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Predicting synergistic effects of resources and predators on foraging decisions by juvenile Steller sea lions

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Abstract Many theoretical and experimental studies suggest that synergistic interactions between resources and predators influence foraging decisions and their fitness consequences. This framework, however, has been ignored almost completely by hypotheses on causes of the population decline of Steller sea lions (SSLs) (*Eumetopias jubatus*) in western Alaska. By comparing predictions from a dynamic state variable model to empirical data on the behaviour of individuals instrumented with satellite-linked time-at-depth recorders, we develop and find preliminary support for the hypothesis that, during winter in Prince William Sound, juvenile SSLs (a) underutilise walleye pollock, a predictable resource in deep strata, due to predation risk from Pacific sleeper sharks, and (b) underutilise the potential energy bonanza of inshore aggregations of Pacific herring due to risk from either killer whales, larger conspecifics, or both. Further, under conditions of resource scarcity—induced by overfishing, long-term oceanographic cycles, or their combination—trade-offs between mortality risk and energy gain may influence demographic parameters. Accordingly, computer simulations illustrated the theoretical plausibility that a decline of Pacific herring in shallow strata would greatly increase the number of deep foraging dives, thereby increasing exposure to sleeper sharks and mortality rates. These results suggest that hypotheses on the decline of SSLs should consider synergistic effects of predators and resources on behaviour and mortality rates. Empirical support for our model, however, is limited and we outline tasks for empirical research that emerge from these limitations. More generally, in the context of today's conservation crises, our work illustrates that the greater the dearth of system-specific data, the greater the need to apply principles of behavioural ecology toward the understanding and management of large-scale marine systems.

Keywords Alaska · Diving behaviour ·
Dynamic state variable model · Optimal foraging ·
Predation risk

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Introduction

Marine foragers that breathe air make time allocation decisions, including number and duration of dives to different strata, that may signal spatiotemporal shifts in the abundance and distribution of fish or other food resources

(Monaghan 1996; Mori and Boyd 2004). Accordingly, studies of at-sea behaviour have aimed to elucidate the role of resource scarcity in the population trajectories of air-breathing vertebrates (Lewis et al. 2006), including endangered Steller sea lions (SSLs; *Eumetopias jubatus*) in western Alaska (e.g. Loughlin et al. 2003).

Resources, however, are not the only drivers of foraging decisions. Virtually all animal taxa optimise trade-offs between energy gain and risk of mortality by underutilising resources—using them less than expected from their energetic profitability—when access to resources requires greater risks. In other words, functional loss of resources and lost energetic opportunities are nonlethal effects of predators on their prey (Lima and Dill 1990; Wirsing et al. 2008). In spite of their general ecological importance, nonlethal effects of predators rarely have been considered as potential influences on foraging decisions by air-breathing vertebrates (Frid et al. 2007a). Further, although predators are the most common form of perceived danger, risk from larger conspecifics may lead to behavioural decisions that, functionally, do not differ from those managing predator avoidance (e.g. Ben-David et al. 2004).

In this paper we apply the framework of risk–energy trade-offs and optimisation theory to seek insight into the drivers of foraging decisions by two-year-old SSLs (hereon, "juvenile SSLs") in Prince William Sound (PWS), western Alaska. Specifically, we derive a dynamic state variable model (Clark and Mangel 2000) of foraging decisions under different risk scenarios and compare predictions to empirical data. These analyses are motivated by the decline of SSLs and other pinnipeds in western Alaska, which began in the late 1970s. Leading hypotheses for causes of the decline have emphasized top-down and bottom-up influences as independent factors (reviewed in Wolf et al. 2006). Although the concurrent importance of predation, competition and resource availability has gained recent recognition (Guénette et al. 2006; Wolf et al. 2006), an understanding is still required of how behavioural mechanisms might influence synergistic effects of resources and predators on population parameters, as experiments in other systems demonstrate (e.g. Anholt and Werner 1995; Biro et al. 2003).

The framework of risk–energy trade-offs is relevant to our case study because empirical data suggest that juvenile SSLs underutilise an abundant near-surface resource with very high energy density: adult herring (*Clupea palassi*) aggregations overwintering in inshore waters (hereon, "inshore herring"). One set of studies, which could not determine the age–sex class and identities of individual SSLs, found strong correlations at fine spatial scales between the density of inshore herring and sea lion numbers (Thomas and Thorne 2001; Thorne 2004). In contrast, juvenile SSLs instrumented with satellite tags rarely used

the locations of inshore herring (Briggs 2005; this study). We are unaware of any studies documenting adults as a form of intraspecific risk for juvenile SSLs. Nonetheless, we speculate that SSLs foraging on inshore herring tend to be adults, and that juvenile SSLs underutilise this resource to reduce the threat of intraspecific aggression. Alternatively, mammal-eating killer whales (*Orcinus orca*) might be a source of elevated risk during winter at inshore herring aggregations, and juvenile SSLs might be less willing to face that risk than older conspecifics. This possibility, however, cannot be examined empirically, because killer whale studies have been limited to non-winter months (Saulitis et al. 2000; Matkin et al. 2003). Regardless of its source, elevated risk at herring inshore aggregations should, theoretically, produce the same functional outcome: resource underutilisation.

Further, in the open basin of PWS, where juvenile SSLs do much of their winter foraging, herring are an unpredictable resource because their near-surface aggregations are widely dispersed and often ephemeral. In contrast, walleye pollock (*Theragra chalcogramma*) have lower energy density than herring, but their larger size and more continuous distribution potentially makes them the more predictable and profitable resource in the long term (Gende and Sigler 2006; Frid et al. 2007b). Most juvenile SSLs studied to date in PWS, however, rarely dived to strata where pollock are abundant (Briggs 2005, this study), suggesting that these individuals incurred a functional loss of resources due to predation risk, possibly from Pacific sleeper sharks (*Somniosus pacificus*) which overlap spatially with pollock (Frid et al. 2007b).

Given this backdrop, we used the model to investigate the plausibility that perceived risk causes juvenile SSLs to underutilise walleye pollock in deep strata and inshore herring aggregations. We also investigated the use of other foraging locations and sought the theoretical scenarios which best fit the empirical data.

Methods

Capture and instrumentation of SSLs studied in the field

Seven juvenile SSLs (17 months old at the time of instrumentation) were monitored using external dive-recording satellite tags between November 2003 and July 2004, but the data presented here are only for March 2004. Captures took place during November 2003 at the Glacier Island haulout in PWS (Rehberg and Burns 2008). Sea lions were categorized as juveniles based on length, mass, tooth eruption pattern and canine length (King et al. 2007), and assumed to have been born on 1 June (Pitcher et al. 2001). They were captured with underwater dive-capture

techniques (Raum-Suryan et al. 2004) and transferred by skiff to a research vessel for processing under isoflurane anaesthesia (Heath et al. 1997). Once anaesthetized, satellite-relay data loggers (SRDL, Model 7000, Sea Mammal Research Unit, St. Andrews, Scotland, 300 g) were attached to the fur on the top of the head of each animal using cool-setting epoxy (10 min Epoxy No. 14255, ITW Devcon, Danvers, MA, USA). A pressure transducer and conductivity sensor monitored instrument depth and immersion status (wet or dry) every 4 s. These data were aggregated into measures of diving behaviour (Fedak et al. 2001), and stored in on-board memory prior to transmission to the Argos satellite data-relay system (Argos/CLS 2000). SRDLs reported the date, time, maximum depth and duration of all dives longer than 8 s and deeper than 8 m. However, due to uplink bandwidth constraints, only a subset of dives was successfully relayed by the Argos satellite system. Animal locations received from Service Argos were screened by an iterative forward/backward averaging filter that identified and excluded locations that would require rates of travel greater than 4 m s^{-1} (Vincent et al. 2002). These positions were then used to reconstruct a trackline so that locations could be estimated for all dives (Fedak 2001). Dives were then coded as occurring during the day (sun above the horizon) or night (sun below the horizon), as determined from solar elevation at the time and location of the dive. Behavioural and positional information was then integrated into Access databases, and

exported into ArcGIS (ESRI, Inc., Redlands, CA, USA) so that dives could be associated with the nearest neighbour values for bottom elevation with respect to the mean lower low water datum. In this process, bathymetric data (Rehberg and Gellat 2003) were projected to UTM Zone 6, WGS 1984 coordinates, and then interpolated into a grid with 250 m^2 cells.

Once each dive was associated with the latitude, longitude, and seafloor depth at which it occurred, it was placed into one of five location–depth strata categories corresponding to the foraging locations represented by the model (Fig. 1). The inshore herring aggregation was located at Two Moon Bay, between 146.383° and 146.700°W longitude, and 60.716° and 60.783°N latitude, provided that the bathymetric depth was ≤65 m. Nearshore shallow strata were areas outside the inshore herring aggregation where both seafloor and dive depths were ≤65 m. Offshore habitats were regions where the seafloor was ≥200 m deep; this habitat was further categorized by dive depth into offshore shallow strata with dive depths ≤65 m, offshore mid-depth strata with dive depths of 65.01–105 m, and offshore deep strata with dive depths of 105.1–305 m.

For each individual, daily averages for each location–depth strata category and diel period were calculated for maximum diving depth (m), and the duration (s) of post-dive surface interval (to a maximum duration of 6 min), vertical travel, and bottom time (assumed to represent time
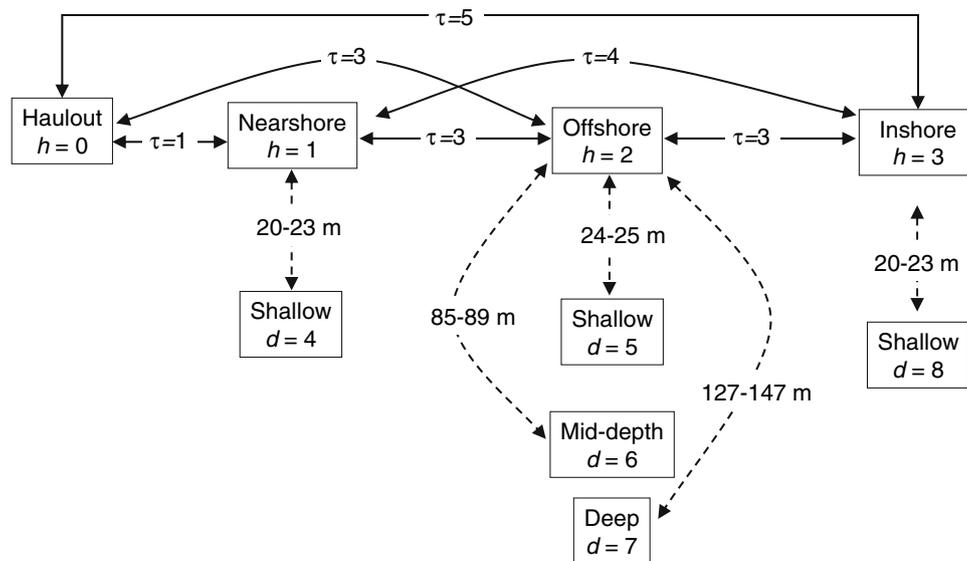

Fig. 1 Spatial structure of the juvenile Stellar sea lion (*Eumetopias jubatus*) foraging decision model. Locations (*h*) are represented by *boxes* that include descriptive names and the numerical labels used in the model. One-way travel times (τ) between locations linked by *solid arrows* are given in 1-h units. *Dashed arrows* represent potential foraging dives within each location; numerical labels contained in *boxes* identify the decision to dive (*d*) to a specific resource patch; the range of diel-dependent depths associated with each decision is superimposed on the *arrows* (see Table S1 in the "Electronic supplementary material"). Locations are ordered, from *left* to *right*, according to increasing distance from the haulout; Table 1 describes resources characterising each location. The inshore location is a large bay, while the nearshore and offshore locations represent more exposed waters near and far from shore, respectively

at a foraging patch, and defined operationally as time spent at >85% of maximum depth). Overall mean durations of different dive cycle components were estimated from daily averages. (Table S1 in the "Electronic supplementary material".)

The model

This section summarises the main assumptions and structure of the model. Model derivation and parameterisation are detailed in the "Electronic supplementary material".

Although SSLs might prey on several fish species, the model considers only Pacific herring and walleye pollock. This simplification is justified because these species comprise the two dominant fish biomasses of PWS (Thorne 2004) and are major prey items. During winter, pollock and herring remains had frequencies of occurrence of 56.2 and 22.8%, respectively, in sea lion scats collected at haulouts adjacent to PWS (Sinclair and Zeppelin 2002; data cannot stratify results by age–sex classes and are for that study's region 1).

In the model, both killer whales and Pacific sleeper sharks are potential predators. While evidence that killer whales prey on SSLs is strong (e.g. Heise et al. 2003), an analysis of stomach contents of sleeper sharks in the Gulf of Alaska found cephalopods to be a major prey item but no evidence of shark predation on SSLs (Sigler et al. 2006). The stomach content data, however, include only sharks with precaudal lengths of <2.5 m, much smaller than the maximum total lengths of >4 m reported by other studies (e.g. Yano et al. 2007). Sharks generally undergo ontogenetic diet shifts, and recent data collected by Yano et al. (2007) for Pacific sleeper sharks and two close relatives (*S. microcephalus* and *S. antarcticus*) suggest that cephalopods are a major prey item for small to mid-sized sharks, yet marine mammals and teleost fish become more important prey items as sharks become larger. This backdrop, along with vast evidence that prey modify their behaviour in response to perceived risk, even if lethal interactions occur only rarely (e.g. Lima and Dill 1990; Wirsing et al. 2008), justify sleeper sharks as sources of perceived risk in the model.

The model depicts spatial variation in risk–energy trade-offs across four locations: (1) the haulout, which is safe from predators but lacks food, (2) a nearshore location containing equal proportions of Age 1, Age 2, and adult herring in shallow strata, (3) an offshore location containing a shallow strata with adult herring, a mid-depth strata with equal proportions of adult pollock, juvenile pollock, and adult herring, and a deep strata containing adult pollock, and (4) an inshore herring aggregation in shallow strata (Fig. 1, Table 1). Killer whales are the main potential predator at or near the surface but are rare to absent in

Table 1 Parameter values characterizing resources

Foraging location[a]	Resource type	Mean wet mass per fish (g)	Mean energy density (kJ g^{-1}, wet)	Mean density (kg m^{-3})		Instantaneous probability of capturing a fish[b]		Volume of water with fish[b] (proportion)	
				Night	Day	Night	Day	Night	Day
Nearshore shallow	1/3 proportions of adult, age 1 and age 2 herring (A)	60.0 (A)	5.14 (A)	8.80×10^{-2} (A)	8.80×10^{-2} (A)	1.46×10^{-2} (A)	9.98×10^{-3}	0.51 (A)	0.51 (A)
Offshore shallow	Ad. herring (A)	131.0 (A)	5.80 (A)	1.11×10^{-5}	3.64×10^{-5}	1.58×10^{-3}	2.17×10^{-3}	0.27	0.24
Offshore mid-depth	1/3 proportions of ad. herring, juv. pollock and ad. pollock (A)	299.9 (A)	4.48 (A)	1.11×10^{-5}	2.10×10^{-5}	3.44×10^{-3}	2.42×10^{-3}	0.90	0.69
Offshore deep	Ad. pollock	711.4	4.08	4.49×10^{-5} (A)	4.49×10^{-5}	2.62×10^{-3}	2.62×10^{-3}	0.96	0.96 (A)
Inshore herring	Ad. herring	131.0	5.80	8.80×10^{-2}	8.80×10^{-2} (A)	1.36×10^{-2}	9.32×10^{-3}	0.51	0.51 (A)

Values derive from data, except when (A) indicates assumed values. See Table S2 and related text in the "Electronic supplementary material" for sources and rationale

[a] See Fig. 1

[b] See Eq. S4 and related text in the "Electronic supplementary material"

deeper strata. The probability of predation by sleeper sharks is very low near the surface but increases with depth (Table 2, Eqs. S1–S3 in the "Electronic supplementary material"). Depending on the theoretical scenario, risk from adult SSLs and/or killer whales may increase the probability of mortality at inshore herring aggregations.

Simulations cover 30 days of March, when adult herring are still aggregated in the inshore waters where they overwinter (Thomas and Thorne 2001, 2003; Thorne 2004). The terminal horizon is T, at which point herring aggregations disperse into open water. The time preceding T is divided into 720 1-h basic periods, t, when decisions d are made. At the onset of simulations, sea lions are at the haulout, where they can remain or travel to a foraging location. At a foraging location, sea lions may remain at the surface, switch foraging locations, return to the haulout, or dive to a resource patch. The number of basic time periods t required for one-way travel between surface locations (Fig. 1), τ is based on the relative locations of the Glacier Island haulout, the location of fish resources (Table S2 in the "Electronic supplementary material"), and areas where instrumented SSLs spent substantial amounts of time diving. To estimate τ, we assumed a surface swimming speed of 2 m s^{-1} (7.2 km h^{-1}), which is approximately the speed of minimum cost of transport (Rosen and Trites 2002).

The model uses two internal states, energy reserves $X(t) = x$ and stomach fill $G(t) = g$, representing the energetic equivalent of lipid stores and the mass of captured fish in stomach at t, respectively. Thus, $G(t) = g$ is a digestive constraint forcing sea lions to optimise trade-offs between the availability and energy density of pollock and herring (Table 1; Eqs. S4–S6 in), as well as the decision to leave a foraging location and return to the haulout—at an energetic and time cost of travel—to digest without predation risk.

The environmental state variable $H(t) = h$ depicts the haulout and the at-sea locations where foraging dives can occur (Fig. 1). Although components of a dive cycle (time at the surface, traveling the water column, and at a foraging patch) have flexible durations that likely respond to resources and predation risk (Frid et al. 2007a), the model's 1-h basic period required that foraging bouts comprise contiguous dive cycles with fixed durations (Table S1).

To maximise expected fitness, juvenile SSLs must optimise risk–energy trade-offs such that they avoid predation and survive to T with energy reserves that are as high as possible (Eqs. S7–S12 in the "Electronic supplementary material").

Computer experiments and empirical testing

The solution to the dynamic programming equation generates an optimal decision matrix for all combinations of state variables and time periods. Based on this matrix, we used forward iterations to conduct computer experiments (Clark and Mangel 2000). Throughout, killer whale risk, μ_w, remained fixed at $\mu_w = 2.00 \times 10^{-8}$. Shark risk, μ_s, varied experimentally as a multiple of μ_w; it is expressed as the relative value $\mu_s\mu_w^{-1}$ (e.g., $\mu_s\mu_w^{-1} = 50$ is equivalent to $\mu_s = 1.00 \times 10^{-6}$). Risk at inshore herring aggregations (hereon, "inshore risk"), $\eta_{3,d}$, varied experimentally as a multiplier for μ_w only at this location. Our a priori factorial design considered 14 theoretical scenarios: seven levels of shark risk (including none) combined with the absence and presence of elevated inshore risk, $\eta_{3,d} = 1$ and 2, respectively (Table 3; Eqs. S1–S3). To ensure that a wider range of parameter values for inshore risk would not alter conclusions on the relative effect of shark and inshore risk on sea lion behaviour, post hoc analyses examined a third and higher level of inshore risk, $\eta_{3,d} = 3$ (Table S4 in the "Electronic supplementary material"). Throughout, initial energy state was fixed at $X(0) = 4$ (13.3% of the maximum attainable), but its effect was assessed in sensitivity analyses (Fig. S6 in the "Electronic supplementary material").

We then selected the theoretical scenario that best fit the empirical data on the proportion of dives by juvenile SSLs to different locations during each diel period. As a preliminary selection procedure, the level of shark risk corresponding to the scenario with the lowest residual sum of squares (RSS) was chosen as the potentially most plausible one. RSS values were calculated as the sum of squared differences between predicted and observed

Table 2 Proportions of time spent by each predator type at each depth range considered by the model

Depth (m)	Diel period	Proportion of time spent by killer whales (W_p)[a]	Proportion of time spent by sharks (S_p)[b]
Surface (0–10)	Day	0.58	0
Shallow (11–65)	Day	0.16	1.13×10^{-3}
Mid (66–105)	Day	6.78×10^{-3}	2.27×10^{-2}
Deep (106–205)	Day	3.43×10^{-4}	4.86×10^{-2}
Surface (0–10)	Night	0.64	0
Shallow (11–65)	Night	0.164	4.65×10^{-3}
Mid (66–105)	Night	4.33×10^{-3}	2.71×10^{-2}
Deep (106–205)	Night	1.09×10^{-5}	5.55×10^{-2}

These are the empirical inputs into Eqs. S1 and S3. The 0–10 m depth range applies only to surface locations. Values are averaged from the 10-m depth intervals presented in Fig. 1a, b of Frid et al. (2007b)

[a] Based on unpublished data from P.J.O. Miller, A.D. Shapiro and V.B. Deecke for ten mammal-eating killer whales collected in southeast Alaska during June–July 2006

[b] Based on Hulbert et al. (2006). The sum of proportions within a diel period is <1 because sleeper sharks also used strata deeper than 205 m

Table 3 Theoretical scenarios simulated in computer experiments and their fit to the empirical data

Scenario	Relative shark risk $\mu_s\mu_w^{-1}$[a]	Inshore risk $\eta_{3,d}$[b]	RSS by individual sea lion							Total RSS[c]	Number of predation risk parameters[d,e]	AICc[d]	W_i[d]
			446PW	445PW	441PW	438PW	449PW	437PW	435PW				
1	0	1	0.70	0.12	0.51	0.66	0.41	0.91	0.83	4.15	1	−195.64	1.28×10^{-11}
2	1	1	0.69	0.12	0.50	0.66	0.40	0.90	0.82	4.10			
3	5	1	0.79	0.90	0.77	0.82	0.63	1.03	0.94	5.89			
4	10	1	0.79	0.91	0.77	0.82	0.63	1.03	0.94	5.89			
5	15	1	0.79	0.91	0.77	0.82	0.63	1.03	0.94	5.89	2	−169.06	2.16×10^{-17}
6	25	1	0.78	0.90	0.77	0.81	0.62	1.02	0.93	5.83			
7	50	1	0.74	0.87	0.73	0.77	0.58	0.98	0.89	5.56			
8	0	2	0.70	0.11	0.50	0.65	0.42	0.88	0.81	4.08	2	−194.80	8.38×10^{-12}
9	1	2	0.71	0.10	0.50	0.66	0.42	0.89	0.82	4.10			
10	5	2	0.66	0.09	0.48	0.62	0.41	0.85	0.76	3.86			
11	10	2	0.62	0.08	0.45	0.58	0.38	0.80	0.71	3.61			
12	15	2	0.17	0.57	0.30	0.21	0.46	0.10	0.09	1.91	3	−245.81	≈ 0.99
13	25	2	0.18	0.58	0.31	0.21	0.46	0.10	0.09	1.93			
14	50	2	0.18	0.58	0.31	0.21	0.47	0.08	0.10	1.95			

[a] Killer whale risk was fixed at $\mu_w = 2.00 \times 10^{-8}$ and, for simplicity, shark risk, μ_s, is represented as a relative value according to the ratio $\mu_s\mu_w^{-1}$ (e.g. $\mu_s\mu_w^{-1} = 15$ is equivalent to $\mu_s = 3.00 \times 10^{-7}$). Note that in Eq. S1, $\mu_s\mu_w^{-1} = 0$ is equivalent to excluding a shark risk parameter

[b] Value is a multiplier for μ_w at inshore aggregations. Note that in Eq. S1, $\eta_{3,d} = 1$ is equivalent to excluding an inshore risk parameter. See Table S4 for assessments of a wider range of parameter values

[c] Sum of RSS by individual sea lions

[d] Applies only to scenarios selected during preliminary selection procedures (see "Methods")

[e] The predation risk parameters considered during model selection were killer whale risk, shark risk, and elevated inshore risk (Eq. S1). The table provides details for the latter two, which varied experimentally, but not for killer whale risk, which was present in all models at a constant level. Also, the number of resource-related parameters remained constant throughout, and did not affect model selection procedures

proportions of dives for each combination of five foraging locations, two diel periods and seven individual sea lions ($N = 70$ differences per scenario).

A final selection procedure compared to the empirical data four alternative scenarios that differed in their number or type of fitted predation risk parameters. These scenarios were (1) killer whale risk only, (2) killer whale and elevated inshore risk, (3) shark risk at the level determined by preliminary model selection and killer whale risk, and (4) killer whale, shark, and elevated inshore risk. (Excluding shark and inshore risk parameters is equivalent to using $\mu_s\mu_w^{-1} = 0$ and $\eta_{3,d} = 1$, respectively, in Eq. S1.) Akaike information criterion corrected for small sample size (AICc: reviewed in Johnson and Omland 2004) tested whether empirical data were best described by including or excluding inshore and/or shark risk parameters in the model. Uncertainty of the fit of the "best" scenario was assessed with Akaike weights W_i, representing the probability that a given combination of parameters is best among the alternatives considered (reviewed in Johnson and Omland 2004).

Results

Empirical results

Four of seven individuals (435PW, 437PW, 438PW, 446PW) dove to offshore deep strata only rarely or not at all (0–3% of dives) and primarily used nearshore shallow strata (50–83% of dives). Most remaining dives by these individuals (16–43%) were to offshore shallow strata; mid-depth strata were used rarely or not all (0–6% of dives). Diel use of nearshore shallow strata ranged from primarily nocturnal (435PW) or diurnal (437PW) to no preference (438PW, 446PW). These four individuals, however, used offshore shallow strata mainly at night (Fig. 2).

The remaining three individuals made 13, 51 and 21% of their dives to offshore deep strata (individuals 441PW, 445PW and 449PW, respectively), primarily during the day (Fig. 2). Most remaining dives by 445PW, the most frequent deep diver, were to mid-depth strata (21%), primarily during the day. Individuals 441PW and 449PW did most remaining dives (43 and 28%, respectively) to offshore shallow strata, mainly at night, but also used mid-depth

Fig. 2 Empirical data on the number of dives during night (*black bars*) and day (*clear bars*) to different locations by seven juvenile SSLs during March 2004. Each *panel* represents a different individual, and the *legend* indicates its identification (three digits and the suffix PW), gender (*F*, female; *M*, male), mass at time of capture (kg), and number of dives analyzed (*N*)
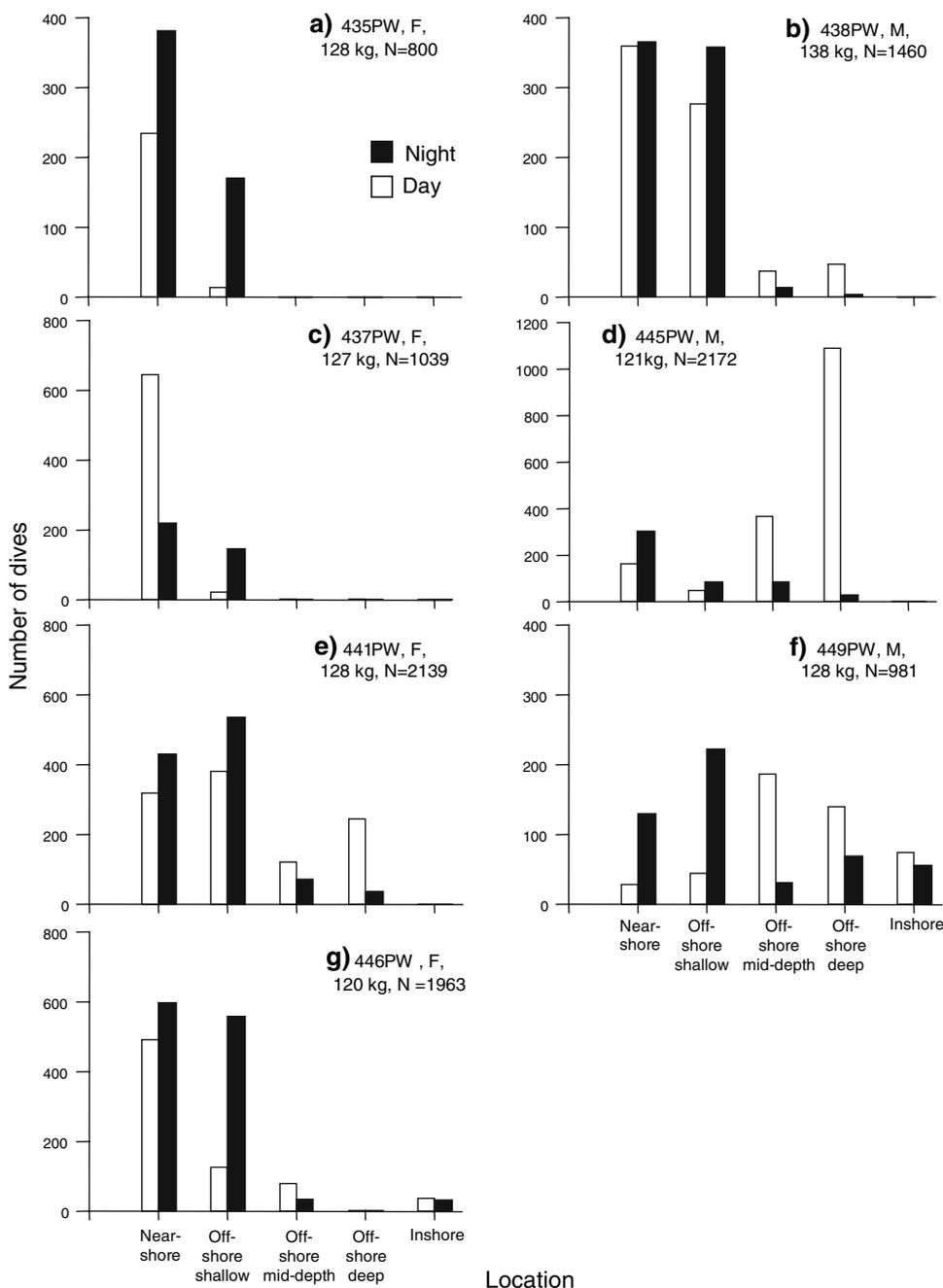
strata (9 and 22% of dives, respectively), primarily during the day (Fig. 2).

Notably, five of seven individuals did not use the inshore herring aggregation. The exceptions were 446PW and 449PW, which made 4 and 14% of their dives, respectively, at that location (Fig. 2).

Although allometric constraints on diving capacity can influence depth preferences (e.g. Richmond et al. 2006), individual differences appeared to not depend on mass at time of capture. The most frequent deep diver also was the second lightest individual (445PW), while the heaviest

individual (438PW) dove shallow almost exclusively. Mass at time of capture also does not appear to have strongly influenced depth preferences by the remaining five individuals (Fig. 2).

Simulation results

Under some treatment combinations, the model predicted substantial use of offshore deep strata, inshore herring aggregations, and nearshore shallow strata (Fig. 3). Dives to mid-depth strata, however, were infrequent under all

Fig. 3 Predicted proportions of dives to nearshore (**a, b**), offshore (**c, d**) and inshore (**e, d**) locations during night (*left column*) and day (*right column*) for low ($\eta_{3,d} = 1$, *black circle*) and high ($\eta_{3,d} = 2$, *open circle*) inshore risk scenarios. Data are the means ($\pm$1SD) of 1,000 forward iterations per treatment (minus 10–24 simulations in which mortalities due to starvation or predation occurred, depending on treatment combination)
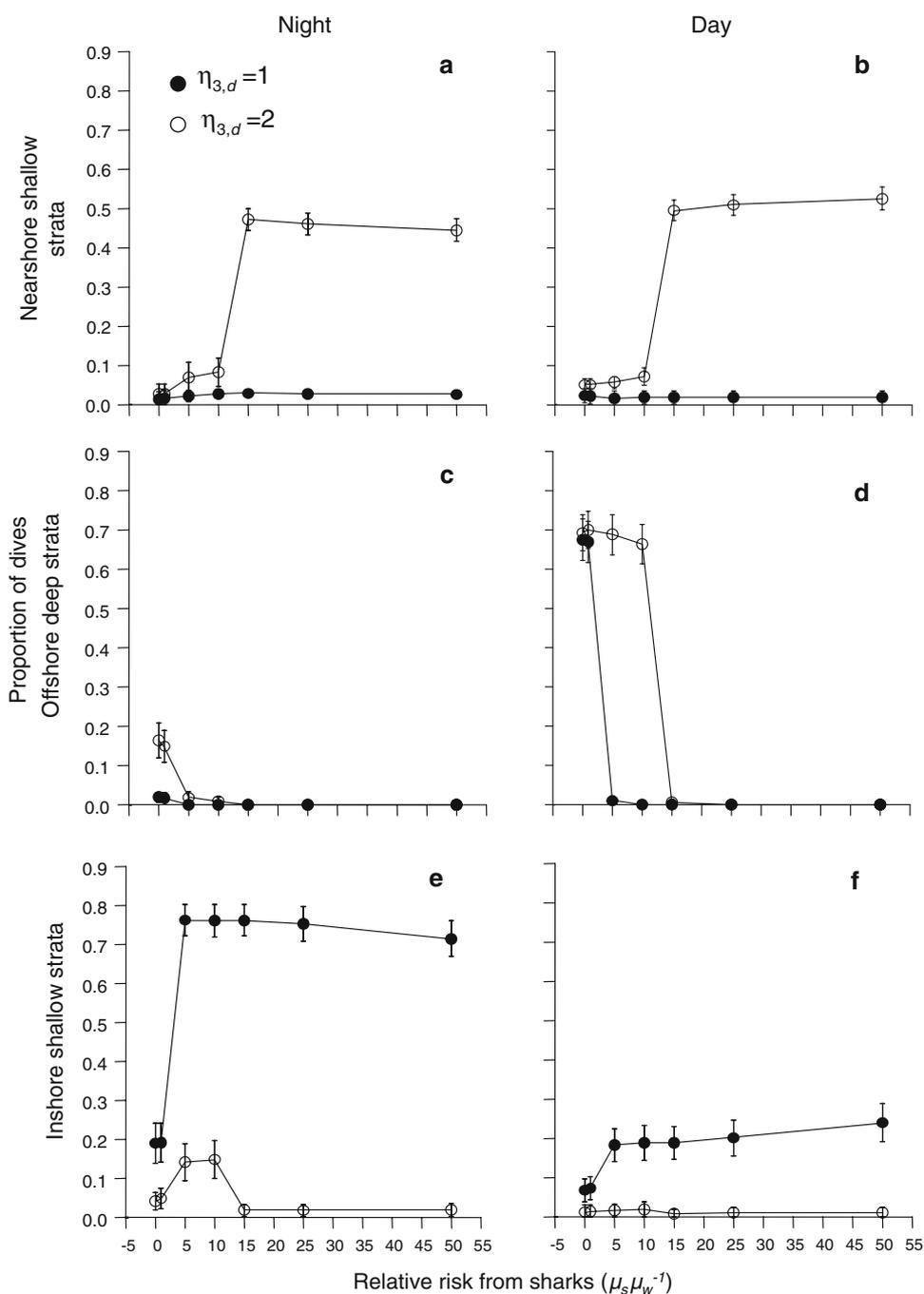
conditions (Fig. S2 in the "Electronic supplementary material") and use of offshore shallow strata, which would have yielded net energetic losses (Fig. S1), did not occur.

If shark risk was absent or very low ($\mu_s \mu_w^{-1} \leq 1$), most dives were deep and diurnal. Under elevated inshore risk ($\eta_{3,d} = 2$), diurnal deep dives also were the most frequent dive type at moderate levels of shark risk ($\mu_s \mu_w^{-1} = 5$ or 10) and—if shark risk was absent or low—the proportion of nocturnal deep dives increased (Fig. 3c, d); these increases in rates of deep diving were compensatory

responses to the avoidance of inshore herring aggregations under elevated risk (Fig. 3e, f). The effect of shark risk reached an asymptote, such that the proportion of dives to different strata differed little between low and mid levels of shark risk ($\mu_s \mu_w^{-1} = 5$–15, depending on inshore risk) and very high levels of shark risk ($\mu_s \mu_w^{-1} > 15$).

Depending on inshore risk, a rise in shark risk may or may not increase the use of inshore herring aggregations or nearshore shallow strata. If $\eta_{3,d} = 2$, inshore herring aggregations are used little, regardless of shark risk

(Fig. 3e, f), but use of nearshore shallow strata increases as shark risk rises as a compensatory response to concurrent avoidance of offshore deep strata and inshore herring aggregations; diel period has little influence on this relationship (Fig. 3a, b). In contrast, if $\eta_{3,d} = 1$, nearshore shallow strata are used little, regardless of shark risk (Fig. 3a, b), and use of inshore herring aggregations—which is greater at night than during the day—increases rapidly to an asymptote as shark risk rises (Fig. 3e, f).

We note that when shark risk is absent or low, the model predicts that most dives will be to offshore deep strata, even if $\eta_{3,d} = 1$ (i.e., contrast Fig. 3d, e at $\mu_s \mu_w^{-1} = 0, 1$), for two reasons. First, exposure to killer whales is reduced when diving in deep strata. Second, although herring aggregations are potentially the largest energy bonanza, resources at offshore deep strata are sufficient to allow optimisation of energy gain and killer whale avoidance (Table 1; also see Fig. 1a, b of Frid et al. 2007b).

Depending on the theoretical scenario, rates of predator-inflicted mortality ranged between 0.8 and 2.0%, and starvation occurred in an additional 0.1–0.5% of simulations ($N = 1,000$ simulations per treatment). The mean energy state of individuals surviving to the end of simulations, however, was high (mean $\pm$ SD = 91.8 $\pm$ 4.5% to 93.9 $\pm$ 3.8% of the maximum attainable; $N = 1,000$ simulations per treatment). Thus, under the current range of parameter values, energy losses resulting from avoidance of risky habitats could be compensated by increasing dive rates elsewhere.

Fit between model predictions and empirical data

Preliminary model selection found that theoretical scenario 12, which included elevated inshore risk ($\eta_{3,d} = 2$) and a shark risk of $\mu_s \mu_w^{-1} = 15$, had the lowest RSS value (Table 3), as calculated from differences between predicted and observed proportions of dives (Fig. S3 in the "Electronic supplementary material"). Small-sample unbiased Akaike information (AIC_c) and Akaike weights W_i confirmed that scenario 12 explained empirical data better than alternative models lacking shark and/or inshore risk parameters (Table 3). During post hoc analyses, a greater level of inshore risk ($\eta_{3,d} = 3$) neither improved the fit to the data nor altered conclusions about the theoretical importance of shark risk influencing sea lion behaviour (Table S4).

In spite of being the best fit scenario for the overall behaviour of all SSLs, scenario 12 underpredicted diurnal use of mid-depth and deep strata for the three individuals that tended to be deeper divers (notably 445PW, but also 449PW and 441PW to a lesser extent: Fig. S3). Scenario 12 also overpredicted use of nearshore shallow strata for most individuals, and underpredicted use of offshore shallow

strata for all individuals. The prediction that few dives would occur in inshore herring aggregations was generally consistent with the behaviour of each individual (Fig. S3).

Discussion

Our analyses are first steps towards understanding how trade-offs between energy gain and risk of predation might influence the behaviour and fitness of juvenile SSLs in a declining population. Our inferences, which contain both the strength of general principles and the weaknesses of small sample sizes and some untested assumptions, are useful for at least two reasons. First, insufficient data dominate the science and conservation of large-scale marine systems. It is therefore unrealistic—and arguably irresponsible—to not attempt scientific interpretations and management decisions with the data at hand (Johannes 1998). Second, "(t)he power of mathematical methods is that they let us approach apparently disparate problems with the same kind of machinery" (Mangel 2006, p. xi). Thus, general principles provide a rigorous tool for short-listing the most plausible drivers and fitness consequences of foraging decisions by juvenile SSLs, particularly because data on predation risk are scarce (see Mangel and Wolf 2006). To this end, we highlight both the more conclusive and the weakest aspects of our study, and suggest directions for empirical research.

Juvenile SSLs appear to manage risk from Pacific sleeper sharks by underutilising important resources in offshore deep strata, thereby incurring lost energetic opportunities. This inference, though clearly limited by our small sample of SSLs, is consistent with the behaviour of sympatric harbour seals, which appeared to also compromise access to resources by underutilising offshore deep strata (Frid et al. 2007b). It also has broader ecological implications (Heithaus et al. 2008). Pacific sleeper sharks are caught as bycatch in groundfish fisheries, and sharks in general are vulnerable to overexploitation. A decline of Pacific sleeper sharks could potentially alter behaviourally mediated trophic cascades via the spatial and diet shifts of SSLs and harbour seals responding to the release of shark intimidation. For instance, rates of pinniped-inflicted mortality could increase and decrease for pollock and herring, respectively, if sharks were to decline (Frid et al. 2008). Clearly, empirical research should look further into lethal and nonlethal interactions between pinnipeds and Pacific sleeper sharks.

Elevated risk at inshore herring aggregations, whether from adult SSLs, killer whales, or both, appears important. These results suggest that juvenile SSLs might generally forego the energy bonanza of herring aggregations in response to perceived risk. To evaluate sources of this

potential risk, empirical research should assess spatial overlap during winter by mammal-eating killer whales and inshore herring aggregations. The possibility that risk from larger conspecifics might influence use of inshore herring aggregations by juvenile SSLs also requires further investigation, perhaps by building on the observational research of Thomas and Thorne (2001, 2003).

The extent to which clumped spatial distributions of fish (e.g. tight schooling surrounded by empty space) interact with mean fish density to determine the probability of an SSL encountering fish might be important (Eq. S4; Fig. S5). Concurrent measures of the distribution of resources, foraging locations, and rates of prey capture are needed to address this issue.

In spite of the reasonable success of the best-fit theoretical scenario in predicting use of deep strata, mid-depth strata, and inshore herring aggregations for most individuals, the model overpredicted use of nearshore shallow strata for most individuals (Fig. S3) and underpredicted use of offshore shallow strata for all individuals. These shortcomings reflect a lack of data for the parameterisation of fish availability at these locations, as adequate data were available only for inshore herring aggregations at night, offshore deep strata during the day, and mid-depth strata (Table S2). Empirical studies on the density, size, species and age–class composition of fish are needed for the location and diel period combinations for which data are lacking.

Overall, our work provides a basis for further developing and testing the hypothesis that predation risk and resource distributions combine synergistically to affect foraging decisions by juvenile SSLs. This framework could be relevant to demographic analyses of the population decline. For instance, resource scarcity—induced by fisheries, long-term oceanographic cycles or both (Trites et al. 2007)—might limit the scope of antipredator behaviour, thereby increasing predation rates (Frid et al. 2006). We briefly illustrate this point with computer simulations contrasting theoretical scenario 12 (which had the best fit to empirical data: Table 3) under baseline levels of herring density (Table 1) against a 90% decline of herring density (see the "Electronic supplementary material"), which approximates a recently documented decline (Thomas and Thorne 2003). Herring scarcity greatly increased the proportion of deep dives while greatly decreasing the proportion of dives in nearshore shallow strata; the proportion of dives in inshore herring aggregations increased also (Fig. 4a). These changes in the spatial distribution of foraging effort caused predator-inflicted mortality rates to increase from 1.7% under baseline conditions to 2.9% under herring scarcity ($N = 1,000$ per treatment). The spatial distribution of predation events mirrored the habitat shifts. Under baseline conditions, predation rates were
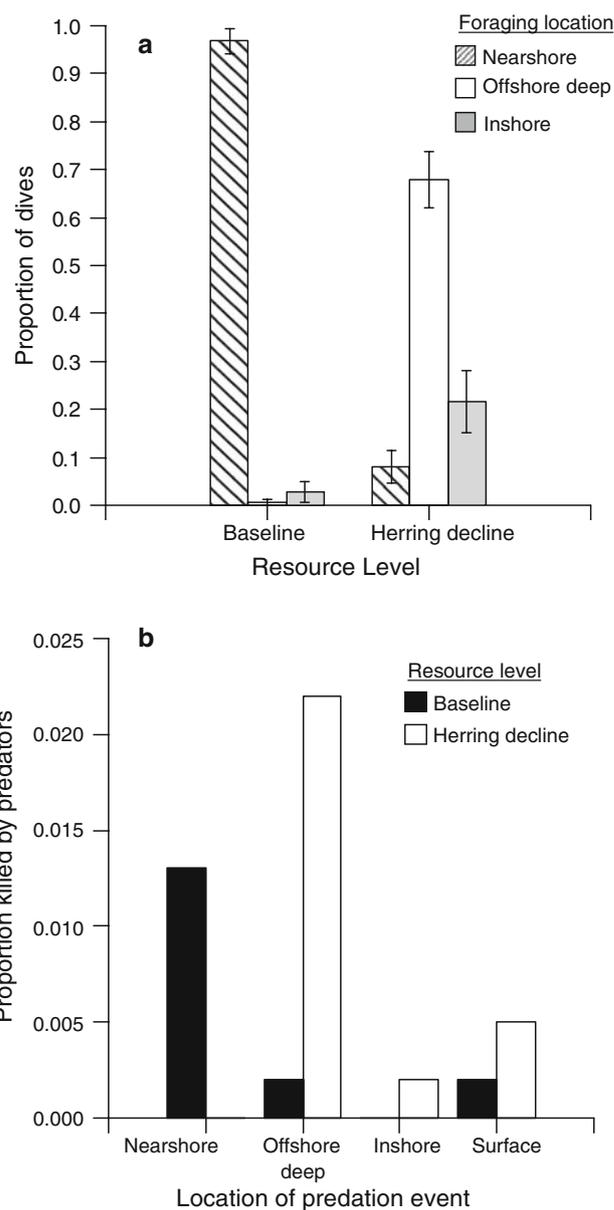

Fig. 4 Predicted effect of a 90% decline in herring density on **a** the mean ($\pm$ SD) proportion of foraging dives to three principal foraging locations (nearshore, offshore deep, and inshore) and on **b** predator-inflicted mortality rates while foraging at these locations or while at the surface during travel or rest ($N = 1,000$ forward iterations per treatment, but **a** excludes simulations in which mortalities occurred). The "baseline" resource level is that described in Table 1 and Fig. S1; the "Electronic supplementary material" details the 90% herring decline. Predation risk was set at the conditions of theoretical scenario 12 (Table 3)

highest at nearshore shallow strata, where killer whales were the main predator. Under herring scarcity, however, predation rates were highest in offshore deep strata, where sharks were the main predator (Fig. 4b).

These predictions are consistent with a body of work supporting the framework that synergistic interactions

between resources and predators influence population processes (e.g. McNamara and Houston 1987). In an elegant experiment, for instance, Anholt and Werner (1995) exposed tadpoles to predatory dragonfly larvae and manipulated resource levels. A 22% decline in food density resulted in 1.5-fold increases in the tadpoles' activity levels and movement rates, and the increased exposure raised their predation rates by 60%, despite predator densities remaining constant. Field studies of vertebrate systems amenable to experimentation (e.g. Krebs et al. 1995; Biro et al. 2003; Zanette et al. 2003) or with access to long-term correlative data sets (e.g. Sinclair and Arcese 1995) also demonstrated synergistic effects of resources and predators on population processes. For instance, the interactive effect on song bird reproductive success of relaxed predation risk and supplementary food was almost twice as large as the additive effect of the two factors (Zanette et al. 2003).

Hypotheses on the decline of SSLs have recently begun to incorporate these concepts, but only incipiently. An ECOSIM model suggested that killer whale predation on SSLs in southeast Alaska would increase if feeding time increased under resource scarcity (Guénette et al. 2006). Although ECOSIM models have the advantage of including large numbers of species, they also treat feeding time and antipredator behaviour (i.e. activity reduction) as fixed parameters (Guénette et al. 2006). The exclusion of adaptive decision-making could limit their predictive power. A recent analysis of bottom-up effects on the SSL decline mentions the possibility that "(d)ecreased prey availability could potentially have increased foraging times and thus the risk of predation" (Trites et al. 2007, p. 50), yet provides neither analyses nor a theoretical context. Other analyses build a case for concurrent effects of resource scarcity, predation, and competition, but their focus is on the independent effects of these factors (Guénette et al. 2006; Wolf et al. 2006). These nascent discussions are important but need to go farther (Heithaus et al. 2008). Also relevant to the behaviour and conservation of SSLs is the theoretical plausibility that increased predation risk might create functional resource scarcity without any resources actually declining (Lima and Dill 1990; Wirsing et al. 2008).

Testing predictions that incorporate the influence of adaptive decision-making on population parameters will be difficult. Measuring individual reproductive rates, sequential changes in body condition, and cause and location of mortality is quite doable in some systems (e.g. Krebs et al. 1995; Zanette et al. 2003), but difficult to near-impossible for northeast Pacific pinnipeds. Immeasurability, however, is unrelated to the potential importance of a process. In the context of empirical limitations and today's conservation crises, our study is one example of how the greater the dearth of system-specific data, the greater the need to apply general principles of behavioural ecology toward the understanding and management of large-scale marine systems (Mangel and Wolf 2006; Frid et al. 2008; Heithaus et al. 2008).

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