

# Do resource declines increase predation rates on North Pacific harbor seals? A behavior-based plausibility model

Alejandro Frid<sup>1,\*</sup>, Gregory G. Baker<sup>2</sup>, Lawrence M. Dill<sup>1</sup>

<sup>1</sup>Behavioural Ecology Research Group, Department of Biological Sciences, and <sup>2</sup>School of Computing Science, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

*Marine Ecology Progress Series 312:265–275 (2006)*

**Appendix 1.** *Phoca vitulina*. Derivation of a dynamic state variable model of foraging decisions by harbor seals in Prince William Sound, Alaska

The model's terminal horizon,  $T$ , is when condition-dependent reproduction occurs. The time span preceding  $T$  is divided into 20 s time units,  $t$ , and decisions are made every  $t$ . The model has 2 internal state variables:  $X(t) = x$  represents energy reserves at  $t$  and  $Y(t) = y$  represents oxygen stores at  $t$ . Their 'discretized' values (see Appendix 2) are 0 to 45 and 0 to 11, respectively.

An environmental state,  $H(t) = h$ , represents location at  $t$  (Fig. 1). We will use the notation  $depth(H(t))$  to indicate the depth (in meters) from the surface to  $H(t)$ , and  $dist(H(t))$  to represent the distance (in meters) from the refuge. The spatial structure of environmental states is as follows.  $H(t) = 0$  represents a predation refuge lacking food where  $depth(0) = 0$  and  $dist(0) = 0$  (i. e. the haulout) and seals must be there by  $T$  to reproduce.  $H(t) = 25$  represents the surface of a nearshore, shallow habitat with  $dist(25) = 500$ , and  $depth(25) = 0$ .  $H(t) = 150$  is the surface of an offshore, deep habitat with  $dist(150) = 3000$  and  $depth(150) = 0$ ; this is 2500 m from Location 25.  $H(t) = 2$  is a demersal foraging patch available from location 25 with  $depth(2) = 40$ .  $H(t) = 1$  is a pelagic foraging patch available from Location 150 with  $depth(1) = 20$ .  $H(t) = 5$  is a demersal foraging patch available from Location 150 with  $depth(5) = 100$ . We will refer to Locations 0, 25, and 150 as *habitats*, with the latter 2 further qualified as foraging habitats, and Locations 1, 2 and 5 as *depths* or *patches* (Fig. 1).

The decision variable is  $D(x, y, h, t) = d$ , where  $d$  is the future location (at either  $t + 1$  or  $t + \text{travel time}$ , see below) chosen by a seal from Location  $h$  and at Time  $t$ . Decisions are unconstrained by time of day or night but limited by the value of  $h$ , as described in state dynamics (below). We assume a travel speed of  $1 \text{ m s}^{-1}$  between habitats and depths. The notation  $time(h, d)$  will indicate the travel time (in 20 s time units) from Locations  $h$  to  $d$ , which is  $|dist(h) - dist(d)|/20$  for surface transit and  $|depth(h) - depth(d)|/20$  for diving. Thus, the values of  $H(t) = h$  listed earlier correspond to the number of 20 s time units required to travel to the given location from either the refuge (if switching surface habitats) or from the surface (if diving). We will use  $\Pr\{h, d\}$  to indicate the probability of surviving the transition from  $h$  to  $d$ . So,  $\Pr\{h, d\} = p$  indicates that there is a  $1-p$  probability of predation during the behavior in question. See Appendix 2 for parameter values.

## State dynamics

Here we describe how decisions affect state variables at the subsequent time period. A seal at the refuge or at a surface habitat can decide to remain or switch habitats. If it stays at the current habitat,

$$\begin{aligned} X(t+1) &= x - \alpha_{h,d} \\ Y(t+1) &= \begin{cases} y_k & \text{if } h=0, \\ y + \beta e^{-zy} & \text{if } h=25 \text{ or } 150 \end{cases} \\ H(t+1) &= d \\ \Pr\{h, d\} &= 1 - \mu_{\text{shark}}(h, d) - \mu_{\text{orca}}(h, d) + \mu_{\text{shark}}(h, d)\mu_{\text{orca}}(h, d) \end{aligned} \quad (\text{A1})$$

where  $\alpha_{h,d}$  is the energetic cost of Decision  $d$  made at Location  $h$ ; the constant  $y_k = 6$  represents oxygen stores when not diving (i.e. at the refuge or during surface transit);  $\beta = 1693$  and  $z = 0.0007$  are scalars (Appendix 2) determining the shape of the oxygen-gain curve as a decelerating function of  $Y(t) = y$  (see Kramer 1988);  $\mu_{\text{shark}}(h, d)$  and  $\mu_{\text{orca}}(h, d)$  are the probabilities of predation by sleeper sharks *Somniosus pacificus* and killer whales *Orcinus orca*, respectively, when making Decision  $d$  at Location  $h$ .

If seals decide to switch habitats,  $D(x, y, h, t) = d$ , with  $(h, d)$  one of (0, 25), (25, 0), (0, 150), (150, 0), (25, 150), or (150, 25), and

$$\begin{aligned} X(t + \text{time}(h, d)) &= x - \text{time}(h, d)\alpha_{h,d} \\ Y(t + \text{time}(h, d)) &= y_k \\ H(t + \text{time}(h, d)) &= d \\ \Pr\{h, d\} &= [1 - \mu_{\text{shark}}(h, d) - \mu_{\text{orca}}(h, d) + \mu_{\text{shark}}(h, d)\mu_{\text{orca}}(h, d)]^{\text{time}(h, d)} \end{aligned} \quad (\text{A2})$$

If a seal at the surface of a foraging habitat chooses to dive, or a seal at a foraging patch chooses to ascend, then  $D(x, y, h, t) = d$ , with  $(h, d)$  one of (150, 1), (1, 150), (150, 5), (5, 150), (25, 2), or (2, 25) and

Appendix 1 (continued)

$$\begin{aligned}
 X(t + \text{time}(h, d)) &= x - \text{time}(h, d)\alpha_{h,d} \\
 Y(t + \text{time}(h, d)) &= y - \text{time}(h, d)u_{h,d} \\
 H(t + \text{time}(h, d)) &= d \\
 \Pr \{h, d\} &= [1 - \mu_{\text{shark}}(h, d) - \mu_{\text{orca}}(h, d) + \mu_{\text{shark}}(h, d)\mu_{\text{orca}}(h, d)]^{\text{time}(h, d)}
 \end{aligned} \tag{A3}$$

where  $u_{h,d}$  is the oxygen cost of Decision  $d$  made at Location  $h$ .

When a seal at a depth stratum ( $h = 1, 2, 5$ ) chooses to remain ( $h = d$ ), there are 2 possible outcomes. First, the seal may encounter and capture prey with probability  $\lambda_h$  and then

$$\begin{aligned}
 X(t+1) &= x + g_h - c\alpha_{h,d} \\
 Y(t+1) &= y - cu_{h,d} \\
 H(t+1) &= d \\
 \Pr \{h, d\} &= 1 - \mu_{\text{shark}}(h, d) - \mu_{\text{orca}}(h, d) + \mu_{\text{shark}}(h, d)\mu_{\text{orca}}(h, d)
 \end{aligned} \tag{A4}$$

where  $g_h$  is energy gain at location  $h$  if prey are captured and  $c = 2$  is a constant representing the added expenditure of chasing and handling prey.

If the seal does not encounter prey, with probability  $1 - \lambda_h$ , then

$$\begin{aligned}
 X(t+1) &= x - \alpha_{h,d} \\
 Y(t+1) &= y - u_{h,d} \\
 H(t+1) &= d \\
 \Pr \{h, d\} &= 1 - \mu_{\text{shark}}(h, d) - \mu_{\text{orca}}(h, d) + \mu_{\text{shark}}(h, d)\mu_{\text{orca}}(h, d)
 \end{aligned} \tag{A5}$$

Let  $F(x, y, h, t)$  be the maximum expected reproductive success at  $T$ , given that  $X(t) = x$ ,  $Y(t) = y$ ,  $H(t) = h$ , and the seal behaves optimally from  $t + 1$  until  $T$ . Let  $V_d(x, y, h, t)$  be the fitness value of decision  $d$ , as determined by Eqs.(A1) to (A5), for a given time period and set of states. Then, the dynamic programming equations (Clark & Mangel 2000), which are solved by backwards iteration from the terminal fitness function described later, are as follows for the possible locations:

$$\begin{aligned}
 F(x, y, 0, t) &= \max[V_0(x, y, 0, t), V_{25}(x, y, 0, t), V_{150}(x, y, 0, t)] \\
 F(x, y, 25, t) &= \max[V_0(x, y, 25, t), V_2(x, y, 25, t), V_{25}(x, y, 25, t), V_{150}(x, y, 25, t)] \\
 F(x, y, 150, t) &= \max[V_0(x, y, 150, t), V_1(x, y, 150, t), V_5(x, y, 1, 50, t) \\
 &\quad V_{25}(x, y, 150, t), V_{150}(x, y, 150, t)] \\
 F(x, y, 2, t) &= \max[V_2(x, y, 2, t), V_{25}(x, y, 2, t)] \\
 F(x, y, 1, t) &= \max[V_1(x, y, 1, t), V_{150}(x, y, 1, t)] \\
 F(x, y, 5, t) &= \max[V_5(x, y, 5, t), V_{150}(x, y, 5, t)]
 \end{aligned} \tag{A6}$$

**Terminal fitness function**

Next, we assume that  $\psi$  and  $\sigma$  are, respectively, the probabilities of producing an offspring that will survive until weaning, and of surviving from  $T$  to the following reproductive season, given that  $X(T) = x$ . After  $T$ , the expected number of pups produced over the remaining lifespan of 20 yr is given by  $\phi$ . Then, the terminal fitness function becomes:

$$F(x, y, h, T) = \psi + \sigma\phi \tag{A7}$$

where  $\psi$  and  $\sigma$  depend on  $X(T) = x$  such that

$$\psi = \begin{cases} 0 & \text{if } X(T) < 8 \text{ or } H(t) \neq 0, \\ -0.00002x^3 + 0.00161x^2 - 0.01134x & \text{if } X(T) \geq 8 \text{ and } H(t) = 0 \end{cases} \tag{A8}$$

and

$$\sigma = 0.77x^{0.041} \tag{A9}$$

Eq. (A8) describes an assumed shape. We chose this increasing sigmoid function because body mass, which correlates with energy stores (Bowen et al. 2001), may influence fertility (Boyd 2000) and offspring survival (Bowen et al. 2001). Thus, Eq. (A8) depicts our assumption that seals in the lowest range of energy states have no possibility of reproducing that year, but current fitness rises and then decelerates with increasing values of  $X(T)$ . Eq. (A9) was constructed by running a preliminary model with baseline parameters values (Tables 1 & 2) and using Eq. (A8) as the terminal fitness function. We ran 9 sets of forward iterations (1000 replicates per treatment) in which initial energy state varied in 5 U increments from  $X(0) = 5$  to  $X(0) = 45$ . These bounds correspond, respectively, to  $0.11x_{\text{max}}$  and  $x_{\text{max}}$ . Eq. (A9) was the estimated survival probability from  $t = 0$  to  $T$  as a function of  $X(0)=x$ . We assume that this function applies to survival from  $T$  to the next reproductive season.

## Appendix 1 (continued)

Finally,  $\phi = 5.78$ , is the expected number of pups produced after  $T$  during the potential remaining lifespan of 20 yr, and was calculated as

$$\phi = \sum_{y=1}^{20} l_x^y m_x \quad (\text{A10})$$

where  $y$  represents years after  $T$ . Survival probability from  $y-1$  to  $y$ ,  $l_x = 0.87$ , is the average  $\sigma$  (from Eq. 9) for all values of  $X(0)=x$ . Fecundity at  $y$ ,  $m_x = 0.92$ , was calculated as the average  $\psi$  (from Eq. A8) for all seals that survived to  $T$  during the forward iterations described above. Our simplifying assumption is that the seal's performance in one year does not predict future performance. We solved Eq. (A6) through backward iteration from Eq. (A7) (Clark & Mangel 2000).

### Forward simulations

Solutions to the dynamic programming equations provided values for an optimal decision matrix for all combinations of state variables and time periods. Based on this matrix, we used forward iterations (Clark & Mangel 2000) to predict behavior and fitness of seals.

While forward iterations covered 120 d, computer memory limited the decision matrix to the last 20 d preceding potential reproduction, or Periods  $T-1$ ,  $T-2$ , ...,  $T-86400$ . The decision matrix, however, had reached stationarity by that point, and we assumed that the optimal policy for the first period of the 20th day prior to the terminal horizon ( $T-86400$ ) also was optimal for earlier periods. 'Stationarity' at  $T-86400$  was determined indirectly as follows: we ran forward iterations simulating the 120 d season based on baseline parameter values and 2 decision matrices (1000 replicates/matrix). The first matrix was generated with a run of 86 400 periods, or 20 d; the second with a run of 82 080 periods, or 19 d. The time spent at any location during forward iterations was nearly identical when using either matrix.

Experimental treatments (see 'Computer experiments' in 'Methods') were simulated 1000 times each and we interpret results as predicted responses by seal populations with initial sizes of 1000 individuals under the simplifying assumption of no density dependence (Clark & Mangel 2000). Except for the *predator manipulations* (see below), behavioral data include only individuals that survived to  $T$ , thus simulating the 'risk' manipulations of empirical studies in which modified predators threaten but cannot kill. Comparing our simulations of seals that evaded predators to empirical experiments with sublethal predators is valid because in our simulations only luck, not 'phenotype', differs between surviving and depredated seals.

We quantify the relative size of trait- and density-mediated indirect effects of top predators on fish as the proportional reductions of the number of fish eaten by seals due to risk avoidance versus density reduction, respectively. Following Luttbeg et al. (2003).

$$TMII = 1 - \frac{\text{fish eaten (risk manipulation)}}{\text{fish eaten (no manipulation)}} \quad (\text{A11})$$

and

$$DMII = 1 - \frac{\text{fish eaten (predator manipulation)}}{\text{fish eaten (risk manipulation)}} \quad (\text{A12})$$

where *fish eaten* is the mean number of fish eaten by individual seals during the 120 d simulation period under the given manipulation scenario. The *risk manipulation* consisted of simulations in which mortality risk per time period from at least 1 predator type was  $>0$ , but included only replicates in which seals avoided predation (i.e. *fish eaten* = sum of fish eaten by non-depredated seals/number of non-depredated seals). The *predator manipulation* had the same predation risk as *risk manipulation*, but included all replicates (i.e. *fish eaten* = sum of fish eaten by all seals up the point of depredation or the terminal horizon, divided by 1000, the initial population size). *No manipulation* consisted of simulations without predation risk and also included all replicates (i.e. *fish eaten* = sum of fish eaten by all seals/1000).

## Appendix 2. *Phoca vitulina*. Parameterization of a dynamic state model of foraging decisions by harbor seals in Prince William Sound, Alaska

### Internal state variables

For energy state  $X(t)$ , we assumed an energy density of 15923.53 kJ kg<sup>-1</sup> (see Bowen et al. 2001) and that body weights ranged from 50 to 85 kg, such that  $x_{\min} = 796176.47$  kJ and  $x_{\max} = 1353500.00$  kJ. From the range  $x_{\max} - x_{\min} = 557323.53$  kJ and Eq. (2.3) of Clark & Mangel (2000), we created the 46 computer values of  $X(t)$ : 0 to 45, with 0 implying death by starvation.

For oxygen state  $Y(t)$ , we assumed that 105.11 ml of oxygen are consumed per 20 s time unit and that oxygen level can rise from  $y_{\max} = 0$  to  $y_{\max} = 3322.21$  ml during a 120 s surface interval, with  $y_{\max}$  allowing a maximum dive duration of 640 s. From the range  $y_{\max} - y_{\min} = 3322.21$  ml and Eq. (2.3) of Clark & Mangel (2000), we created the 11 computer values (0 to 10) of  $Y(t)$ . The oxygen gain function in Eq. (A1) was constructed so that the resulting surface and dive durations were consistent with the range recorded during preliminary observations (A. Frid unpubl. data). Activity-specific energy and oxygen costs are detailed in Table 1.

### Resource-related parameters

In SW Prince William Sound (PWS) during February and March of 2004, 9 harbor seals instrumented with VHF headmounts were tracked from a moving vessel during day and night (A. Frid unpubl. data). While lagging approximately 0.5 to 2 km behind the seal, depth-specific fish biomass was estimated every 1 s and averaged every 1 min using a BioSonics DT4000 echosounder at 70 kHz (Thomas & Thorne 2003 and references within). Data were averaged for 30 min sampling periods and 10 m depth intervals, and stratified into 2 habi-

## Appendix 2 (continued)

tats according to bottom depth (which correlates with distance from the refuge): (1) 35 to 45 m deep, and (2) 90 to 120 m deep (their surface locations being represented in the model by  $H(t) = 25$  and  $H(t) = 150$ , respectively). Using mean biomass values from the 30 min sampling periods as individual data points, we determined for each habitat the depth strata where median biomass (combined for day and night) was highest (A. Frid & R. E. Thorne unpubl. data). Depths represented in the model as  $H(t) = 1, 2, 5$  were based on these biomass peaks. Baseline parameter values for the location-specific probabilities of encountering and capturing prey,  $\lambda_h$  (Table 2) were calculated as  $\lambda_h = S(\text{MdnBiom})$ , where MdnBiom is the median biomass at a given location of all 30 min sampling periods, scaled by  $S = 2000$ . Medians were chosen over means to reduce bias from a few isolated fish schools that were very large.

Individual fish were not caught for ground-truthing acoustic targets, and species and sizes (Table 2) were assumed based on previous surveys in the area at similar times of year (Thomas & Thorne 2003, R. E. Thorne unpubl. data). For walleye pollock *Theragra chalcogramma*, length was converted to weight (525 g) with equations from [www.fishbase.org](http://www.fishbase.org). For herring *Clupea pallas*, weight (115 g) was taken from spring data in the area (R. E. Thorne unpubl. data). Energy gain per fish caught (Table 2) was calculated from energy densities in Anthony et al. (2000; their Appendix B) discounted by the seal's assimilation efficiency, assumed to be 0.9.

### Predation risk

Time-at-depth data during day and night were available for three 2.1 to 2.5 m-long sleeper sharks *Somniosus pacificus* instrumented with recording devices in PWS (L. Hulbert unpubl. data). Data were available for 6 mo (January through June) for 1 shark, 2 mo (January and February) for the second, and 1 mo (May) for the third. Location-specific risk from sharks  $\mu_{\text{shark}}(h, d)$  when  $d = h$  (Table 2) was calculated as  $\mu_{\text{shark}}(h, d) = S(\text{MPD})$ , where MPD is the overall mean (weighted by the number of months sampled) of the mean proportions of time each shark spent at a given depth, scaled by  $S = 1.00\text{E-}7$ .

For risk from killer whales *Orcinus orca*,  $\mu_{\text{orca}}(h, d)$  when  $d = h$  (Table 2), relative differences between depths were assumed based on limited data suggesting that mammal-eating transient killer whales generally use depths  $\leq 20$  m, use 20 to 40 m to some extent, and rarely forage deeper than 60 m, with some depth difference between night and day. The same data set suggests that travel speed is about a third slower during the night, possibly implying less hunting activity (Baird 1994, R.W. Baird unpubl. data), and thus risk at night was parameterized as two thirds of daytime risk. For a given depth, we made killer whale risk twice as high nearshore than offshore. The rationale is that killer whales might have higher encounter rates with their pinniped prey when patrolling the vicinity of haulouts, and researchers in PWS encounter transient killer whales on average twice as often nearshore as offshore (average for 7 survey zones estimated from Fig. 3. of Scheel et al. 2001). Further, 7 of 10 killer whale kills of harbor seal were observed nearshore (Saulitis et al. 2000). (In some survey zones, killer whales were found more frequently offshore, possibly because they were targeting porpoises rather than seals; Scheel et al. 2001, C. Matkin pers. comm.)

### Diurnal versus nocturnal parameter values

Both predation risk and resource-related parameter values depend on whether decisions occur during night or day, which in the model last 9 and 13 h per diel cycle, respectively (means for February through May at PWS). Specifically, let  $\text{day\_len} = 4320$ , the number of 20 s time units  $t$  in a day. Daytime parameter values are used if  $(\text{day\_len} - t \bmod \text{day\_len}) \geq \frac{9}{24} \text{day\_len}$ , otherwise nighttime values are used.

### Limited seasonality

One of the model's simplifications is lack of seasonality during the 120 d considered in forward simulations. For this period, February to May, parameter values are based either on year-round averages (shark predation risk), summer data (killer whale risk and energy content of prey), or late February and early March distributions of resources, as described above.