

Integrating diet and movement data to identify hot spots of predation risk and areas of conservation concern for endangered species

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Abstract

Effective management of threatened and endangered species requires an understanding of how species of conservation concern are distributed spatially, as well as the spatial distribution of risks to the population, such as predation or human impacts (fishing, pollution, and loss of habitat). Identifying high-risk areas is particularly important when designing reserves or protected areas. Our novel approach incorporates data on distribution, movement, and diet of a generalist marine predator (harbor seals) to identify and map “hot spots” of predation risk for an endangered prey species (rockfish). Areas with high concentrations of seals (including some current marine reserves) are also estimated hot spots for rockfish predation. Although marine reserve planning currently targets areas with good habitat and low human disturbance, our modeling suggests that future terrestrial and marine reserve design may be made more effective by incorporating other components of the food web that either directly or indirectly interact with target species.

Introduction

Conservation and recovery of protected species is increasingly characterized by conflicts among species (Roemer & Wayne 2003). Successful management requires understanding the nature of conflicts and the development of strategies to address trade-offs among species. The range of interactions is as rich as the endangered species themselves, including competition (Livezey 2010), parasitism (Rothstein & Cook 2000), and habitat alteration (e.g., Garcia *et al.* 2011). Conflicts between protected predators and prey seem to engender the most discussion, perhaps because of the public value of predators (Martin-Lopez *et al.* 2008). For example, the endangered San Clemente loggerhead shrike is threatened by predation by the San Clemente Island fox, a “species of concern” under the US Endangered Species Act (ESA; Roemer & Wayne 2003). Similarly, predation by birds (Good *et al.* 2007) and seals

(Wright *et al.* 2007) have been implicated as a factor preventing recovery of ESA-listed salmon in the Columbia River basin.

In this article, we explore potential conflicts between recovery of depleted rockfish (*Sebastes* spp.) and a generalist predator, harbor seals (*Phoca vitulina*). In 1999, 13 species of rockfish were petitioned for ESA listing in Puget Sound, USA. In 2010, one of these (bocaccio, *S. paucispinis*) was listed as endangered and two (canary rockfish, *S. pinniger* and yelloweye rockfish, *S. ruberrimus*) were listed as threatened. Three additional rockfishes (brown rockfish, *S. auriculatus*; copper rockfish, *S. caurinus*; and quillback rockfish, *S. maliger*) are now considered federal species of concern, and the remaining seven species are listed as species of concern by the state of Washington (Palsson *et al.* 2009). Conflicts between harbor seals and the abundance of their commercially valuable prey have

been recognized across multiple continents for centuries (Perrin *et al.* 2002); on the Pacific coast of the United States, state-funded hunts designed to control population levels continued through the 1960s. In Washington State, approximately 17,000 seals were harvested from 1943 to 1960 (Newby 1973). All seal harvests stopped after the 1972 Marine Mammal Protection Act (MMPA), and in the absence of significant predation, numbers of harbor seals in Puget Sound and the adjacent Strait of Georgia have increased exponentially, from several thousand in 1970 to more than 39,000 in recent years (Jeffries *et al.* 2003; DFO 2010).

The decline of rockfish in Puget Sound was clearly the result of historical overfishing (Williams *et al.* 2010), but other factors, including predation, have been implicated as causes for a lack of recovery (Palsson *et al.* 2009; Drake *et al.* 2010). Even a 1.2% increase in predation mortality on juvenile rockfish has been shown to eliminate any benefit from a fishing moratorium (Ruckelshaus 2009). Like other slow growing vertebrate species, the life histories of rockfishes (Palsson *et al.* 2009) make them particularly susceptible to effects of increased mortality, as a result of fishing or predation by marine mammals or other fishes, such as lingcod (Beadreau & Essington 2007).

As predators, seals are super-generalists. Because rockfishes are not a dominant item in their diet (Lance & Jeffries 2007), their rarity means that spatial patterns of seal predation are ostensibly dictated by other, more common, prey. Consequently, the spatial pattern of rockfish recovery may be indirectly mediated by the combined dynamics of a prey assemblage and their shared predator (DeCesare *et al.* 2010). For example, rockfish in locations with high densities of salmon (a preferred prey of seals in summer months; Lance & Jeffries 2007) may experience greater rates of mortality than in regions with lower salmon densities. Understanding patterns and causes of spatial variability in predation pressure is increasingly important as ocean-use policy moves toward spatial management (Lubchenco & Sutley 2010). Marine spatial planning requires that we protect marine species and resources in a manner that decreases conflicts (Crowder & Norse 2008), and it is clear that an essential part of this planning must be consideration of predator–prey interactions (Mangel & Levin 2005).

A key element of marine spatial planning is marine protected areas (MPAs)—regions where fishing is restricted to some degree. Currently, the state of Washington manages 123 MPAs with restricted fishing, and 20 MPAs that prohibit all fishing (Van Cleve *et al.* 2009). MPAs have been proposed as important management components for rockfish in Puget Sound (WDFW 2010) because they can positively influence rockfish abundance. However, the efficacy of MPAs for rockfish

recovery may ultimately depend on their location relative to foraging patterns of their predators.

In this article, we integrated data on seal movement and diet to develop predictions of the spatial distribution of the predation risk on rockfish. We first asked what proportion of the seal diet is comprised of rockfish, and how this varies seasonally and annually. Second, we used data from satellite tagged seals to develop a hierarchical Bayesian movement model with multiple foraging states (traveling, resting), to describe harbor seal movement behavior. Finally, using data on the spatial distribution of harbor seals, their diet and movement behavior, we constructed maps of rockfish predation risk in Puget Sound.

Methods

Quantifying intra- and interannual variation in harbor seal diet

To quantify harbor seal diet, we collected 1,686 scat samples from harbor seals in the vicinity of the San Juan Islands, during 2005–2008 (Lance & Jeffries 2007; Figure 1; Appendix). We concentrated on this region because the largest component of the harbor seal population in Washington State is aggregated there at terrestrial haul-out sites (Figure 2; Jeffries *et al.* 2003; Lance & Jeffries 2007). Scat samples were collected throughout the year, with the majority occurring in spring ($n = 358$) and summer ($n = 1,190$) months. Identification to the species level was not possible for all of the recovered fish bones and otoliths, so prey were aggregated into broader taxonomic groupings (Lance & Jeffries 2007). For the purpose of this analysis, we considered four prey groups (“salmon,” “gadids,” “herring,” and “rockfish”).

Previous studies have recognized the importance of salmon in harbor seal diets (Scordino 2010); although five species may be found in and around Puget Sound, pink salmon (*Oncorhynchus gorbuscha*) are consumed most frequently (Lance & Jeffries 2006; Appendix). Pink salmon are typically smaller than other salmon, but larger than the majority of nonsalmon species, such as Pacific herring (*Clupea pallasii*). Pink salmon have a strict 2-year life cycle, and in the Puget Sound region, are only available as prey during the odd years (Quinn 2005). To account for the importance of pink salmon, scat samples were aggregated into years when pink salmon were absent (2006, 2008) and years with pink salmon present (2005, 2007).

Collecting seal movement and behavior data

To estimate the movement behavior of individual seals, 36 harbor seals were tagged in 2007–2008. Adult harbor

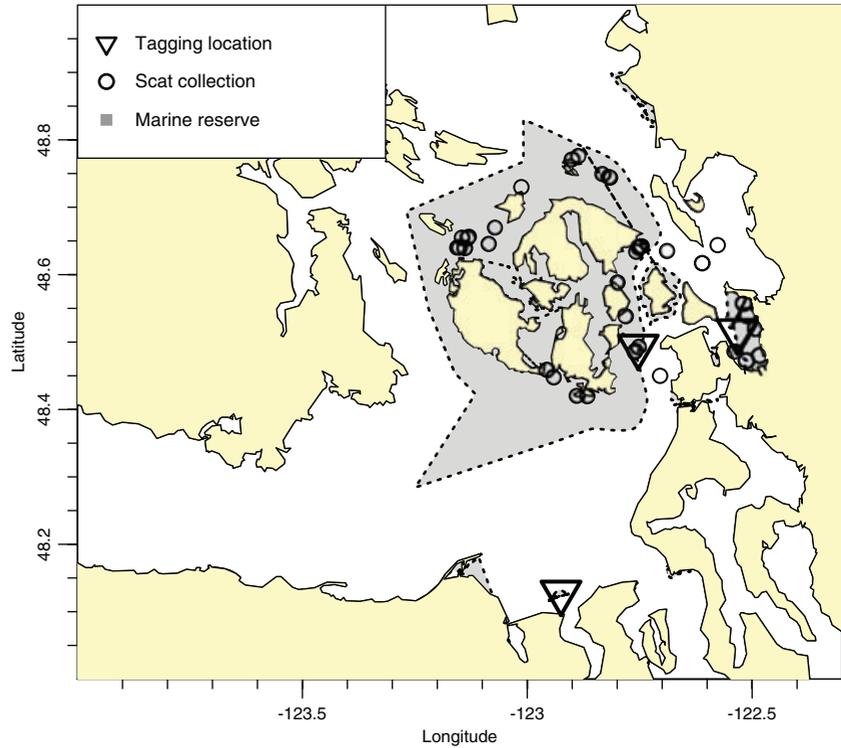


Figure 1 Map of locations in Washington State (San Juan Islands) where harbor seals were tagged for our tracking study, and where scat samples were collected. The gray region represents the extent of marine protected areas in the region.

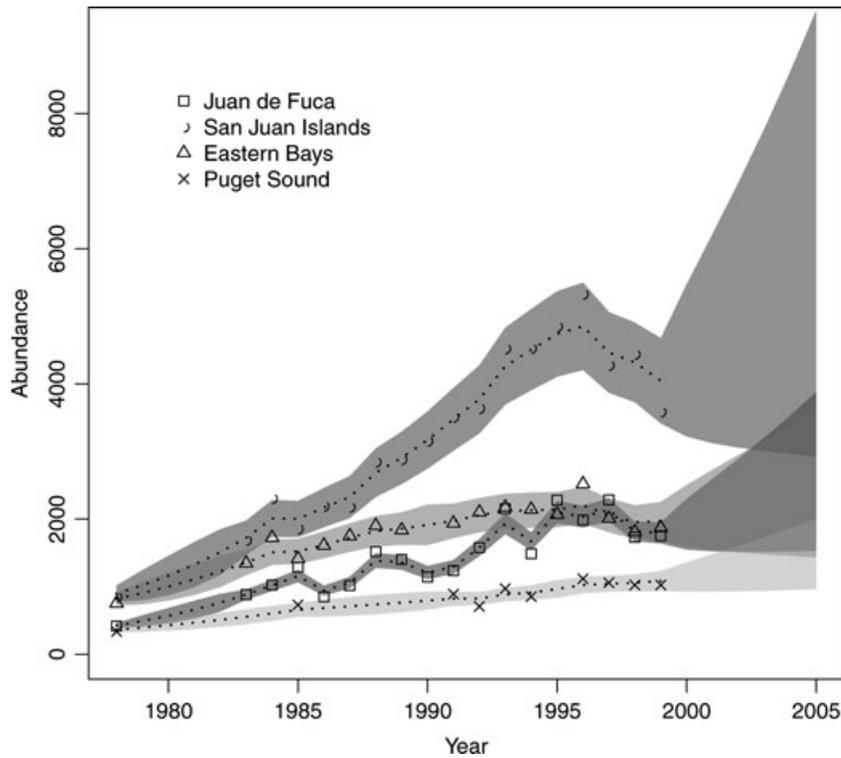


Figure 2 Historical abundance of harbor seals in four subregions of inland Washington waters (Eastern Bays, Puget Sound, Strait of Juan de Fuca, and San Juan Islands). Abundance estimates are given as points, and the state-space model estimates are indicated as dotted lines (shaded regions represent 95% confidence intervals).

seals were captured at three sites: Padilla Bay, Bird/Belle Rocks, and Protection Island (Figure 1). Seals were tagged with time-depth recorders, and satellite tags glued to the pelage of the animal. Data from individual seals was collected by orbiting Argos satellites (Landover, MD; further details in the Appendix).

Modeling harbor seal movement

Correlated random walk models have been widely used to describe the distributions of the lengths and turning angles that describe the trajectory of an individual across a landscape (Turchin 1998). In the last decade, these models have evolved statistically to estimate uncertainty in both observation error (representing errors in measurements, such as those caused by errors in GPS receivers), and process variance (representing the stochastic nature of movement; Jonsen *et al.* 2005). These state-space movement models have become ubiquitous because of their ability to partition these two types of uncertainty, resulting in more precise prediction of locations (Jonsen *et al.* 2005; Patterson *et al.* 2008). A second advancement in movement models has been the development of state-space switching models (SSSMs), where at each time step individuals are allowed to transition between multiple latent categorical states (Morales *et al.* 2004; Eckert *et al.* 2008). For the analysis of our harbor seal movement data, we fit models with two states, representing fast and slow movement, corresponding to periods of seals resting (generally on land, at haul-out sites), or traveling (further details in the Appendix).

Building on previous applications of Bayesian SSSMs, we extend the SSSM modeling framework to be hierarchical for the 36 seals in our analysis. At each time step, each seal was allowed to have a unique movement state (traveling/foraging or resting). Locations were allowed to be independent, but movement rates for each seal were drawn from a shared, global distribution of movement rates across seals. For individual i at time t in state s , velocity was modeled as $\log(v_{i,t,s}) \sim \text{Normal}(a_{i,s}, b_s)$, where $a_{i,s}$ is an individual and state-specific parameter representing mean movement, and b_s is a state-specific variance (shared among individuals). Mean movements were modeled as hierarchical random effects, so that $a_{i,s} \sim \text{Normal}(u_s, \sigma_s)$. The global hyper-parameters (u_s, σ_s) allow us to estimate the variability among all seals for each movement state. Thus, for the 36 seals in our analysis, we estimated 36 individual deviations in mean movement from the global mean for each of the two movement states.

We also extended previous SSSM models to include random effects in transition probabilities between fast/slow movement states. Treating these probabilities as

being drawn from a common distribution assumes similar behavioral traits among seals. By analyzing all seals simultaneously, we are able to allow some parameters, such as observation error variance, to be shared among individuals.

Constructing maps of predation risk

Because the majority of seal scat samples are collected in August and September, we constructed maps of predation risk for these late summer months. The first step in creating maps of predation risk involved distributing seals according to their relative abundances. Simulated populations were initialized by resampling known haul-out locations of seals in Washington State (Jeffries *et al.* 2000); these locations were drawn with replacement and weighted by the estimated abundance at each haul-out site (Jeffries *et al.* 2000). For each seal, we projected movement over a 60-day window, by resampling from the global posterior distributions of estimated movement rates (e.g., u_s, σ_s) and transition probabilities.

The second component of creating maps of predation risk involved simulating the frequency of rockfish in harbor seal diets. Given the estimated frequency of rockfish in summer months (Figure 3), we simulated diets in two scenarios: years with pink salmon present (odd years) and years without pink salmon (even years). At each simulated location, we sampled a random proportion according to the estimated mean and standard error (Figure 3). Locations were then divided into a 200×200 cell grid, and the mean frequency of rockfish of occurrence was calculated for each cell.

Results

Harbor seal diet

Herring, salmon, and gadids (Pacific cod, hake, and wall-eye Pollock) occurred frequently in harbor seal diets (Figure 3). In spring, approximately 80% of harbor seal scat samples included herring, and in contrast, salmon occurred in less than 10% of the spring scat samples. In summer months, the frequency of harbor seal scat sample containing salmon increased fivefold, although the frequency of herring in scat samples declined by half (Figure 3).

Although summer consumption of salmon is high in all years, salmon occurs in 63% of seal scats in years with pink salmon and 49% of scats in years without pink salmon (Figure 3). In years when pink salmon were absent from Puget Sound, this decrease in salmon consumption is accompanied by an increase in the frequency of occurrence of other species, including gadids and

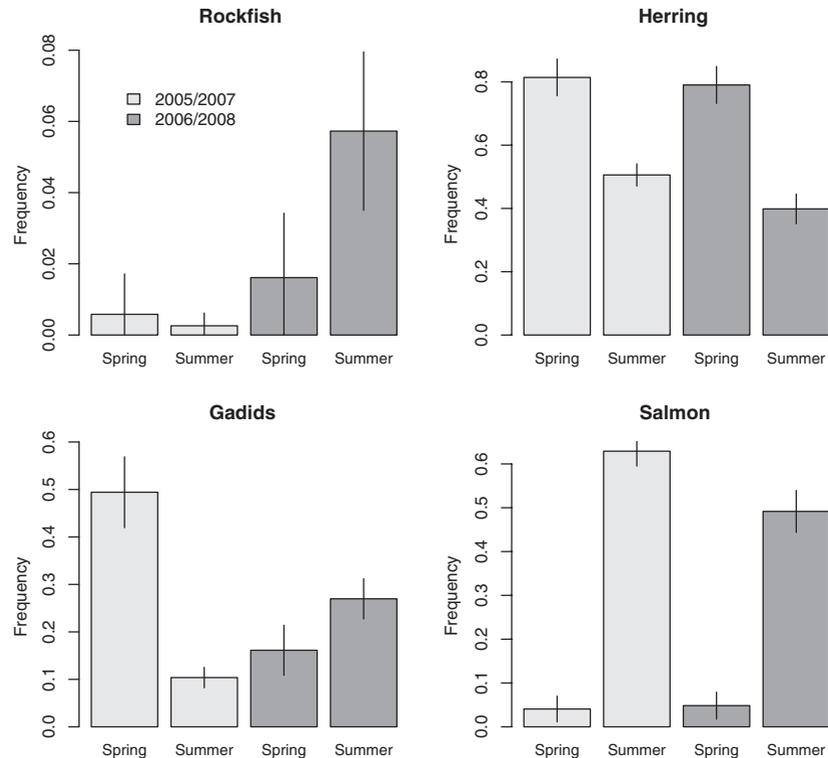


Figure 3 Estimated relative diet contribution of four fish species to harbor seal diet. Estimates represent the frequency of occurrences in collected scat samples (note: most plots have different y-axes). Data are combined into years with pink salmon present (odd years) and years when pink salmon are absent (even years), and are stratified within a year (spring and summer). Mean estimates are given, with 95% confidence intervals.

rockfishes (Figure 3). The increase in the frequency of rockfish is particularly large, approximately 22 times higher. In years when pink salmon are not present, salmon continues to be present in seal diets because of the consumption of other species.

Harbor seal movement

The raw satellite location data revealed a diversity of movement behavior, including potential mixing of previously identified stocks (Jeffries *et al.* 2003). Of the 36-tagged seals, several made roundtrip foraging trips >200 km, from the location of the tagging (Figure 1) to the Pacific outer coast. Previous analyses have shown differences in movement or range size are not influenced by sex or season (Hardee 2008). When harbor seals are in a traveling behavioral mode, our hierarchical Bayesian SSSM model estimated global mean movement rates that ranged from 0.7 to 4.1 m/s with a median of 2.2 m/s. The upper bound of our estimates is consistent with maximum burst velocities observed in laboratory settings (~4.9 m/s, Figure 4; Williams & Kooyman 1985). When in a resting state, estimated mean movement rates ranged from 0 to 0.3 m/s with a median of 0.1 m/s.

The mean transition probabilities from the fast to slow state was 4.6%, and from the slow to fast state 8.1% (Figure 4). These transition probabilities may be used to calculate geometric waiting times to estimate the amount of

time seals spend foraging. For example, an average “fast” trip (representing traveling and feeding) would be expected to last 21.7 hours ($1/0.046$), and an average “slow” trip (representing resting) would be expected to last 12.3 hours ($1/0.081$).

Spatial distribution of predation risk

By integrating diet, movement, and distribution data of harbor seals, we were able to generate predictions about the spatial pattern of predation risk on rockfish. In general, the highest risk of predation was associated with the highest densities of harbor seal haul-out sites. Thus, our simulation maps indicated relatively low predation risk to rockfish in south Puget Sound (Figure 5c and d) and the Strait of Juan de Fuca (Figure 6c and d). In contrast, high relative predation risk occurred in the San Juan Islands (Figure 6a and b), corresponding to the highest density of haul-out sites. Average home range sizes of seals (266–862 km²; Hardee 2008) were at least an order magnitude larger than the average area of marine reserves in Washington State (21.9 km²; Van Cleve 2009). Although the spatial variability in predation risk is important, there are large differences between years with and without pink salmon (odd and even years, respectively). The change in relative predation risk between odd and even years may be highest for areas with low risk to

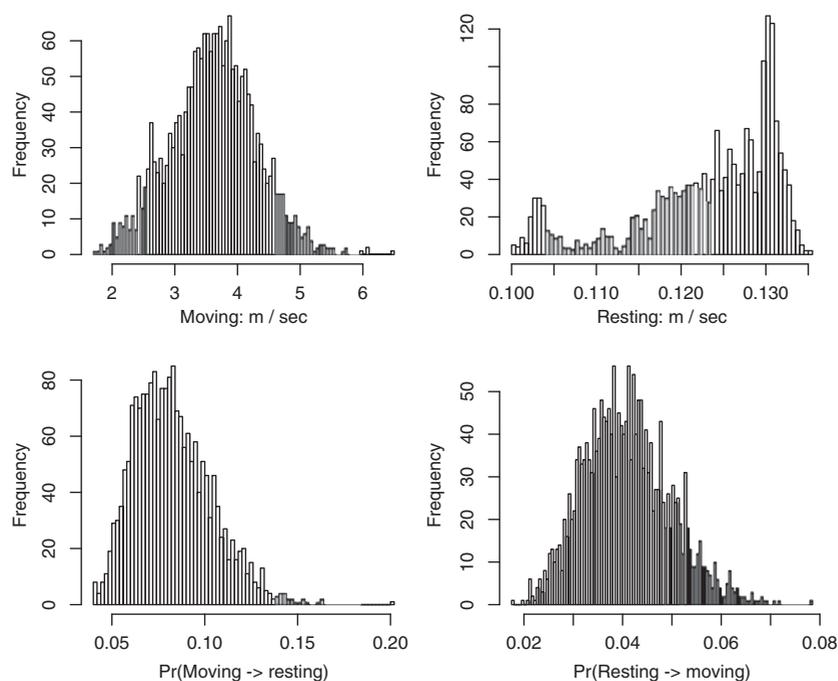


Figure 4 Posterior distributions of movement rates and transition probabilities for one seal from the hierarchical Bayesian state-space switching model. The two movement rates (m/sec) represent traveling and nontraveling behaviors. The transition probabilities represent the probabilities of changing behavior at each time step (hourly).

begin with (south Puget Sound and Strait of Juan de Fuca; Figures 5 and 6). In years without pink salmon, predation risk to rockfish becomes >20 times higher (Figure 3)—but these changes may be significantly increased by the dispersal of seals from high density (San Juan Islands) to low density areas.

Discussion

As countries around the globe move to adopt marine spatial planning as a means to manage ocean resources (Foley *et al.* 2010), it is increasingly important to understand spatial variability in species interactions. Here, we developed predictions of the spatial distribution of predation risk by harbor seals on threatened and endangered rockfish by integrating diet data with seal movement. Given the potential importance of predation in the ecology of MPAs (Babcock *et al.* 2010) and for rockfish recovery (Drake *et al.* 2010), understanding how predation risk varies is critical for conservation planning. Although our approach includes detailed data on individual movement, this framework could be generalized to more poor data situations by using knowledge about home range size, or by using proxies for predator density (such as density of haul-out sites).

Our results highlight two important considerations relevant for conservation planning. First, salmon, herring, and gadid fishes are dominant prey items of harbor seals (Lance & Jeffries 2007; Figure 3), suggesting that the distribution of these prey species may determine both

the spatial distribution of seals and spatial distribution of seal predation on rockfish. Because prey species like pink salmon are highly migratory and have a complex life cycle making them abundant every other year, the efficacy of spatial planning may be improved by also considering a temporal dimension. For instance, the reserve boundaries or harvest regulations could be allowed to change both seasonally and between years. Typically, MPA planning considers a suite of sociological, economic, and biological factors (such as diversity; Van Cleve *et al.* 2009). When assemblages of species are targeted for conservation, specific factors may include larval dispersal, habitat preference, or adult movement (Gleason *et al.* 2010). Our results suggest MPA planning for rockfish recovery would be served by moving beyond single species traits and by also considering the distribution of species that indirectly interact with rockfish via shared predators.

Spatial planning will likely benefit by considering how these interactions change over time. For example, of the 127 MPAs in Washington State, at least 43% were established before the passage of the MMPA, when seal predation was greatly diminished. Thus, historically, an analysis of the sort we conducted would have been unlikely to alter MPA planning. Moving forward, however, our results provide the basis for adding to or adapting the existing MPA network. Future networks may benefit from considering the potential spatial and temporal distributions of both apex- and meso-predators.

Our results point to the San Juan Islands as a location of high predation risk from seals. This region has

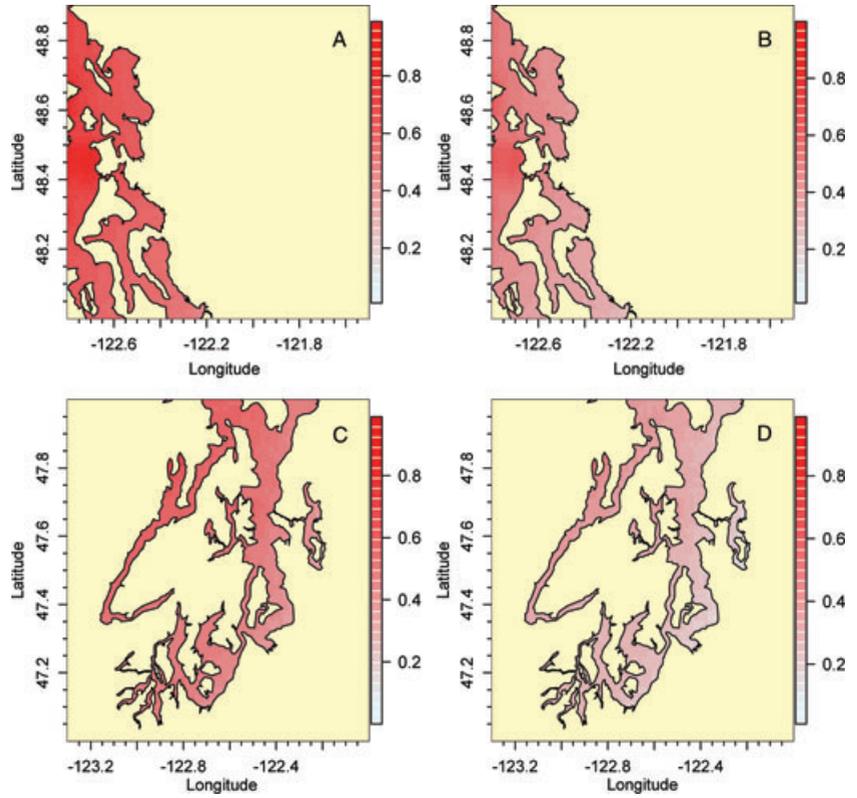


Figure 5 Maps of estimated relative predation risk for rockfish in the Eastern Bays and Puget Sound regions. Red areas represent high risk, white areas represent low risk.

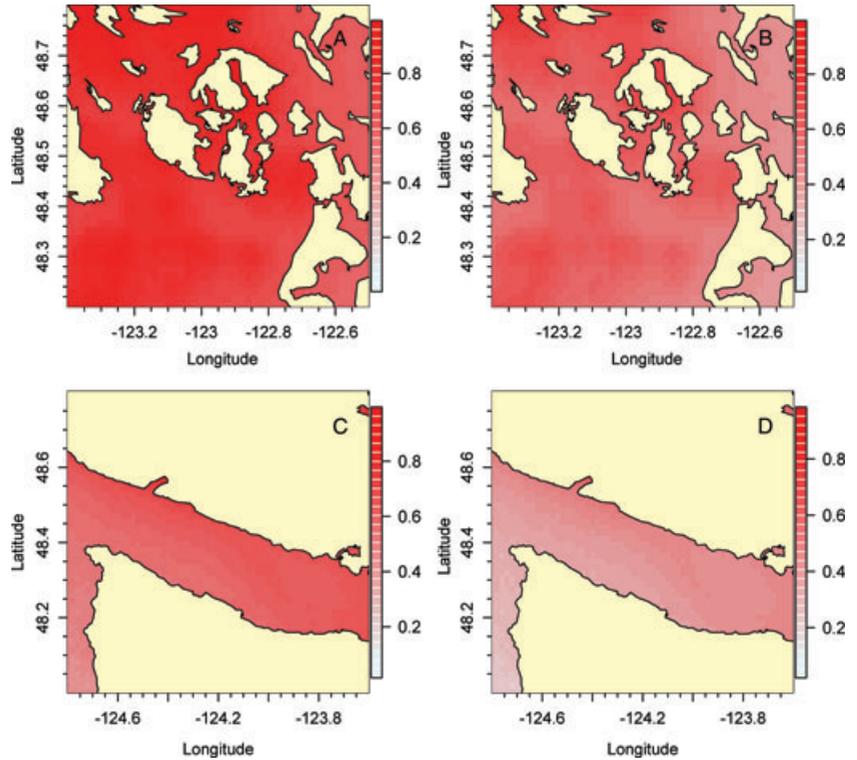


Figure 6 Maps of estimated relative predation risk for rockfish in the Strait of Juan de Fuca and San Juan Islands regions. Red areas represent high risk, white areas represent low risk.

been a focus of a number of rockfish recovery efforts (Palsson *et al.* 2003), in part because of ample rockfish habitat available. By maintaining or increasing current biodiversity, reserves in the region may directly support greater predator abundance, by increasing total prey biomass, or the reliability of available prey via an increase in prey diversity (MacArthur 1955). In contrast with the San Juan Islands, historical records indicate that threatened canary rockfish and endangered bocaccio were once abundant in areas in southern Puget Sound (Drake *et al.* 2010). This region experiences much lower use by harbor seals, and may provide an opportunity as a node of long-term recovery. Although no single MPA is designed to meet all recovery goals (biodiversity, long-term viability, and harvest), new reserves with rockfish-specific goals, such as recruitment or juvenile survival, could be added to the existing reserve network in low seal predation areas.

Constructing reserves based on predator–prey interactions illustrate one of the many challenges in managing complex ecosystems (Levin & Lubchenco 2008). Although the recovery of harbor seals in Washington State following the MMPA may help prevent the recovery of other protected species (canary, yelloweye, and bocaccio rockfishes listed under ESA in 2010), harbor seals may have direct and indirect effects on a variety of other species that offer other challenges. Harbor seals and other pinnipeds have a quantifiable impact on commercial fishermen (e.g., Hjermann *et al.* 2004). Seals in inland Washington may also have indirect impacts on local populations of other apex predators, including killer whales (listed under ESA in 2005), via a shared prey base (salmon). Effective multispecies management requires identifying multiple recovery objectives and potential conflicts between them, as well as potential consequences of actions. Controlling seal abundance may also have deleterious effects for rockfish, particularly if it results in an increase of a species like lingcod that preys on juvenile rockfish (Palsson *et al.* 2003; Lessard *et al.* 2005).

The recovery of depleted predators is the primary objective of many spatial conservation plans and would certainly be considered a conservation success. Such success, however, will clearly produce challenges when prey species are imperiled. The approach we develop here provides groundwork for predicting predation hot spots, and thus can provide the foundation for conservation planning that explicitly considers predator–prey interactions.

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Appendix

Collection of scat samples

In 2005–2006 (pink salmon present) and 2006–2007 (pink salmon absent), scientists from the Washington Department of Fish and Wildlife collected scat samples from 38 locations in the San Juan Islands (Lance and Jeffries 2006, 2007). At a finer spatial scale within the San Juan Islands, sampling regions are designated as: “South Strait of Georgia,” “North Rosario Strait,” “Eastern Bays,” “South Rosario Strait,” “South San Juan Channel,” and “North San Juan Channel.” Sampling in each area was stratified by season (winter, spring, summer/fall), with two to three collection events per season. In 2005–2006, a total of 509 scats were collected (Lance and Jeffries 2006). Thirty salmon otoliths were identifiable to species, with pink salmon representing 83% (25). Of the 26 juvenile salmon present, only 4 were identifiable to the species level, and all were Chinook. In 2006–2007, a total of 398 scats were collected (Lance and Jeffries 2007). Twenty-four adult otoliths were identifiable to the species level (1 pink salmon, 13 chum, 7 sockeye, 2 coho, 1 Chinook). Of the 10 juvenile otoliths identifiable (of $n = 22$), 8 were Chinook, in addition to 1 coho and 1 sockeye. While salmon remains a commonly occurring item in the diets of each year, the big difference between years is that when pink salmon is absent from Puget Sound, it is replaced by other species.

Tagging and collection of location data

To estimate the movement behavior of individual seals, we tagged 36 harbor seals in 2007–2008 (seals tagged in April/May). Adult harbor seals were captured following the methods of (Jeffries *et al.* 1993) at three sites: Padilla Bay, Bird/Belle Rocks, and Protection Island (Figure 1). Seals were tagged with time-depth recorders (TDRs; Wildlife Computers, Redmond, WA, Mk-9, or Mk-10F), and satellite tags (Wildlife Computers, Redmond, WA, Spot 5). Tags were glued to the pelage of the animal using 5-min epoxy. TDR tags were placed along the dorsal midline of the animal between the shoulders and satellite tags were placed on top of the head.

Each satellite tag was programmed to be on for two hours and off for one, except during haul-out periods when transmissions ceased until the tag was re-submerged. Tags transmitted every day with a maximum of 350 transmissions per day. In addition to dive data, Mk-10F tags were set to record GPS positions continuously for two weeks each month for the first three months of deployment, and then continuously for the entire month until the battery was exhausted. GPS tags

were set to record a maximum of 150 acquisitions per day. All TDR tags were equipped with an Eco-tech floatation pack and a VHF transmitter to allow for tracking and recovery after it became detached during the seals annual molt between August and October. This tag duration (from spring to late summer) captured the diet of seals in summer months.

We tracked individual seals via data collected by polar orbiting satellites operated by Service Argos. Argos (2007) assigns a location quality based on the number of uplinks received by a passing satellite. The ARGOS positioning system classifies points in decreasing precision ($3 > 2 > 1 > 0 > A > B$); this uncertainty was built into the movement model by estimating standard deviations for each level of classification (constrained to be more imprecise than the level above it). Standard locations need > 4 uplinks from the tag and are designated quality 1, 2, or 3, with 68th percentile predicted accuracies of approximately $< 1,000$ m, 350–150 m, and < 150 m, respectively (Argos 2007). Auxiliary locations receive ≤ 4 uplinks. Locations with four uplinks are level 0, with $> 1,000$ m predicted accuracy and locations with three and two uplinks are labeled A or B, respectively, with no predicted accuracy (Argos 2007). Satellite locations were used to determine the movements of each seal. Historically, all auxiliary locations (those with ≤ 4 satellite uplinks) were excluded from analyses due to the lack of accuracy associated with the estimated error for these location classes. Alternative procedures for preserving data include applying filters to remove erroneous locations (McConnell *et al.* 1992; Lowry *et al.* 1998; Bonadonna *et al.* 2000; Guinet *et al.* 2001). In this analysis, we attempted to make full use of all locations, with varying levels of precision (modeling details below).

Hierarchical Bayesian State Space Switching Model

For our hierarchical State Space Switching Model (SSSM), we assumed that seals transitioned between 2 states, representing slow and fast movement. For each state, we assumed the movement velocity of individual i at time t in behavioral state s to be lognormally distributed, $\log(v_{i,t,s}) \text{ Normal}(a_{i,s}, b_s)$. This parameterization allowed each individual to have a unique mean velocity a , and each behavioral state to have a unique standard deviation b . To enable convergence, we assumed that the variances of the log-velocities to be shared among individuals. Velocities were converted to predicted step lengths by multiplying by the minutes traveled (interval between transmissions); uncertainty in step lengths is proportional to t^2 , following methods for diffusion approximation. The second component of our hierarchical

SSSM is the distribution of turn angles. We used the wrapped Cauchy distribution proposed by Morales (2004). Following Eckert *et al.* (2008), we assumed the mean turn angle to be 0.

To allow for transitioning between states, the SSSM requires estimation of the transition probabilities from state 1 to 2 (q_{12}) and the transition probability from state 2 to 1 (q_{21}). In our hierarchical model, we assumed that there were mean transition probabilities, and that each individual had a slight deviation from the mean. To avoid (0, 1) constraints, these deviations were estimated in logit space, so that the transition probabilities for seal j can be described by

$$\eta_{12,j} \sim \text{Normal}(\text{logit}(\bar{q}_{12}), \sigma_{12}); \quad q_{12,j} = \text{logit}^{-1}(\eta_{12,j})$$

$$\eta_{21,j} \sim \text{Normal}(\text{logit}(\bar{q}_{21}), \sigma_{21}); \quad q_{21,j} = \text{logit}^{-1}(\eta_{21,j}).$$

The mean transition probabilities (\bar{q}_{12} , \bar{q}_{21}) were assigned uniform priors in normal space, and the standard deviations of the random effects assigned uniform priors (Gelman 2008).

For the observation error model, we assumed observation error variances to be shared among all seals. Because our coordinates were in UTM's, we subtracted 5,000 km from longitude to make it on same scale as latitude. We assumed that the errors were normally distributed, and identical in each dimension. After removing locations with the poorest location quality ("Z"), we were left with 6 remaining classes, each receiving its own variance ("3" > "2" > "1" > "0" > "A" > "B"). The advantage of using such an approach is that we can use almost all locations, rather than throwing out 30% or more of data (Tremblay *et al.* 2009). The variance of the most precise location quality was assigned an inverse gamma prior, $r_3 \sim \text{InvGamma}(0.001, 0.001)$. To constrain other location estimates to be less certain, we assigned Half-normal (0, 1) before the difference between variances: $(r_2 - r_3) \sim \text{Normal}(0, 1)[0,]$, $(r_1 - r_2) \sim \text{Normal}(0, 1)[0,]$, etc.

Model diagnostics and tests for convergence were done using R (the "coda" and "boa" packages). All plotting and mapping was also done in R, using the "PBSmapping" package.