. Understanding the drivers and predictability of pop-

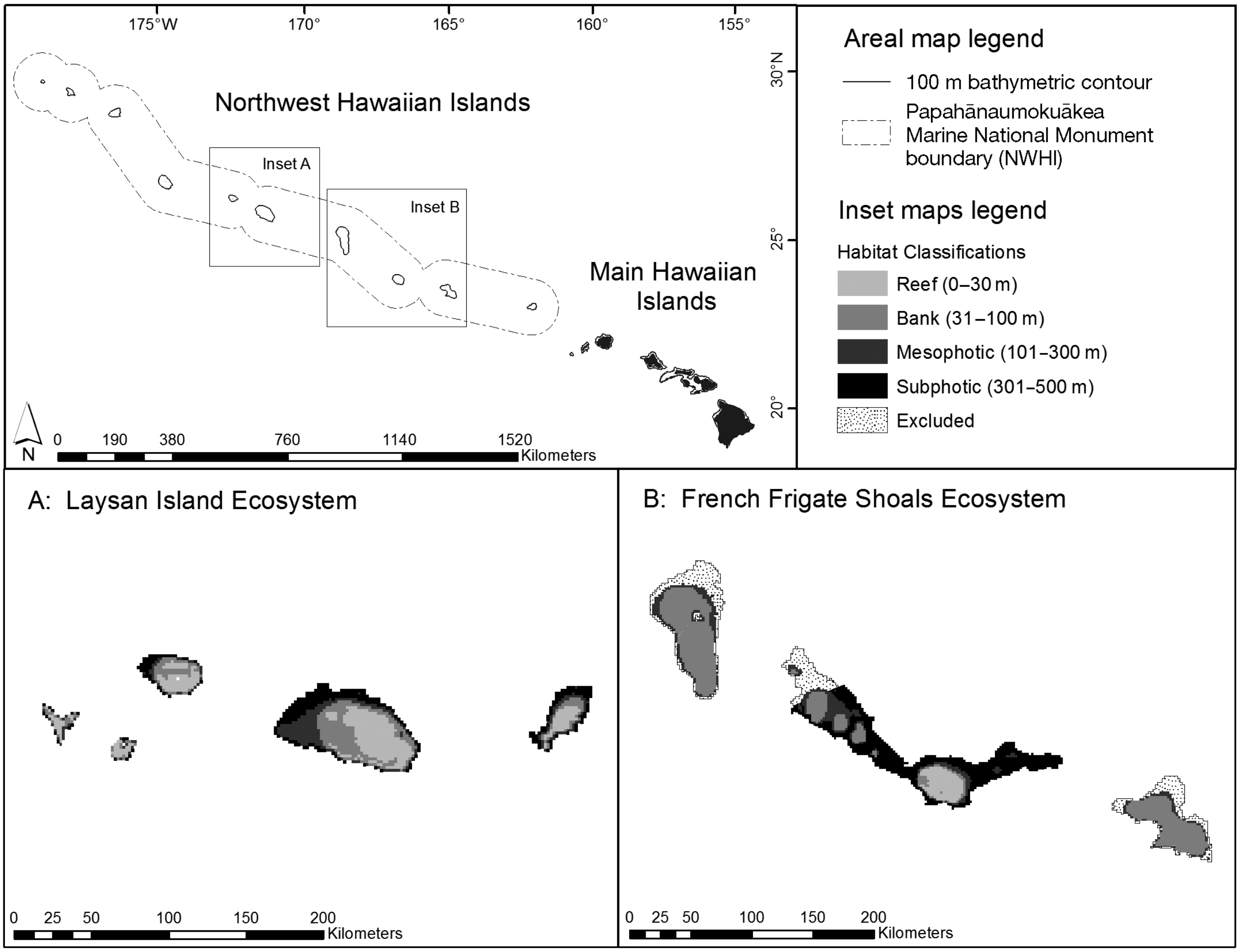

Fig. 1. The wide area map (top) shows the study areas in context of the Hawaiian Archipelago. Insets (bottom) show the distribution of habitat types around (A) Laysan Island and (B) French Frigate Shoals

ulation trends will illuminate areas of focus for Hawaiian monk seal recovery efforts.

METHODS

To address the objectives and test our hypotheses we conducted 2 types of simulations, sensitivity and hindcast simulations (Table 1) using the Ecopath with Ecosim modeling software.

Ecopath with Ecosim

Ecopath with Ecosim (EwE) version 6.4.4 (Christensen et al. 2008) was used for understanding the ecosystem's structure and dynamics. Ecopath is a steady-state mass-balanced model, determined largely by trophic interactions and fishery removals (Polovina 1984, Walters et al. 1997). This modeling approach is based on a master equation that describes the production term and another equation for the energy balance for each group. To parameterize, simultaneous linear equations for each functional group (species with similar life history characteristics and ecological role) in the system are set up and Ecopath solves this set for 1 of the 4 following ecological input parameters biomass (B), production to biomass ratio (P:B), consumption to biomass ratio (C:B), or ecotrophic efficiency (EE). The other 3 parameters, along with catches, diet composition, assimilation, net migration rate, and biomass accumulation rate, must be entered for each group (Christensen & Walters 2004). EE is the proportion of the production that is utilized in the system and ranges between 0 and 1. The most robust approach

Table 1. Details of model simulations. PDO: Pacific Decadal Oscillation

Objective: System understanding

Sensitivity simulations	Time span	Model fitting
Base — compare static structural ecosystem composition between Laysan and French Frigate Shoals	50 yr	No
Predation — 30 % decrease in biomass of main predators (based on principal component analyses of predator–prey relationships; Supplement 5) in the ecosystem (through an increase in fishing mortality) to evaluate the role of predators in structuring the food web (top-down control)	50 yr	No
Prey availability — 30 % decrease in biomass of main monk seal prey groups (based on principal component analyses of predator–prey relationships; Supplement 5) to compare the role of prey in structuring the monk seal population (waist control)	50 yr	No
Primary productivity — change productivity annually by 10 % for both phytoplankton and benthic algae (through an annual forcing factor of 0.9 and 1.1 on both groups) to evaluate the role of primary productivity in food web structure (bottom-up control)	50 yr	No

Objective: Evaluation of drivers of monk seal population dynamics

Hindcast simulations	Time span	Model fitting
Fishery	1998–2015	Yes, to 2 (monk seal and benthic bottomfish) biomass time series and 5 catch time series
PDO	1998–2015	Yes, to 2 biomass time series and primary production
Additional monk seal removal	1998–2015	Yes, to 2 biomass time series and additional monk seal removal time series
Fishery and PDO	1998–2015	Yes, to 2 biomass time series, 5 catch time series, and primary production
Fishery and additional monk seal removal	1998–2015	Yes, to 2 biomass time series, 5 catch time series, and additional monk seal removal time series
Fishery, PDO, and additional monk seal removal	1998–2015	Yes, to 2 biomass time series, 5 catch time series, primary production, and additional monk seal removal time series

for model development is to enter B, P:B, and C:B and allow the model to estimate EE, providing a check for mass balance because EE cannot be greater than 1 (Polovina 1984).

Ecosim is the temporal component of the EwE suite (Christensen & Walters 2004). It accounts for the biomass flux between groups using coupled differential equations derived from the Ecopath master equations. Change in biomass is determined by growth efficiency, consumption, immigration, and loss due to predation, emigration, natural mortality, and removal by fisheries or other sources. Consumption rates are calculated based on vulnerable and invulnerable components of the prey biomass to their predators (vulnerability). Vulnerability determines whether control is bottom up (the prey can remain hidden or defended against predation, value is close to 1) top down (predation mortality is proportional to the product of prey and predator abundance, i.e. Lotka–Volterra relationship, value is >~2.5) or of an intermediate type (value is 2; Christensen & Walters 2004). When vulnerability values are set too high (e.g. 10) it can cause some groups to reach extinction. During the model fitting procedure, we manually adjusted these vulnerability coefficients between 1 and 3 with incremental steps of 0.1 to find the best-fit model based on the least-square fitting criterion. Note, however, that we needed to increase some vulnerability values to 10 to obtain a better fit.

Model components

Ecosystems and boundaries

FFS and Laysan are 2 of 8 atolls and islands serving as Hawaiian monk seal haul-out and breeding sites in the NWHI (Fig. 1). Additional seamounts and reefs in the area extend monk seal foraging habitat beyond the islands and atolls at Laysan and FFS. While both sites share broadly similar fauna and habitats, the bathymetric profiles and habitat distribution around each site differ, potentially influencing community dynamics. We designated the study area around Laysan Island based on monk seal foraging ranges and dive depths (Supplement 1 in the Supplement at www.int-res.com/articles/suppl/m582p215_supp.pdf) using habitat designations from Parrish et al. (2012). The extent of the areas typically visited by monk seals that have been satellite tracked from Laysan was determined by using satellite tag data for 27 seals (Stewart et al. 2006). The total habitat area was 4970 km^2 (Fig. 1, Table 2). For FFS, we used the same habitat areas as described in Parrish et al. (2012).

Functional groups

For ease of comparison with Laysan, we used the same functional groups as used in FFS (Parrish et al. 2012). We updated the species composition of each functional group (Supplement 2 in the Supplement) based on surveys where available. Bottomfish, an important prey group for monk seals, were separated into 2 groups based on their diet. Monk seals primarily eat bottomfish species that feed on benthic prey sources ('benthic bottomfish') and to a lesser degree on species that feed on prey in the water column above the substrate ('demersal bottomfish'). Supplement 3 details the sources for biomass data, data on vital rates, and diet composition, and Supplement 4 shows all the input values in tables with their uncertainty or 'pedigree' as defined by Christensen & Walters (2004). These uncertainties were used in Monte Carlo simulations (see 'Model simulations').

Environmental data

Following the approach in Parrish et al. (2012), we used the monthly PDO index to simulate regional environmental trends in the model. Monthly values of the PDO from 1998 to 2015 were obtained from the index's data server (http://research.jisao.washington.edu/pdo/PDO.latest). These values were scaled to the maximum PDO value and used as a monthly forcing factor for primary productivity of the phytoplankton and benthic algae (we assumed a linear relationship by multiplying the scaled index by biomass).

Table 2. Habitat types classified in accordance with Parrish et al. (2012) for Laysan and French Frigate Shoals (FFS)

Habitat type	Depth (m)	Area (km^2) (% of total) FFS	Laysan
Atoll	0–30	1003 (9%)	1642 (33%)
Bank	30–100	5807 (49%)	1256 (25%)
Mesophotic	100–300	1831 (15%)	1005 (20%)
Subphotic	300–500	3209 (27%)	1066 (21%)
Total		11850	4970

Fishery removals

Commercial fishery data came from the Hawaii Division of Aquatic Resources commercial catch for the reporting zones of Raita Bank (16925E), Maro Reef (17025 A,B,C,D), Laysan (17125 G,H), and Northampton (17225 C,E,F). These landings were allocated to 4 fishing fleets — bottomfish, bank jacks, reef jacks, lobster (macroheterotrophs) — based on the species caught. In contrast to FFS, no shark landings were reported for the Laysan study area.

Additional monk seal biomass reduction

Given the observed downward trends in monk seal populations, it is possible that extra mortality sources explain these patterns. To explore this possibility, a monk seal 'fishery' was included as an annual constant percentage mortality. This percentage was incrementally increased to achieve the best model fit for monk seals. The purpose for estimating arbitrary mortality factors was twofold: (1) to determine whether environmental or fisheries drivers explain the fit between model-predicted and observational data better than an arbitrary downward trend, and (2) to evaluate the role of the ecosystem structure versus particular sources of excess mortality in the decline of monk seals. Many mortality sources are extrinsic to the food web (e.g. entanglement) and/or impact populations disproportionately to the biomass removed. For example, though it is captured in the diet matrix, shark predation on monk seals disproportionately (almost entirely) impacts seal pups, which leads to a skewed age distribution that dramatically reduces reproductive potential and population productivity.

Model simulations

To understand the energetic flows and dynamics in the 2 ecosystems, we simulated perturbations to the food web models for a time span of 50 yr and looked for evidence of top-down, bottom-up, or waist control by comparing the mean of the last 5 yr of a perturbation against the baseline scenario). We simulated these scenarios with no external forcing except for the perturbation detailed in Table 1. Predator–prey vulnerabilities were set at 2 (intermediate control) to avoid over-parameterization.

Apart from the simulation to increase our understanding of the drivers of the system dynamics, we also performed (1998–2015) hindcast simulations to evaluate the importance of various historical stressors to the monk seal population dynamics by selecting the best-fit model for monk seal biomass time series. Stressors included were (1) fishing with time series based on commercial fishery data, (2) environment with time series of the monthly PDO index as a multiplier for primary productivity, (3) additional mortality simulated with a constant removal of monk seals of varied intensities, and (4) combinations of these 3 stressors (Table 1). Time series data of monk seal biomass and benthic bottomfish biomass, as well as catch time series of bank sharks (only for FFS), benthic and demersal bottomfish, bank jacks, and macroheterotrophs (lobster) were loaded into Ecosim for model fitting. Additionally, we incrementally adjusted vulnerability values of important predator–prey linkages based on the results from the perturbation scenarios. We applied the Monte Carlo routine in Ecosim (Supplement 4) to select the best model considering the uncertainty in Ecopath input parameters. The best fit model was determined by minimizing the residuals between predicted and observed time series using a least-squares fitting criterion, which gave us a measure of fit as the sum of squared deviations (SS). Additionally, we calculated the Akaike's information criterion (AIC), which penalizes for fitting too many parameters based on the number of time series used for estimating the SS. AIC was calculated according to Scott et al. (2016):

$$\mathrm{AIC} = n \times \log(\mathrm{minSS} / n) + 2K \tag{1}$$

where n is the total number of loaded time series values, minSS is the minimum sum of squares from the Monte Carlo routine, and K is the number of parameters estimated (e.g. for FFS this was 71: 40 for 7 catch time series treating each catch year as an independent parameter and 31 for 2 biomass time series). Hence, the AIC value combines the goodness of fit of all time series (catch and biomass). To address the small sample size, we also calculated the corrected AIC ($\mathrm{AIC_c}$) (Scott et al. 2016):

$$\mathrm{AIC_c} = \mathrm{AIC} + 2K \times (K - 1) / (n - K - 1) \tag{2}$$

RESULTS

Fitting Ecopath food web model for Laysan

Pre-balance diagnostics for the Laysan Ecopath model (Supplement 6 in the Supplement) indicated that it conformed to general ecological principles, and that the model was suitable for balancing and dynamic applications with the input parameters (Link 2010). To mass balance the Laysan Ecopath model, we needed to make some adjustments. We increased the biomass of benthic bottomfish by 20% (from 0.180 to 0.215 t m^{-2}), which is still within the confidence limits (30%; Supplement 4 in the Supplement). The mass-balance Ecopath model showed that estimated monk seal biomass (0.0085 t km^{-2}) compared reasonably well with the observed biomass at Laysan (0.0074 t km^{-2}). However, reef shark biomass at Laysan was less well represented by the model with 0.1 t km^{-2} compared with 0.9 t km^{-2} from survey data (PIFSC unpubl. towed-diver data). This discrepancy could be because in general sharks are attracted to divers in non-fished areas; hence, diver surveys likely overestimate actual shark biomass (Richards et al. 2011).

Comparison of ecosystem structure and energy dynamics between FFS and Laysan

Static structural differences

A quantitative analysis of the ecosystem structure showed differences between the biomass per trophic level of FFS and Laysan; biomass was 4 times higher per trophic level for Laysan compared with FFS (Fig. 2). Predator biomass (tiger sharks and reef sharks) was 12 times higher, and food competitors' biomass (reef and bank jacks and sharks) was 9 times higher (Fig. 2). This higher productivity was partly sustained by a 5-fold higher benthic algal community in Laysan. However, the composition per trophic level was very similar (Table 3) indicating that the trophic structure was comparable between the 2 systems but the overall productivity was higher in the Laysan area.

Ecosystem indicators for the Laysan and FFS models (Table 3) show that the Laysan ecosystem structure may be more stable (mature sensu Odum 1969) than the FFS structure based on a higher net system production, lower production-to-respiration ratio, slightly higher energy flow from detritus, and a higher value for Finn's cycling index (Christensen et al. 2005). However, the transfer energy from primary

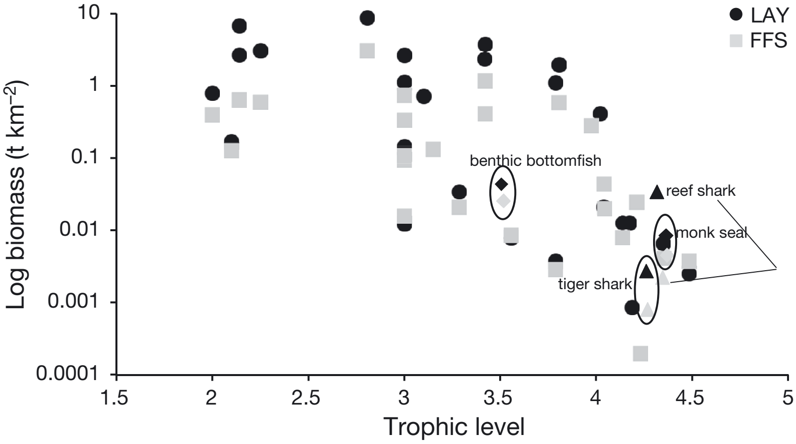

Fig. 2. Biomass density (t km^{-2}) of functional species groups at trophic level in the French Frigate Shoals (FFS, gray symbols) and Laysan (LAY, black symbols) modeled areas. Main prey (benthic bottomfish) and predators (tiger and reef sharks) of monk seals are indicated with different symbols as well as the monk seal biomass

Table 3. Ecosystem structure and energy flows for the Laysan and French Frigate Shoals ecosystem models

Ecosystem structure	Laysan		FFS	
Net system production (t km^{-2} yr^{-1})	85.51		64.53	
Total primary production/total respiration	1.13		1.50	
Throughput cycled (excl. detritus) (t km^{-2} yr^{-1})	145.21		27.02	
Finn's cycling index (% of total throughput)	15.91		10.80	
Predatory cycling index (% of throughput without detritus)	8.99		7.32	
Total transfer efficiency (%)	15.00		16.80	
Transfer efficiency from primary producers (%)	13.80		14.90	
Transfer efficiency from detritus (%)	17.40		20.90	
Energy flows (t km^{-2} yr^{-1})	Value	%	Value	%
Flow from primary production	726.3	0.67	194.1	0.75
Flow from phytoplankton	159.6	0.22	68.8	0.35
Flow from algae	566.7	0.78	125.3	0.65
Flow from detritus	359.6	0.33	65.7	0.25

producers was below 20%, indicating that most of the primary production is not directly used, but enters the food web through heterotrophic benthic organisms. The predator cycling index was very high, suggesting the importance of predation in the structure and functioning of these ecosystems at higher trophic levels.

Perturbation scenarios to evaluate food web structure and energy flows

The static structural differences between Laysan and FFS resulted in different system adjustments to the simulated perturbations. In general, bottom-up forcing was important for the ecosystem structure and energy flows in both models as is evident from the overall biomass increase of 512% (average of 16% per group) and 583% (average of 18% per group) in Laysan and FFS, respectively, with the simulated increase in primary productivity of 10%. Monk seals responded similarly to the change in productivity in the 2 areas (Fig. 3).

The Laysan system is secondarily influenced by predation. A 30% reduction in the biomass of the main monk seal predator (reef sharks) led to a 4% and 2% increase in monk seal biomass in Laysan and FFS, respectively. However, a 30% reduction in all main ecosystem predator groups (Supplement 5 in the Supplement) led to a counterintuitive 8% decrease in monk seal biomass in Laysan and a 2% increase in FFS (Fig. 4). In Laysan, release of predation pressure led to a 121% decrease in the monk seal prey biomass, including mesophotic piscivores (60%), benthic bottomfish (13%), and mesophotic forage fish (36%; Fig. 5). The same reduction in predators in FFS resulted in a combined reduction of just 16% in the prey groups (Fig. 5). This discrepancy between the 2 systems could be explained by the stronger energetic links between these prey groups and monk seals due to their higher biomass (Fig. 6). These results indicate that predators are an important structuring component of the biological community in Laysan but less so in FFS, which corresponds with the higher Finn's predator cycling index in the Laysan model (Table 3). In contrast, reef sharks play a bigger role (stronger energy pathway; Fig. 6) in structuring the monk seal population in FFS due to the larger proportion of monk seals in their diet compared with Laysan (0.6% in FFS versus 0.1% in Laysan).

The 30% decrease in mesophotic prey groups affected both systems similarly, with a 26% and 30% reduction in monk seal biomass in Laysan and FFS, respectively. The effect size was greater when the benthic bottomfish group was also reduced by 30% (Figs. 5 & 7).

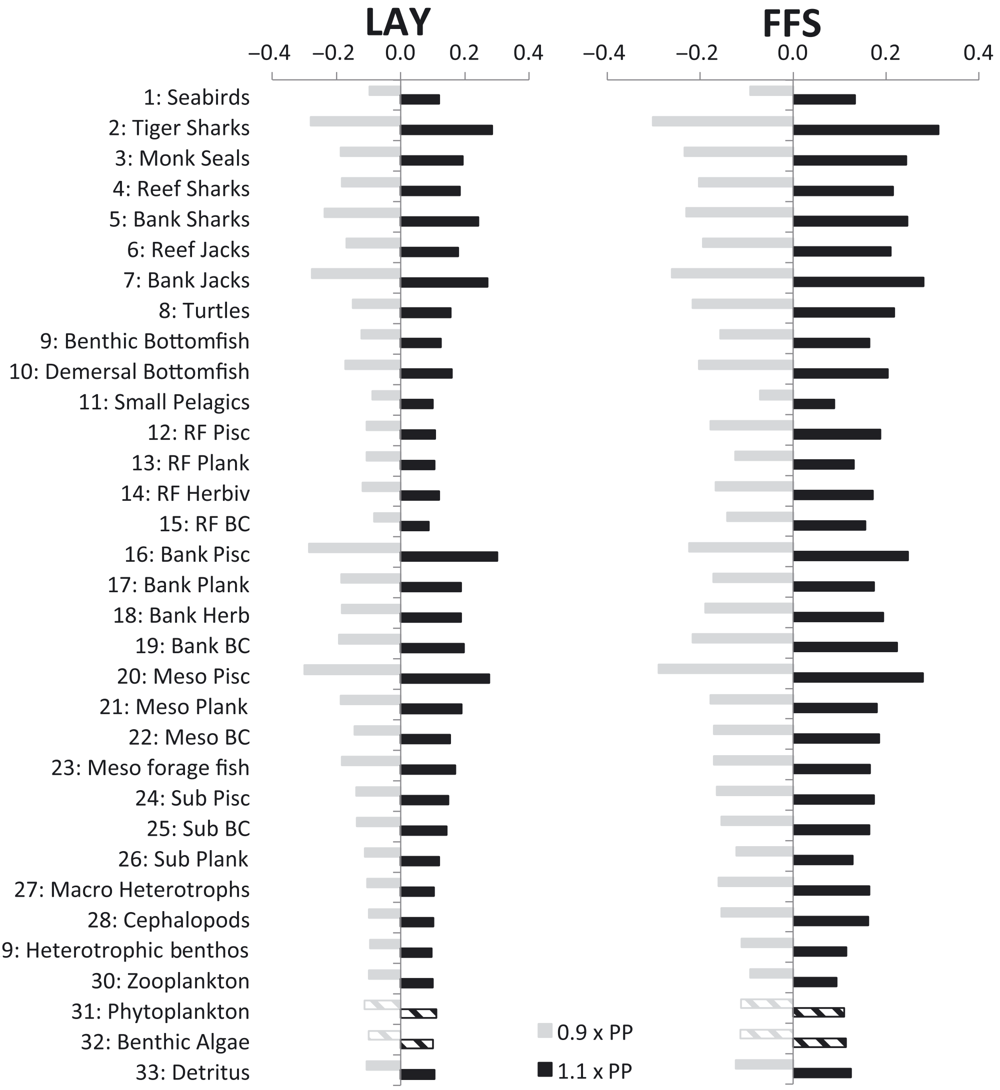

Fig. 3. Response ratio of functional groups to simulated perturbation of a 10% increase and decrease in primary productivity (PP; phytoplankton and benthic algae) in the Laysan (LAY) and French Frigate Shoals (FFS) ecosystems. Values are mean of last 5 yr of a 50-yr simulation of perturbation divided by baseline. Hatched bars represent groups with forced changes according to perturbation scenario. RF: reef; Meso: mesophotic; Sub: subphotic; BC: benthic carnivores

Hindcast simulations to evaluate importance of external drivers

The 2 systems responded differently to the external drivers. The best fit between predicted and observed monk seal biomass was explained by the (cessation of) fishery in Laysan and the cessation of fishery and a 1% additional monk seal mortality (Fig. 8, Table 4). Adding additional monk seal removals improved the fit for the benthic bottomfish trend while it stayed the same for the monk seal biomass. Adding the PDO forcing factor did not improve the Laysan model fit for monk seals or benthic bottomfish. At FFS, the best model in terms of monk seal and benthic bottomfish fit was driven by the fishery and an additional 7% removal of monk seals. (Fig. 9, Table 4). Adding the PDO as a forcing factor to the FFS model allowed us to lower the removal to 3%, but the model fit for both monk seals and (especially) benthic bottomfish decreased (Table 4). The best model based on the AIC_c value for FSS was also the model driven by fishery and a 7% additional monk seal removal (Table 4).

DISCUSSION

Ecosystem structure and dynamics comparison

Comparing the FFS and Laysan ecosystems was useful in elucidating consistent characteristics of

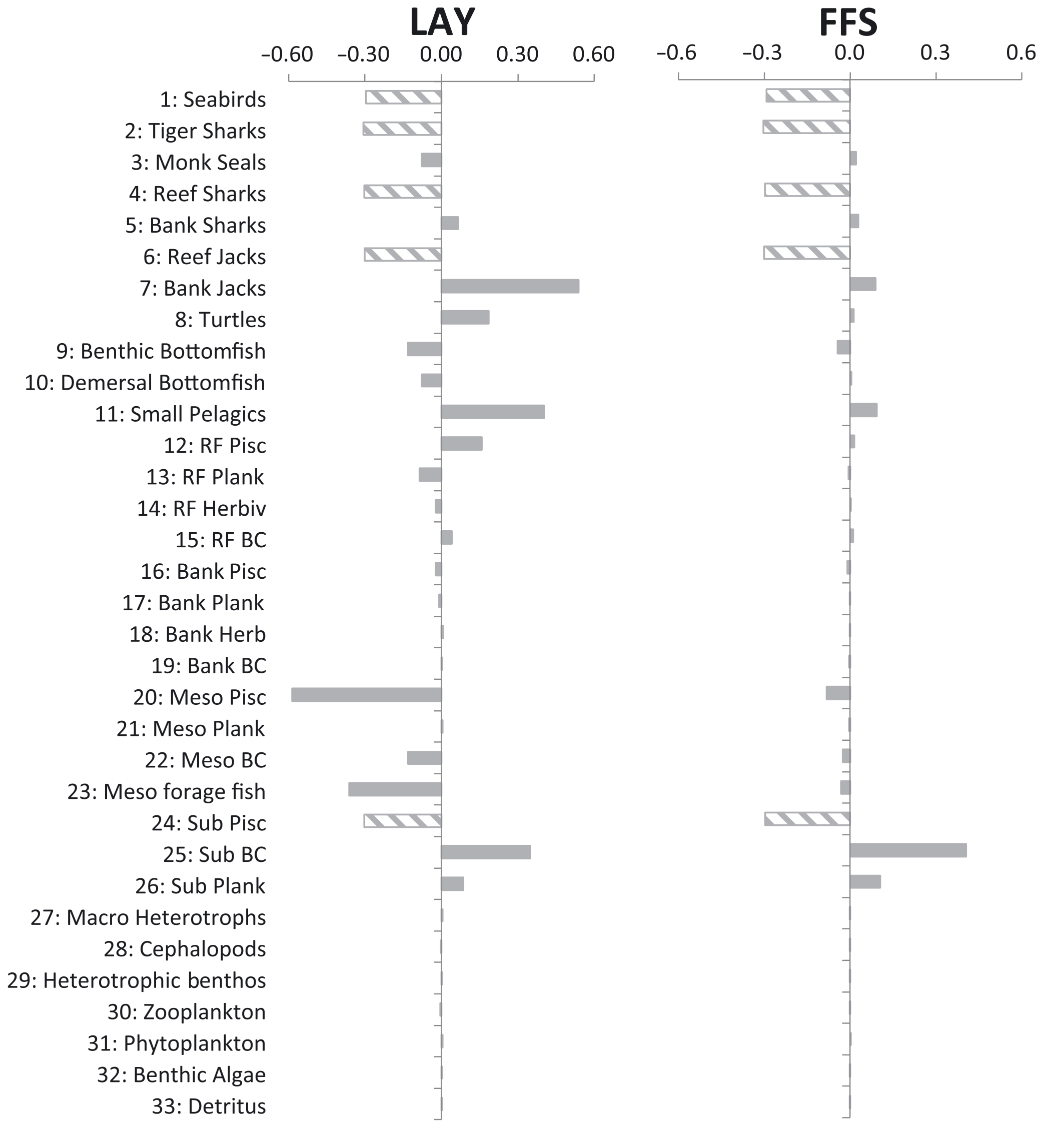

Fig. 4. Response ratio of functional groups to simulated reduction in biomass of predators (seabirds, tiger sharks, reef sharks, reef jacks, and subphotic piscivores) in the Laysan (LAY) and French Frigate Shoals (FFS) ecosystems. Hatched bars represent groups with forced 30% reductions according to perturbation scenario. RF: reef; Meso: mesophotic; Sub: subphotic; BC: benthic carnivores

these ecosystems versus variations that may influence population trends. While overall community composition and trophic structure were similar, the higher productivity and higher energy cycling at Laysan provides insights as to why this site might support more seals per area and showed greater stability despite environmental fluxes. In addition to impacts on the total carrying capacity, the evidence of low productivity at FFS is seen in the growth and development of animals, with high rates of juvenile emaciation (Craig & Ragen 1999, Baker & Thompson 2007) and with FFS females showing delayed age at breeding maturity compared with Laysan (Harting et al. 2007, Baker et al. 2014). While differences in ecosystem productivity and structure help explain differences in capacity of the 2 systems, we looked toward perturbations and other drivers to explain dynamic trajectories over time.

The perturbation scenarios showed that both systems were largely governed by similar bottom-up forcings; however, we saw a different response to decreasing top predators. Because the Laysan system supported higher predator populations (Fig. 6), its ecosystem structure was more influenced by predators than FFS. Cascading effects of predator removal had a negative impact on monk seal populations at Laysan, whereas release from predation and competition led to minor but positive impacts at FFS (Fig. 4).

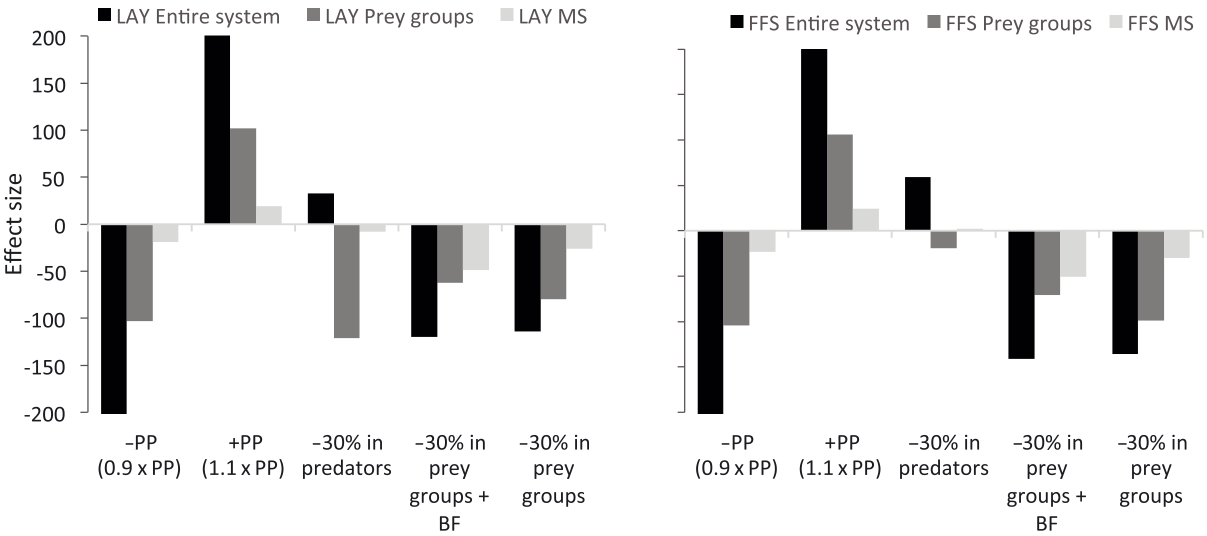

Fig. 5. Effect size of ecosystem perturbation at the end of a 50-yr simulation in the Laysan (LAY) and French Frigate Shoals (FFS) ecosystems. Effect size is calculated as mean of the last 5 yr of perturbation scenario divided by mean of last 5 yr of base scenario (no perturbation). Values are percentages in net changed biomass of functional groups (not incorporating forced declines). Predators were seabirds, tiger sharks, reef sharks, reef jacks, and subphotic piscivores. Prey groups were mesophotic benthic carnivores, mesophotic planktivores, and mesophotic forage fish. BF: benthic bottomfish; MS: monk seal biomass; PP: primary producers (phytoplankton and benthic algae)

This finding suggests that predators have a large but completely different influence on the ecosystem structure with likely trophic cascading effects leading to a decline in monk seal biomass because of prey reductions at Laysan. In FFS, predators (including higher predation on monk seals compared with Laysan) played an important role in the decrease of the monk seal population, and the removal of predation pressure led to a stable or even slightly increasing population.

External drivers

Benthic bottomfish fishery

Given the importance of bottomfish in the monk seal diet, it can be expected that monk seal trends tracked benthic bottomfish removals and projected recovery (after fishing closure). The food web models demonstrated the importance of fish removals in decreasing the systems' capacity to support monk seals. We should note that, because the fishery time series ended when the fishery closed, bottomfish recovery was predicted based on vital rate parameters and predator–prey interactions. Future bottomfish population monitoring data will be valuable in confirming the model-predicted trend.

In the model, the diet matrix determines the influence of a diet item as a driver on its predator. Studies using differing methods to analyze diet components have indicated variable importance of benthic bottomfish vs. other prey items in the monk seal diet. For example, while the fatty acid analyses relied on in this study suggest benthic bottomfish make up as much as 49.5% of the diet (Iverson et al. 2011), analyses of fecal remains suggest that reef fish are far more important (40% reef groups vs. 1.5% benthic bottomfish; Goodman-Lowe 1998, Longenecker et al. 2006). Both fecal and fatty acid analyses have their potential biases. Fecal analysis may be biased toward the meals most recently eaten near shore where feces can be collected (thus biasing toward shallow-water reef fish). Fatty acid analysis relies on mixture models based on extensive prey libraries, and unsampled prey could lead to false assignments of fatty acid signatures (Bowen & Iverson 2013). While both fecal and fatty acid analysis can have biases, fatty acid analysis is thought to better represent the prey that was actually consumed and incorporated into tissue (Iverson et al. 2004) and showed better model fits (Supplement 7 in the Supplement)

PDO

Despite the importance of primary productivity (each modeled ecosystem showed strong bottom-up forcing), PDO did not appear to be a major driver underlying variation observed in these ecosystems.

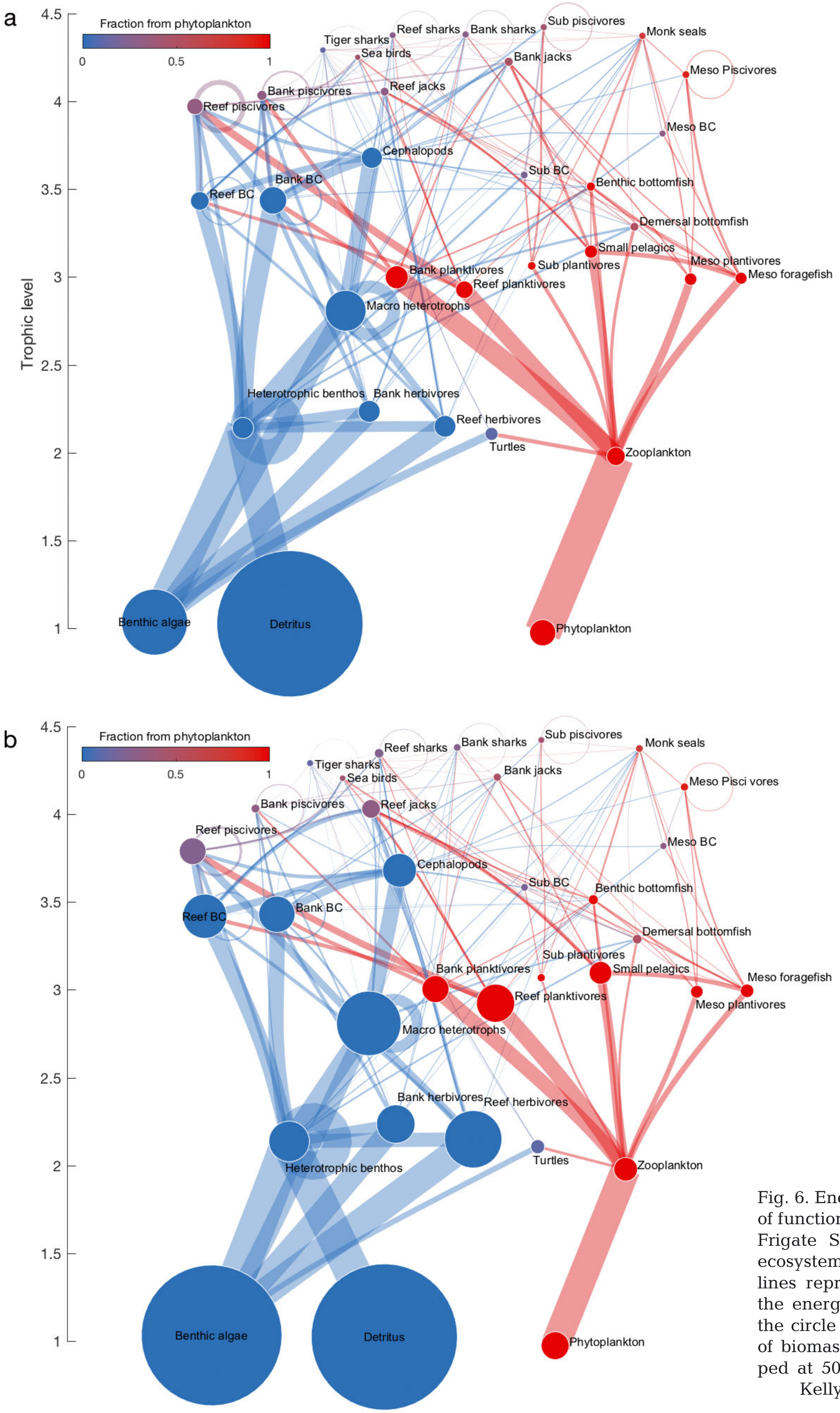

Fig. 6. Energy flows and biomass of functional groups in (a) French Frigate Shoals and (b) Laysan ecosystems. The thickness of the lines represents the strength of the energy pathway, the size of the circle represents the amount of biomass. Circle size was capped at 50 t km^{-2}. Figure credit: Kelly Kearney (NOAA)

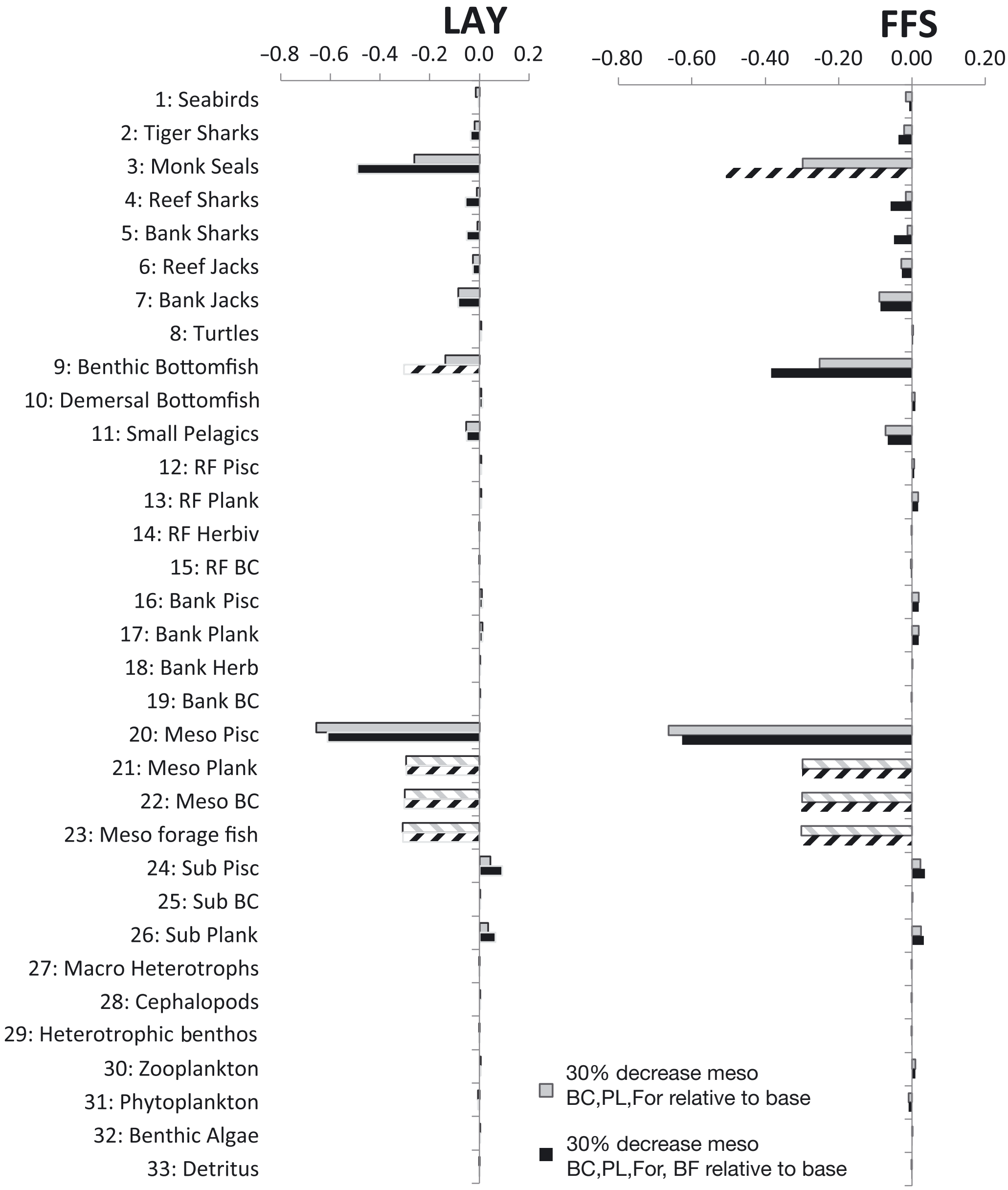

Fig. 7. Response ratio of functional groups to a 30 % decrease of mesophotic prey groups (dark bars) and an additional 30 % decrease in benthic bottomfish (BF, light bars) in the Laysan (LAY) and French Frigate Shoals (FFS) ecosystems. RF: reef; Meso: mesophotic; Sub: subphotic; BC: benthic carnivores; PL: planktivores; For: forage fish. Hatched bars represent groups with forced 30 % reductions according to perturbation scenario

The addition of the PDO to the Laysan model provided only mild improvement to the fit for monk seals once the food web and benthic bottomfish dynamics were accounted for; however, the AIC_c (which is based on 5 catch and 2 biomass time series) was lower primarily as a result of the better fit for benthic bottomfish, suggesting that the PDO is of minor importance (Table 4). The PDO appeared to greatly improve the fit for monk seals in the FFS model; however, it showed a very poor fit for observed benthic bottomfish trends, indicating that the modeled mechanism of PDO driving primary productivity was a poor fit for this system overall. Additionally, as discussed below, the model incorporating an additional monk seal removal provided the best fit to observed time series for both monk seals and benthic bottomfish. The PDO forcing factor in the model may not capture the mechanisms of primary productivity fluctuations or it may not have strong enough effects in this portion of the NWHI chain to increase productivity enough to elicit a response.

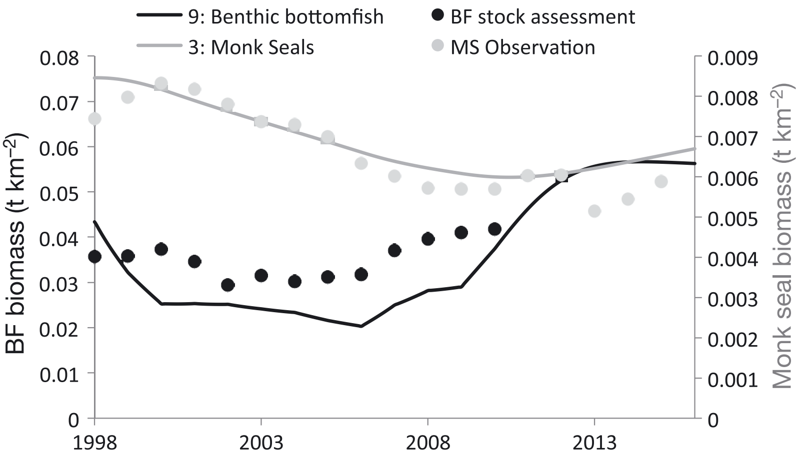

Fig. 8. Biomass trajectories for monk seal (MS) and benthic bottomfish (BF) at Laysan. Projections (solid lines) and observational data (dots) for a hindcast simulation using Ecosim with drivers based on historic fisheries. Vulnerabilities were manually adjusted to reach best fit

This finding represents an important contrast from the results of previous ecosystem models for FFS (Parrish et al. 2012). Additional data since the 2012 study provide some explanation for this difference. First, oceanographic patterns suggest that the increase in productivity from the PDO may not be expected to reach as far southeast as FFS (Polovina et al. 2017). Further, Baker et al. (2012) found that the PDO index was a poor correlate for observed monk seal trends in this region. The addition of a second study system, Laysan, provided greater context in which to evaluate the models for FFS, lending further credibility to the idea that the PDO influence may be minor and monk seal declines were better addressed through additional removals. Though not represented well by the PDO as a productivity forcing factor, climate and oceanographic factors are still likely to impact these systems. For example, Antonelis et al. (2003) found that FFS pups weaned at larger girths in El Niño-Southern Oscillation years.

Additional monk seal biomass reduction

While much of the slow decline in Laysan monk seals could be explained by benthic bottomfish trends, a 1% removal factor improved model fit for monk seals. This small reduction factor may be explained by mortality sources not well captured in the model, which could include marine debris entanglements. A 7% reduction was required to fit the steeper decline in monk seals at FFS and gave a better model fit (both for monk seals and bottomfish) than models incorporating the PDO even when also including the reduction. Moreover, the 6-point difference in AIC$_c$ indicated strong support for the 7% reduction and fishery model over competing models. Though post hoc, the effort to explain this reduction forces us to examine potential changes in the system or mortality sources that might not be well incorporated in the food web model. One potential limitation of the Ecosim model is that all biomass is treated equally, whereas in the

Table 4. Model fits for monk seals and benthic bottomfish under simulation of different external drivers. For the middle 2 columns, goodness of fit was based on the sum of squared deviations calculated by the Ecopath with Ecosim software, the last column gives an overall goodness of fit including the fit for monk seal and bottomfish. Scenarios in *italic* are the ones with the best fit for monk seals for Laysan and French Frigate Shoals. Vulnerability was minimally changed to obtain best fit for each scenario simulation. AIC$_c$: corrected Akaike's information criterion

External driver(s)	Model fit for monk seals	Model fit for bottomfish	Model fit overall (AIC$_c$)
Laysan			
Fishery	*0.07*	1.76	−20.29
Additional removal of 1%	0.78	0.68	−22.38
PDO	0.41	3.47	−16.52
Fishery + Additional removal of 1%	*0.07*	*0.68*	*−23.91*
Fishery + PDO	0.25	3.35	−19.82
Fishery + PDO + Additional removal of 1%	0.23	3.37	−23.10
French Frigate Shoals			
Fishery	1.09	15.08	−21.24
Additional removal of 7%	0.06	0.19	−31.65
PDO	0.91	7.05	−22.30
Fishery + Additional removal of 7%	*0.03*	*0.16*	*−37.61*
Fishery + PDO	0.09	16.38	−25.74
Fishery + PDO + Additional removal of 3%	0.09	5.2	−30.26

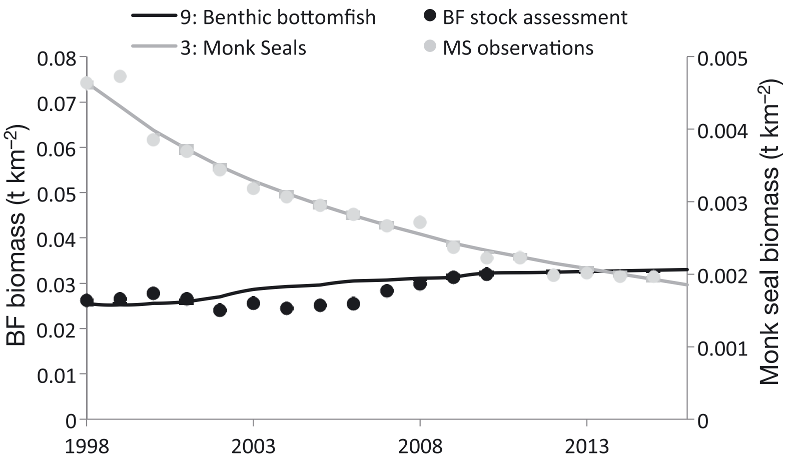

Fig. 9. Biomass trajectories for monk seal (MS) and benthic bottomfish (BF) at French Frigate Shoals. Projections (solid lines) and observational data (dots) for a hindcast simulation using Ecosim with drivers based on historic fisheries and an additional removal of 7% of monk seal biomass per year. Vulnerabilities were manually adjusted to reach best fit

actual population, some biomass losses may have a disproportionate effect on population dynamics and biomass trends in subsequent years. For example, the high shark predation observed at FFS specifically impacts pups (lowest biomass loss per mortality), but these heavy losses of pup recruitment lead to a skewed age structure and loss of breeding potential that may lead to compounding losses for the population (Harting 2010). The perturbation simulation of a 30% decrease in predators that led to a slight increase in monk seals in FFS supports the important role predators play in structuring the monk seal population dynamics in FFS. While our perturbation scenarios indicate that even substantial decreases in primary productivity could not produce the level of decline observed, much lower predator levels at FFS may have allowed the monk seal population to remain stable. Other changes in the FFS system not captured in the dataset could also be responsible for this apparent removal. For instance, declines in prey species could play an important role. Updating survey information for species at many levels in this food web (we only had time series for commercially harvested species to 2009) would be important in further resolving the drivers of this decline.

CONCLUSIONS

Comparison of ecosystem models for 2 systems was useful in understanding fine-scale variations in the NWHI ecosystems and other important factors in the Hawaiian monk seal's decline. Expanding the modeling scope from previous efforts allowed for additional hypothesis testing and improved context for interpretation. We clarified the role of the PDO in driving monk seal dynamics, which appears less than previously suggested by Parrish et al. (2012) at FFS. Instead, we suggest that other factors amplifying mortality played a larger role than the PDO. Fitting the model-derived values for monk seal removal was instructive in identifying data gaps and potential mortality sources; results showed that mitigating shark predation could be a crucial step in slowing the decline of monk seals at FFS and merits further research.

This modeling exercise was valuable for the evaluation of management options. Confirming the limited influence of the PDO at these southern monk seal sites diminishes what might have been a predictive tool (if managers could optimize actions such as animal translocations according to oceanographic data). However, the perturbation scenarios demonstrated the utility of the modeling tools for illuminating complex interactions and evaluating the system-specific impacts of modifications (such as predator removals) that may occur through management actions or resource removals.

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