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Inferring prey perception of relative danger in large-scale marine systems

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ABSTRACT

Problem: Infer relative danger from spatially segregated predators in large-scale marine systems, using individual differences in prey foraging behaviour.

Mathematical models: Optimization of trade-offs between predation risk and energy gain.

Key assumption: Foraging individuals choosing to incur higher risk of predation should experience higher energetic gain than individuals choosing safer foraging options.

Organisms: Alaskan harbour seals foraging under predation risk from killer whales and Pacific sleeper sharks in shallow and deep strata, respectively. Sleeper sharks are elusive predators and their interactions with prey are difficult to measure directly.

Method: Our method infers the relative danger from different predator types that is theoretically most plausible according to intermediate consumer behaviour. We predicted net energy gain and predation risk per foraging dive, parameterizing an analytical model with data on seal behaviour and the spatial distributions of predators and resources. We used assumptions about relative danger from different predator types as treatments in a computer experiment. We sought the treatment combination best supporting the assumption that individuals that risk more should gain more by plotting the individual seals' predicted cumulative energy gain against cumulative predation risk. Improved statistical fit for a positive and monotonic relationship implied greater support.

Conclusions: Our key assumption was best supported when assuming that relative danger from sleeper sharks is much greater than that from killer whales, suggesting that sub-lethal effects of sharks on Alaskan harbour seals might be much stronger than previously thought.

Keywords: diving behaviour, harbour seal, hazardous duty pay, individual variation in risk-taking, killer whale, Pacific herring, Pacific sleeper shark, predation risk, resource distribution, risk–energy trade-offs, sub-lethal effects of predators, walleye pollock.

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INTRODUCTION

The ocean is a challenging environment for studying the sub-lethal effects of top predators on their prey. Much of the action may occur far below the surface, in deep and dark waters that ecologists might glimpse only briefly with the aid of remote-operated cameras or other modern technologies. Nonetheless, we can expect that where there is a top predator there will be scared prey attempting to optimize energy gain and predation risk (Lima and Dill, 1990; Brown and Kotler, 2004). Thus, failure to address sub-lethal effects of top predators can preclude important ecological insights into large-scale marine systems (Frid *et al.*, 2007).

The loss of foraging opportunities is a well-known sub-lethal effect of predators on their prey. Myriad experimental, theoretical, and field studies of intermediate consumers support the hypothesis that resource acquisition demands exposure to predators, and conversely risk avoidance entails a functional loss of resources (Lima and Dill, 1990; Lima, 1998; Brown and Kotler, 2004). Energy state, age, and other factors affecting residual reproductive value determine the optimal trade-off between safety and resource gain that an individual should choose (Lima, 1998; Clark and Mangel, 2000). Furthermore, from principles of natural selection we expect individuals to make more dangerous choices only if the fitness costs of increased predation risk are offset by the fitness benefit of enhanced access to resources (e.g. Abrahams and Dill, 1989). This 'hazardous duty pay' paradigm (*sensu* Brown and Kotler, 2004) is widely supported (Lima and Dill, 1990; Lima, 1998; Brown and Kotler, 2004).

Given this theoretical backdrop, a means for indirectly quantifying the sub-lethal effects of elusive predators on their prey in the ocean should be tenable. Here we pursue that challenge through a case study of harbour seals *Phoca vitulina richardsi* in Prince William Sound, Alaska, foraging under predation risk from killer whales (*Orcinus orca*) and Pacific sleeper sharks (*Somniosus pacificus*). Although we are primarily interested in the role of sleeper sharks, risk from killer whales cannot be ignored because observations at the surface already provide direct evidence for lethal effects (e.g. Saulitis *et al.*, 2000). A key feature of the system, which allows us to pursue our goal, is that two important resources used by seals and both types of predator segregate spatially in the water column. Killer whales hunt at or near the surface, overlapping with Pacific herring (*Clupea pallasi*), while sleeper sharks primarily use depths of more than 100 m (Hulbert *et al.*, 2006), overlapping with walleye pollock (*Theragra chalcogramma*).

To infer the seal's perceived risk from sharks, we analysed individual variation in seal foraging tactics in light of the hazardous duty-pay paradigm (Brown and Kotler, 2004). That is, we assumed that foraging individuals choosing to incur higher risk of predation should experience higher energetic gain than individuals choosing safer foraging options. We then predicted net energy gain and predation risk per foraging dive, parameterizing an analytical model with field data on seal behaviour and resource distributions, and with the available data on use of the water column by sharks and killer whales. We used assumptions about relative danger from different predator types as treatments in a computer experiment. We then sought the treatment combination required to generate the pattern of individual variability in risk-taking and energy gain that would best conform to the hazardous duty pay paradigm. This novel application of predation risk theory suggested that sub-lethal effects of sharks on Alaskan harbour seals might be much stronger than previously thought.

METHODS

Our theoretical search for the relative danger from sharks and killer whales faced by seals required that we first modelled risk–energy trade-offs on a per dive basis, and then obtained the cumulative sum of risks and net energetic gains incurred by individuals over the thousands of dives performed. Although the relative danger from sharks and killer whales was our main interest, the model required that we translate depth-specific fish density into expected foraging success (see equation 1). This task led us to combine different risk scenarios factorially with scenarios in which huge but widely dispersed herring schools – effectively rare bonanzas – had either a weak or strong influence on expected foraging success.

We assume that predation risk is influenced by the predators' (a) distribution, (b) abundance, (c) hunting efficiency, and (d) probability of attack given an encounter, and by (e) the prey's behaviour (e.g. Lima and Dill, 1990; Hugie and Dill, 1994). In the model, (a) and (e) are empirical inputs while (b), (c), and (d) are unknown. Thus, we interpret 'relative danger' as the aggregate contribution to seal mortality risk of a predator's abundance, hunting efficiency, and probability of attack given an encounter.

The model

Dive cycles consist of surface intervals for uploading oxygen, travel between the surface and a resource patch, and foraging at that patch. We define patch residence as time spent within 90% of the dive's maximum depth, and travel time as total dive duration minus patch residence time. We assume that depth choice occurs at the onset of a dive, rather than based upon prey encounters during descent or ascent (Simpkins *et al.*, 2001; Wilson, 2003; Mori *et al.*, 2005). The distribution of predators and resources is influenced by diel period and depth (Fig. 1; see Appendix A online),* and time spent at a stratum affects predation risk and energy gain. The model has no density dependence and therefore does not consider games among seals either in energy intake or risk of predation.

Lacking empirical data on how resource density affects foraging success by seals, we developed a function that converts mean fish density in a given stratum into the expected number of fish caught per unit time spent in that stratum. This function had to take into account that, during late winter, most herring schools are widely dispersed and while most herring schools are small, a few are huge. Specifically, 1.6% of depth-specific fish biomass measurements ($n = 951$; see next section) were more than 10 times greater than the mean, and the largest value was 280 times greater (Appendix A). Nine of these extreme outliers represented herring schools in shallow strata, and only two of the smallest outliers represented walleye pollock aggregations at greater depth. The same sampling regime found that pollock in the deep were more evenly distributed than herring in the shallows (Appendix A). It is quite likely that seals in Prince William Sound exploit rare herring bonanzas in the short term if they happen to come upon them. It is unclear, however, the extent to which these events influence expected foraging success during winter, when herring aggregations are found predictably only within a few bays (Thomas and Thorne, 2001, 2003). Furthermore, while the larger, more aggressive Steller sea lion *Eumetopias jubatus*

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* The URL for the online appendices is: http://evolutionary-ecology.com/data/2178appendices.html.

aggregates to exploit wintering herring in these bays (Thomas and Thorne, 2001, 2003), there is no evidence that harbour seals make long-term use of these locations. [None of the seals that we tracked (see next section) foraged inside these bays and Lowry *et al.* (2001) found few satellite tag locations within these bays.] The function was designed to explore two theoretical scenarios. In the first, herring bonanzas are targeted and predictably found by seals, and fish density outliers strongly influence the expected number of fish caught per unit time. In the second scenario, herring bonanzas are too rare to be found predictably and – in the long-term average – the influence of fish density outliers on the expected number of fish caught per unit time is weak.

Let T represent the total number of 1-s time units t spent at a foraging patch and $t = 1$, $t = 2, \ldots, t = T$. Thus, $P_{l,s,d}$, the expected number of fish caught during $t = 1$ by a seal of length l (Appendix B) in depth stratum s during diel period d, is

$$P_{l,s,d} = a_{\varepsilon} Log_{10}((\varepsilon\delta_{l,s,d}) + 1) \tag{1}$$

where $\delta_{l,s,d}$ is the density of fish of exploitable size for the given conditions [i.e. biomass (Appendix A) divided by the average mass of all fish in that stratum (non-exploitable sizes included) and multiplied by the proportion of fish of exploitable size (Appendix C)]. The parameter ε depicts the influence of extreme outliers of fish density on the expected number of fish caught during $t = 1$. The log-transformed product $\varepsilon\delta_{l,s,d}$ implies that as ε increases, the influence of extreme density outliers weakens. Using a_{ε} as a scaler that bounds gross cumulative energy gain within known limits to digestible energy intake by harbour seals [$\approx 4500\ \text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{day}^{-1}$ for captive seals fed a mixed diet of pollock and herring at high frequency (Trumble and Castellini 2005)], we contrasted strong ($\varepsilon = 100$, $a_{100} = 0.13$) versus weak influence ($\varepsilon = 10{,}000$, $a_{10{,}000} = 0.008$) scenarios in computer experiments (Table 1; Figs. 1c,d).

We assume that the cumulative number of fish caught per dive, $\lambda_{l,s,d}$, is a decelerating function of patch residence time,

$$\lambda_{l,s,d} = \sum_{t=1}^{T} P_{l,s,d} k^{t-1} = P_{l,s,d} \frac{(1 - k^{T})}{1 - k} \tag{2}$$

Table 1. Experimental treatment combinations

	Levels of each treatment		
Experiment	ε*	μ_{shark}	μ_{orca}
1	100	0	5.00×10^{-9}
2	100	5.00×10^{-9}	5.00×10^{-9}
3	100	1.25×10^{-7}	5.00×10^{-9}
4	100	2.5×10^{-7}	5.00×10^{-9}
5	10,000	0	5.00×10^{-9}
6	10,000	5.00×10^{-9}	5.00×10^{-9}
7	10,000	2.5×10^{-7}	5.00×10^{-9}
8	10,000	2.5×10^{-7}	5.00×10^{-9}

* $a_{100} = 0.13$ and $a_{10{,}000} = 0.008$ (equation 1).

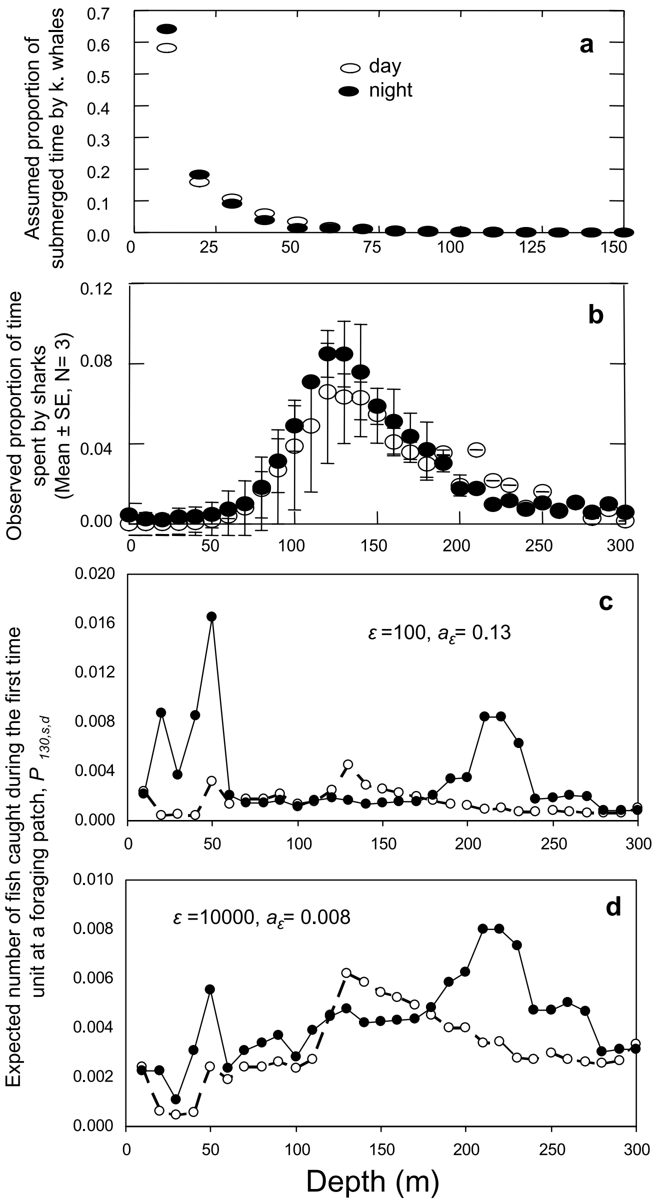

Fig. 1. Factors influencing predation risk and energy gain per dive. (a, b) Proportions of time-at-depth by each predator type were empirically based inputs into equation (6), which, when combined with different μ_{shark} to μ_{orca} ratios (Table 1), were used to predict predation risk per dive under four contrasting assumptions about the relative danger of sharks and killer whales. (c, d) The expected number of fish caught during the first time period at a foraging patch illustrate the two theoretical scenarios used to contrast assumptions about the influence of rare herring bonanzas on foraging success. These scenarios were derived by combining data on fish distributions (Appendices A, C) with different values of ε into equation (1). (The $P_{\leq 115,s,d}$ scenario is not shown; see 'Methods' for details.) Panel (a) is based on P.J.O. Miller, A.D. Shapiro, and V.B. Deecke (unpublished data). Panel (b) is based on a subset of data from Hulbert *et al.* (2006). SE = standard error of the mean.

where $k = 0.99$ is the proportion of resources available at t relative to $t - 1$ (for sensitivity analysis, see Appendix F). Based on the energy content (kJ) of exploitable fish at a given depth (Appendix C), $\psi_{l,s}$, gross gain per dive for a seal of length l, G_l, is

$$G_l = \psi_{l,s}\lambda_{l,s,d} \tag{3}$$

We assumed that the metabolic cost of pausing at the surface for a seal of mass m, r_m, was 0.00154 $\mathrm{kJ \cdot kg^{-1} \cdot s^{-1}}$ if $m \geq 48$ kg or 0.00170 $\mathrm{kJ \cdot kg^{-1} \cdot s^{-1}}$ if $m \leq 40$ kg. These values were converted from oxygen consumption rates when resting at the surface by a 63- and a 33-kg harbour seal, respectively (Williams, 1999). The total cost of pausing at the surface, R_m, is the product of r_m, the individual's mass, and pause duration (s).

Travel rate, ρ, was calculated as vertical distance divided by time spent ascending and descending. Surface swimming is energetically more expensive than vertical travel (see Williams, 1999; Williams *et al.*, 2000), but vertical swimming costs have yet to be measured for harbour seals. Thus, we assumed that the metabolic cost of vertical travel at rate ρ for a seal of mass m, $v_{\rho,m}$, was 65% of the cost of surface swimming at the same rate. To obtain $v_{\rho,m}$, we first estimated oxygen consumption ($V\mathrm{O_2}$ in $\mathrm{ml \cdot min^{-1} \cdot kg^{-1}}$) as $4.6 + 3.1\rho^{1.42}$ if $m \geq 48$ kg or $5.1 + 6.25\rho^{1.42}$ if $m \leq 40$ kg. These equations were derived for a 63- and a 33-kg harbour seal, respectively, swimming at the surface (Davis *et al.*, 1985). Resulting estimates were multiplied by 0.65 and converted to $\mathrm{kJ \cdot kg^{-1} \cdot s^{-1}}$. Seals were assumed to glide passively through a depth-dependent proportion of descent and ascent (Williams *et al.*, 2000) with a metabolic cost equal to r_m. Total travel cost (kJ) per dive, τ_m, is

$$\tau_m = ((\phi - \gamma)v_{\rho,m} + \gamma r_m)m \tag{4}$$

where ϕ is total travel time and γ is seconds spent gliding (Williams *et al.*, 2000). While ρ and ϕ were measured empirically (Appendix D), γ was estimated from Williams and colleagues' (2000) Figure 2. (Negative estimates for shallow dives were treated as zeroes.)

Energetic cost at the foraging patch was estimated from Davis and colleagues' (1985) equations described above for surface swimming costs, and by assuming $\rho = 1\ \mathrm{m \cdot s^{-1}}$. Here we multiplied $V\mathrm{O_2}$ estimates by 0.75 to account for lower energy costs below the surface before converting to $\mathrm{kJ \cdot kg^{-1} \cdot s^{-1}}$. The latter value multiplied by body mass and patch residence time was the per dive cost of foraging at the patch, B_m. Net energetic gain (kJ) per dive, E, is

$$E = G_l - R_m - \tau_m - B_m \tag{5}$$

The probability of predation during dive cycle component ω (surface interval, vertical travel or foraging at the patch) for a dive to stratum s during diel period d, $\mu_{\omega,s,d}$, is

$$\mu_{\omega,s,d} = h_\omega(1 - (1 - \mu_{\mathrm{shark}}\,T_{\mathrm{shark}_{s,d}} - \mu_{\mathrm{orca}}\,T_{\mathrm{orca}_{s,d}} + \mu_{\mathrm{shark}}\,T_{\mathrm{shark}_{s,d}}\mu_{\mathrm{orca}}\,T_{\mathrm{orca}_{s,d}})^{\zeta}) \tag{6}$$

where μ_{shark} and μ_{orca} represent relative danger from the given predator type (see Table 1). Variable $T_{\mathrm{shark}_{s,d}}$ is the empirical estimate for the mean proportion of time sharks spent at s during d, $T_{\mathrm{orca}_{s,d}}$ is the empirical estimate for the mean proportion of subsurface time killer whales spent at s during d (Fig. 1), and ζ is the duration (s) of ω (Appendix D). Variable h_ω represents the assumption that vertical travel is safer than remaining within a stratum, such that $h_\omega = 1$ if $\omega =$ foraging or surface interval and $h_\omega = 0.25$ if $\omega =$ vertical travel. If dives were very deep, risk from killer whales during vertical travel was estimated only for the portion of descent and ascent that crossed the shallower depths used by killer whales.

Background risk from killer whales at the surface, $T_{\mathrm{orca}_{0,d}}$, equalled the value of μ_{orca}. Total predation risk per dive, μ_{dive}, is

$$\mu_{\mathrm{dive}} = \sum_{\omega} \mu_{\omega,s,d} \tag{7}$$

Parameterization

Time allocation by seals

Data on time allocation by seals were empirical inputs for the model's behavioural parameters. During late February 2004 in southwestern Prince William Sound, 28 harbour seals were caught by entanglement in a seine net set near their haulout and transferred to a large vessel where morphometrics were recorded. Capture and handling procedures followed those described in Lowry *et al.* (2001). A subset of 13 harbour seals (Appendix B) were instrumented with time-at-depth recorders (TDRs; Mk9 Wildlife Computers, Redmond, WA) programmed to record depth every 2 s with 0.5-m resolution. The time-at-depth recorders were embedded in flotation packages of syntactic foam glued with Devcon 5 Minute® Epoxy to the seal's back, which released when seals moulted in early summer. Nine time-at-depth recorders were subsequently recovered by tracking the signal of a VHF transmitter embedded in the syntactic foam. Instrument packages were shaped to reduce hydrodynamic drag [i.e. rounded and thinner/narrower at the front; maximum dimensions (excluding VHF antenna): length = 15.3 cm, width = 8.5 cm, thickness = 3.5 cm; weight with instruments = 351 g]. The TDR archived data for 5 months but analyses are for late February through March, when we collected resource distribution data. Seals also were instrumented with head-mounted VHF transmitters (MM 270, Advanced Telemetry Systems, Isanti, MN) for surface tracking.

Time-at-depth data were filtered for analyses. Minimum diving depth was 6 m because methods for quantifying fish biomass were optimized for depths of > 5 m. We excluded data for 24 h after releasing seals, when handling stress might have influenced their behaviour. Dives with surface intervals of > 5 min were excluded because even the longest dives (i.e. > 10 min long) tended to be associated with < 3 min surfacings (both pre- and post-dive), and longer surfacings tended to be associated with extended moves on the surface (as determined from focal follows).

Resource distribution

To estimate $\delta_{l,s,d}$, we collected data on depth-specific fish biomass (Appendix A) during late February and early March 2004. Measures were made along the foraging tracks of seals individually followed from a moving vessel during day and night. While lagging 0.5–2.0 km behind the seal to avoid disturbance, depth-specific fish biomass was estimated for the entire water column every second and averaged every minute with a BioSonics DT4000 echo-sounder at 70 kHz (see Thomas and Thorne, 2003). Sampling periods lasted approximately 30 min, the limit determined by data file size. The towed transducer, however, was unstable when the vessel was stationary; data from these periods were of lower quality and thus excluded, yielding effective sampling period durations of 2–22 min (mean ± standard deviation: 6.9 ± 3.5 min, $n = 86$ sampling periods). Depending on the weather and navigation hazards, we collected multiple samples on the foraging tracks of individual seals during 1.5- to 10-h focal follows (gaps between samples were < 15 min). Effort was spread over nine individuals over 2 weeks. Seals remained in habitats less than 120 m deep during focal follows. The TDR data, however, later showed use of much deeper strata; data for habitats with maximum depths of 400 m were obtained from walleye pollock surveys conducted in the same area during March 2003 (Thorne, 2004). The protocol of pollock surveys was as described above, except the vessel's path was a grid transect and data were recorded only for depths ≥50 m ($n = 16$ sampling periods with mean duration ± standard deviation of 24.8 ± 5.6 min). Data from focal follows and pollock surveys were pooled. Mean fish biomass values ($\mathrm{kg \cdot m^{-3}}$) at each sampling period, stratified by 10-m depth bins, were the units of analyses ($n = 956$; see Appendix A).

Based on surveys conducted during March and April of 2000–2004 (Thomas and Thorne, 2001, 2003; Thorne, 2004), we assumed that fish biomass at 6–55 m and > 95 m depths was dominated by Pacific herring and walleye pollock, respectively, and that equal proportions of these species comprised the biomass at 56–95 m depths. Herring and pollock appear to be dominant items in the diet of seals in southern Prince William Sound (Iverson *et al.*, 1997), and we did not consider other species.

Weights and fork lengths of Pacific herring were estimated from nocturnal purse seine catches in the upper 40 m of the water column during late March and early April 2004 [Alaska Department of Fish and Game test fishery surveys for eastern Prince William Sound (S. Moffitt, unpublished data)]. Walleye pollock sizes were estimated from mid-water trawls at 250-m depths during March 2003 in the general vicinity of seal capture sites [Alaska Department of Fish and Game ground fish surveys (W. Bechtol, unpublished data)].

Data are lacking for the maximum fish sizes consumed by seals in Prince William Sound during winter. Thus, $\delta_{l,s,d}$ estimates assumed that maximum exploitable lengths of fish were 40 and 45 cm, respectively, for seals with standard lengths, l, of 99–115 and 130–157 cm (Appendix B). Based on this assumption, all herring were exploitable (maximum fork tail length = 28.0 cm). Pollock, however, had a maximum fork tail length of 67.2 cm and the assumed exploitable proportion of pollock was 0.66 if $l \leq 115$ cm or 0.80 if $l \geq 130$ cm. [Of 1383 pollock caught in the 2003 trawls, 915 were ≤40 cm and 1108 were ≤45 cm (W. Bechtol, unpublished data).] Appendix C describes average size and energy content of fish under these assumptions (see also sensitivity analyses in Appendix F).

Time-at-depth by sleeper sharks

Parameterization of $T_{\mathbf{shark}_{s,d}}$ was based on the behaviour of three sleeper sharks instrumented in Prince William Sound or adjacent Gulf of Alaska, the subset of sharks studied by Hulbert *et al.* (2006) for which depths were recorded every minute (see their 'Methods'). While the small sample size is not ideal, these sharks' pattern of depth use within the strata used by seals (0–300 m) was qualitatively similar to that of eight other sharks for which coarser behavioural data were available. Namely, all 11 sharks spent more time at depths of 100–300 m than in shallower strata and, with one exception, rarely used depths shallower than 50 m (Table V of Hulbert *et al.*, 2006).

Archived depth data encompassed multiple months, but for each shark we used a 4-week subset approximating the season of our study. For sharks identified as 2, 11, and 21 [Appendix B (see Hulbert *et al.*, 2006)], these periods were March 2002, 15 January to 15 February 2002, and 3 November to 3 December 2002, respectively. The TDR maximum depth resolution was 1000 m for shark 21 but only 200 m for sharks 2 and 11. For the latter two sharks, depths greater than 200 m were pooled into a maximum depth bin (Hulbert *et al.*, 2006), which we excluded from analyses. From these data we estimated the mean proportions of time each shark spent at 10-m depth bins, and used individual means to calculate the overall mean for all sharks (Fig. 1b).

Time-at-depth by killer whales

We parameterized $T_{\mathrm{orca}_{s,d}}$ based on data collected from 29 June to 10 July 2006 for 10 mammal-eating killer whales in Frederick Sound, Stephens Passage, Chatham Strait, and adjacent inlets in Southeast Alaska (P.J.O. Miller, A.D. Shapiro and V.B. Deecke, unpublished data). The whales belonged to eight social groups and their time-at-depth records lasted 1.4–16.4 h per individual. Data from members of the same social group (two different pairs) were collected on different days and should therefore be reasonably independent. Though covering a different season and region of Alaska than our study, these are the only replicated data available. [An unreplicated study in Sumner Strait, Southeast Alaska, found similar patterns of depth use (Baird, 1994).] By diel period, we estimated the mean proportions of submerged time each individual spent at 10-m depth bins (except the shallowest bin, which was 0–15 m), from which we calculated the overall mean, weighted by the duration of each individual's time-at-depth record (Fig. 1a).

Computer experiments and sensitivity analyses

Model assumptions on the relative risk of mortality from each predator type and the influence of rare bonanzas on expected resource encounter rate were treated as variables in a factorial experiment. In this context, the term 'experiment' does not imply stochasticity, as in Monte Carlo simulations (e.g. Clark and Mangel, 2000). Rather, as described below, it refers to the process of determining which combination of assumptions made predictions that were most consistent with the hazardous duty pay paradigm.

There were eight treatment combinations: two levels of ε and four levels of $\mu_{\mathbf{shark}}$ to $\mu_{\mathbf{orca}}$ ratios (Table 1). We determined the set of assumptions that was most consistent with the hazardous duty pay paradigm by plotting the individuals' predicted cumulative net energy gain against predicted cumulative predation risk for each computer experiment. Improved statistical fit (higher R^2) for a positive relationship implied stronger support. Plots were adjusted for differences in the duration of the individuals' behavioural records (range 33.3–36.4 days).

Sensitivity analyses scrutinized four parameters whose values had little or no empirical support and which potentially could produce suspect conclusions. We changed these values and re-ran the computer experiments as described in Appendix F, testing whether the relative fit of plots derived from each treatment combination (Table 1) was robust to re-parameterization.

RESULTS

We first outline the main spatial trade-offs faced by seals under model assumptions. If rare bonanzas are assumed to have a weak influence on long-term foraging success ($\varepsilon = 10{,}000$), the expected number of fish caught upon arriving at a depth stratum (i.e. during $t = 1$; hereafter 'expected fish captures') is greatest at depths of 70–270 m during day and night, overlapping with strata where sharks spend most of their time. The exception is the 50-m stratum at night, which is used little by sharks and is where expected fish captures at depths of less than 200 m are greatest during the night. If rare bonanzas are assumed to strongly influence foraging success ($\varepsilon = 100$), expected fish captures are greatest in strata ≤ 50 m during the night, where killer whales are assumed to spend most of their submerged time and sharks spend little time (Fig. 1). Although herring have a higher energy density than pollock, pollock are larger; consequently, expected energy gain per captured fish is greater at depths of more than 50 than in shallower strata (Appendix C), regardless of ε.

Next we summarize the observed behaviour of seals used as empirical inputs into the model. Individual variability in foraging tactics was manifested as differences in depth choice, total number of dives, and diel periodicity (Fig. 2). Possibly influenced by an increase in expected fish captures nearer to the surface at night (see Figs. 1c,d), dives were shallower and individual differences in depth choice were smaller at night than during the day. Also, seals that preferred shallow strata dove mostly at night while the two deepest diving individuals (af17 and yf22) had the greatest proportion of daytime dives and the least number of total dives (Fig. 2). As predicted by theory (see Frid *et al.*, 2007, and references within),

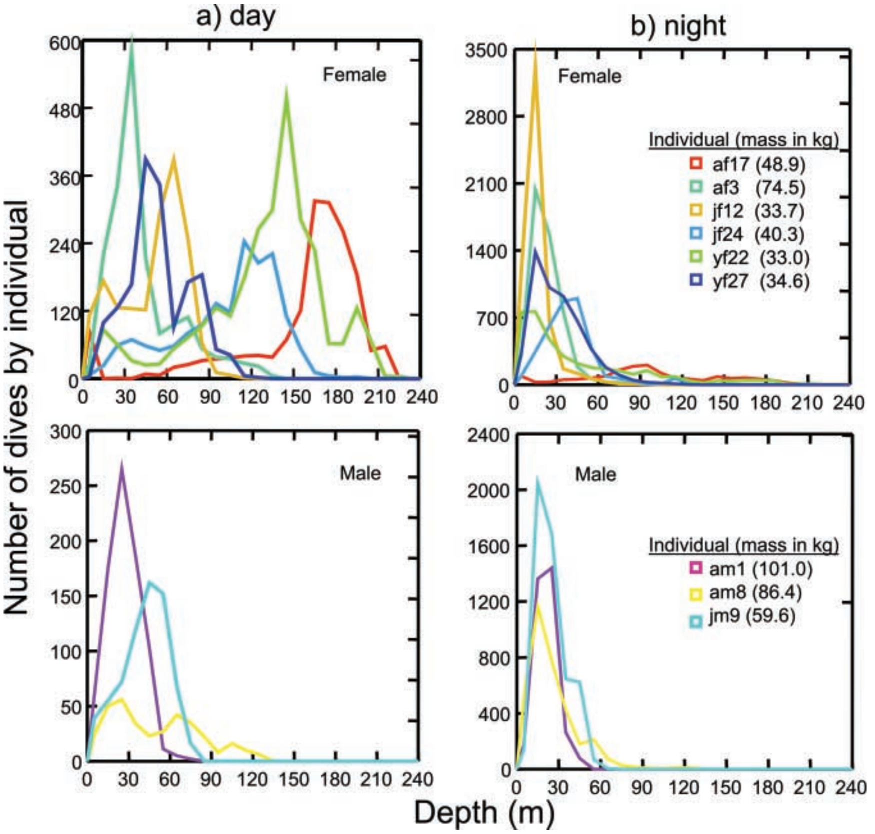

Fig. 2. Individual variation in depth, diel period, and total number of dives by harbour seals in Prince William Sound during late February to 31 March 2004. Letters in the key indicate likely age class (a = adult ≥3 years, j = juvenile 1–2 years, y = yearling <1 year; see Table 1) and gender (f = female, m = male). Frequency polygons are for 10-m depth bins. Note that the y-axis scales differ between panels.

the duration of surface intervals, travel durations, and patch residence times generally increased with depth (Appendix D). In addition, travel rate (average descent and ascent rates combined) increased during deeper dives (Appendix D). There were no apparent effects of body mass or age-class on individual depth preferences (Fig. 2), which is surprising given that mass limits dive capacity and has been found to influence harbour seal diving characteristics in other systems (e.g. Eguchi and Harvey, 2005). Our results and those of others (Costa and Gales, 2000) suggest that interactions between ecological conditions and the individual's state can influence average dive characteristics more strongly than body mass alone.

The outcome of computer experiments was as follows. Given that individuals differed in their diving behaviour, so did their predicted predation risk and energy gain. This was the case on a per dive basis (Appendix E) and for the cumulative sum of risks and net energetic gains incurred by individuals over the thousands of dives performed (Fig. 3). The regression model for plots of individuals' predicted cumulative energy gain against cumulative predation risk had a positive slope and best statistical fit (highest R^2) when assuming a 50 : 1 ratio of $\mu_{\mathbf{shark}}$ to $\mu_{\mathbf{orca}}$ and $\varepsilon = 10{,}000$ (Experiment 8 in Table 1; Fig. 3). The worst fit resulted when killer whales were assumed to be the only dangerous predator, regardless of the value of ε. The fit also was poor when $\varepsilon = 100$ for all ratios of $\mu_{\mathbf{shark}}$ to $\mu_{\mathbf{orca}}$ (Fig. 3). Results were robust to sensitivity analyses (Appendix F).

DISCUSSION

Our objective was to derive the most plausible hypothesis concerning the relative danger from sharks and killer whales faced by seals by applying the hazardous duty pay paradigm (*sensu* Brown and Kotler, 2004). Empirical data on individual variability in seal foraging tactics and the distribution of resources and top predators are inherent to this framework.

Individual seals differed in their observed use of deep strata, where sleeper sharks spent most of their time and net energy gain was predicted to be highest based on the assumption that rare bonanzas have a weak influence on the expected number of fish caught per unit time. From first principles, we expect individuals that risk more to gain more (Abrahams and Dill, 1989; Brown and Kotler, 2004). Accordingly, plots of individual seals' predicted cumulative energy gain against cumulative predation risk had a positive slope and the best statistical fit when relative danger from sleeper sharks was assumed to be 50 times greater than that of killer whales, and the worst fit when sharks were assumed to not be dangerous or only as dangerous as killer whales. During *a posteriori* analyses, statistical fit improved if assuming even greater shark danger ($R^2 = 0.95$ for a $\mu_{\mathbf{shark}}$ to $\mu_{\mathbf{orca}}$ ratio of 75 : 1 and $\varepsilon = 10{,}000$, vs. $R^2 = 0.92$ for the 50 : 1 ratio of Experiment 8). The point is not whether a ratio of 75 : 1 is better and statistically different from 50:1 or 25:1, but that relative danger from sharks must be assumed to be much greater than that of killer whales for predictions on energy gain and predation risk to conform to the hazardous duty pay paradigm. Thus, our model suggests that the system has many more large sharks (i.e. large enough to threaten seals) than killer whales and that seals perceive sharks to be the greater threat. Theoretically, we expect seals that prefer the relative safety of shallow strata to have better energy stores than seals preferring greater depths (Clark and Mangel, 2000; Frid *et al.*, 2006). Unfortunately, our data were limited to nine individuals spread over five age–sex classes and cannot test this prediction.

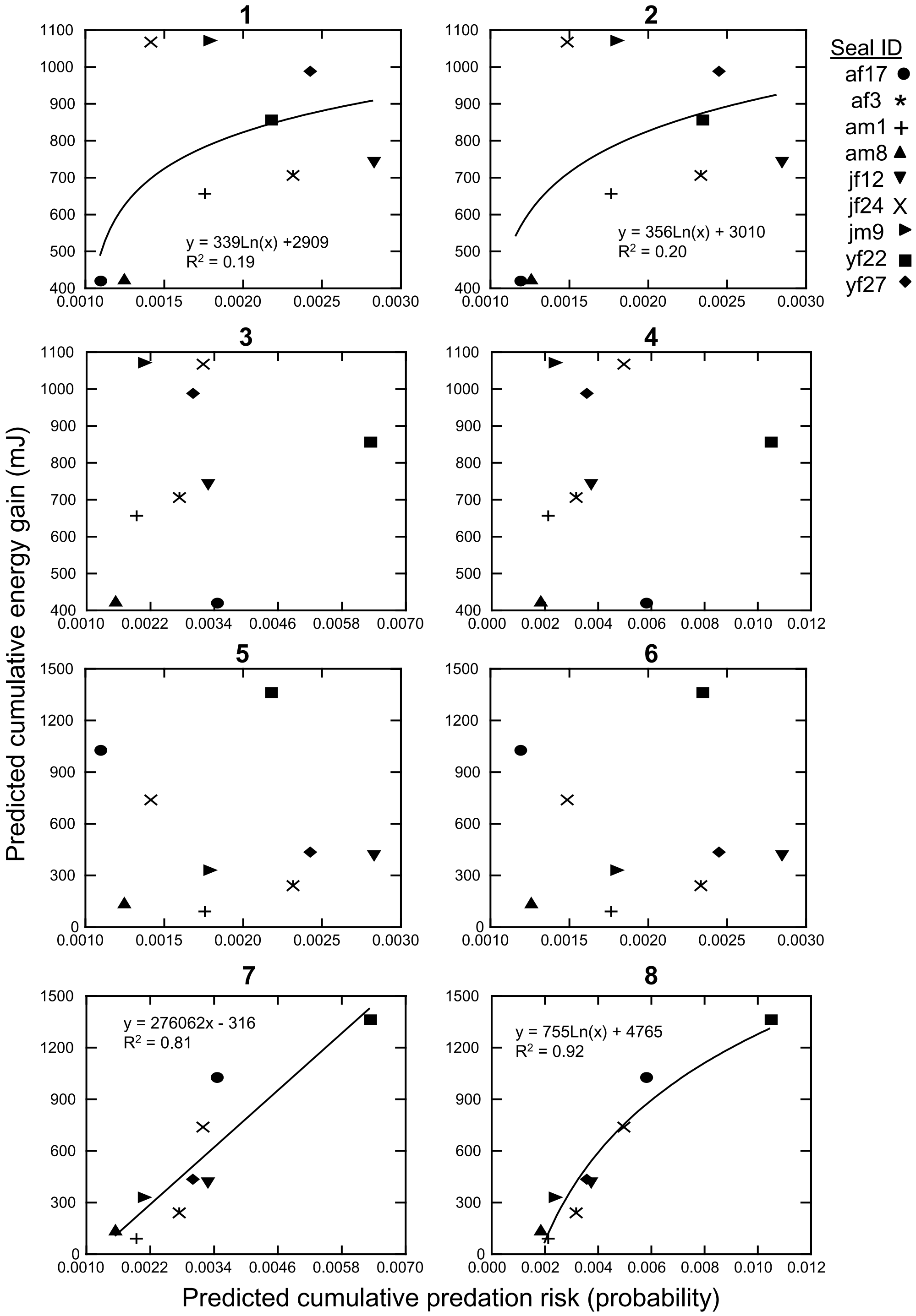

Fig. 3. Outcome of computer experiments. Each data point represents the cumulative sum of risks and net energetic gains incurred by individuals over the thousands of dives performed. Each of the panels represents a different theoretical scenario and their labels correspond to computer experiments described in Table 1.

Results also suggest that rare bonanzas have a weak influence on expected foraging success by Prince William Sound seals during winter. Plots of predicted cumulative energy gain against cumulative predation risk had the positive relationship inherent to the hazardous duty pay paradigm only under this assumption provided that, as detailed above, relative danger from sharks was assumed to be much greater than that of killer whales. All conclusions were robust to sensitivity analyses (Appendix F).

We point out that evidence for lethal effects of sleeper sharks on North Pacific pinnipeds is currently weak (Sigler *et al.*, 2006), yet this has no bearing on our conclusions. As stated in a seminal synthesis, 'antipredator behavior may be so effective that predators are rarely successful' and 'lack of observed predation does not necessarily imply a lack of behavioral sensitivity to the risk of predation' (Lima and Dill, 1990, p. 634). Thus, a small number of top predators can spread fear and elicit anti-predator responses that compromise energy gain across an entire population of intermediate consumers while killing few, if any, individuals (Lima and Dill, 1990; Brown and Kotler, 2004). Such sub-lethal costs inflicted by predators on prey are ubiquitous (Lima, 1998) and are now being documented in a marine mammal–shark system where local conditions are unusually favourable for empirical tests (e.g. Heithaus and Dill, 2006; Wirsing *et al.*, in press).

Our theoretically based method for inferring relative danger from different top predators is not entirely new. Gurung (2003, cited in Brown and Kotler, 2004) inferred the distribution of snow leopards (*Uncia uncia*) from the vigilance of ungulate prey. Alonzo *et al.* (2003, p. 1598) described this general framework as 'an inverse problem in biology where we infer an unknown relationship by examining patterns that are predicted to be the outcome of a given interaction'. Clearly, empirical data on seal–shark interactions are needed to test our interpretations of seal behavioural signals. Such data, however, may require great expense and time to collect. In the meantime, we can 'use what is known about each individual species and ecological interactions in general to understand what is relatively unknown – interactions between particular species' (Alonzo *et al.*, 2003, p. 1598).

A limitation of our method is that it can suggest relative danger from multiple predators only if these are segregated in the water column. Salmon sharks (*Lamna ditropis*), for instance, are abundant in Prince William Sound and primarily use the upper 40-m strata (Hulbert *et al.*, 2005). Although we did not consider them in the model because only fish or cephalopods have been found in their stomachs (Hulbert *et al.*, 2005), what we assumed to be killer whale risk may in fact represent the combined risk from salmon sharks and killer whales. Also, to remain tractable, the model could not consider the energetic needs and foraging decisions of sharks and killer whales. Future work, however, could incorporate game-theoretical approaches that simultaneously predict state-dependent responses of sharks and killer whales to seals and vice versa (e.g. Alonzo *et al.*, 2003). Also, the model assumes that seals dive to forage. This assumption may not be true of every dive, possibly leading to overestimation of energy intake rates. The overestimation, however, would apply to all individual seals and is unlikely to have biased our results.

Our study develops a methodology for inferring the relative danger from different top predators that is theoretically most plausible according to intermediate consumer behaviour. Our general framework could be applied to many types of large-scale ecosystems, including terrestrial ones (e.g. Hernandez *et al.*, 2005), where the sub-lethal effects of rare or elusive predators cannot be measured directly and thus might be under-appreciated.

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