Project Title: Effects of prey availability and predation risk on the foraging ecology and demography of harbor seals in Prince William Sound: development and test of a dynamic state variable model.

Project Period: Date: 1 May 2003 to 30 April 2005.

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Research Priorities Addressed:
Identify up to three priorities from list in RFP (a-g): a, b, d

Summary of Proposed Work (250 words or less):
We will examine the contributions of prey availability and predation risk to the population dynamics of harbor seals (Phoca vitulina) in Prince William Sound. This work has great conservation value because seal numbers have been declining since 1984. Although available prey changed in the late 1970’s, food limitation alone cannot explain the current population trajectory; body condition of pups is presently good, suggesting that mothers are not nutritionally stressed. Harbor seals are preyed on by transient killer whales (Orca orca) and may be under increasing risk from sleeper sharks (Somniosus pacificus). We hypothesize that these predators affect survival and reproduction through both direct mortality and sublethal costs in which seals compromise energy intake while avoiding predator encounters. We hypothesize further that individuals vary in their ability to balance energetic and antipredator demands, and only a subset of those that follow an optimal foraging strategy survive and reproduce. A proportion of the population might consist of poor foragers that initially compromise energy intake to avoid predation and—once energetically stressed—take larger risks to avoid starvation and consequently have greater predation rates. To test these hypotheses, we will model optimal foraging strategies that maximize lifetime reproductive output under different predator and food distributions, and field-test predictions in Prince William Sound. We will expand inferences by comparing our research with existing and ongoing studies in adjacent regions that have stable or increasing seal populations. Because seals and fisheries might compete for prey, computer simulations will explore how alternative fisheries scenarios might influence the foraging ecology and demography of seals.

Funding:
Total NPRB Funding Requested: $172,886 total ($102,290 for year 1; $70,596 for year 2)
Total Matching Funds Used $25,160 total ($12,580 for year 1, $12,580 for year 2)

Legally Binding Authorizing Signature and Affiliation:
Kevin Brooks, Director, Division of Administration, Department of Fish & Game

(300x300)
1. **Project title:** Effects of prey availability and predation risk on the foraging ecology and demography of harbor seals in Prince William Sound: development and test of a dynamic state variable model.

2. **Proposal summary**
We will examine the contributions of prey availability and predation risk to the population dynamics of harbor seals (*Phoca vitulina*) in Prince William Sound. This work has great conservation value because seal numbers have been declining since 1984. Although available prey changed in the late 1970's, food limitation alone cannot explain the current population trajectory; body condition of pups is presently good, suggesting that mothers are not nutritionally stressed. Harbor seals are preyed on by transient killer whales (*Orcinus Orca*) and may be under increasing risk from sleeper sharks (*Somniosus Pacificus*). We hypothesize that these predators affect survival and reproduction through both direct mortality and sublethal costs in which seals compromise energy intake while avoiding predator encounters. We hypothesize further that individuals vary in their ability to balance energetic and antipredator demands, and only a subset of those that follow an optimal foraging strategy survive and reproduce. A proportion of the population might consist of poor foragers that initially compromise energy intake to avoid predation and—once energetically stressed—take larger risks to avoid starvation and consequently have greater predation rates. To test these hypotheses, we will model optimal foraging strategies that maximize lifetime reproductive output under different predator and food distributions, and field-test predictions in Prince William Sound. We will expand inferences by comparing our research with existing and ongoing studies in adjacent regions that have stable or increasing seal populations. Because seals and fisheries might compete for prey, computer simulations will explore how alternative fisheries scenarios might influence the foraging ecology and demography of seals.

3. **Project Responsiveness to NPRB Research Priorities**
Our proposed work is relevant to three of the NPRB research priorities. First, it directly addresses “Endangered and Stressed Species” because we will analyze factors that influence energy gain, survival, and reproduction in a depressed population of marine mammals that has declined for nearly 20 years. Second, our proposed work will increase general understanding of “Marine Ecosystem Structure and Process”, because our holistic approach integrates three trophic levels: seals and their prey and predators. Finally, our research will be relevant to “Fishery Management and Economics”, as inferences from our research will enhance computer simulations exploring how fisheries management can optimize the use of marine resources while simultaneously addressing the conservation of pinnipeds and other biodiversity components of the Gulf of Alaska region.

4. **Project design and conceptual approach**

4.1 **Theoretical background**
A basic premise of our work is that predators may affect prey not only through death or wounds to the captured, but also through the sublethal costs of antipredator behavior to those who managed danger (e.g. Abramsky et al. 2002; Heithaus et al. 2002). Sublethal costs include increased energy expenditure or lower rates of energy gain associated with vigilance, fleeing, or avoidance of habitats where predator encounters are likely. To optimize costs and benefits, investment in antipredator behavior should track changes in perceived risk. Thus, for a given food density, energy intake rates are lowest when perceived risk is highest. The corollary is that abundant and high quality resources may become functionally scarce or unavailable if associated with high risk (reviewed in Frid & Dill 2002; Heithaus & Dill 2002). If perceived risk is sufficiently high and long term, the energetic costs of antipredator behavior could impact body condition and reduce survival and reproductive output. Furthermore, animals in poor condition may experience greater predation rates when trying to avoid starvation by taking greater risks to find
additional food (Sinclair & Arcese 1995). Thus, predators may affect the population dynamics of prey more strongly through interactions between sublethal costs of perceived risk and direct mortality than by direct mortality alone (Brown et al. 1999; Peacock & Werner 2001; Frid & Dill 2002).

Only recently have sublethal costs of predation been considered in the study of dive cycles by aquatic animals that breathe air (Heithaus & Frid in review; Frid et al. in review). Dive cycles consist of time spent at the surface replenishing oxygen stores, travel from and to the surface, and time at a prey patch. While longer surface intervals allow longer dives, and therefore access to deeper prey or more time to feed within a patch, the trade-off is that feeding and breathing are mutually exclusive. Furthermore, physiological constraints make the rate of oxygen gain a decelerating function of time at the surface (Kramer 1988). Most models assume that optimal surface intervals maximize the proportion of a dive cycle spent at a prey patch, or other currencies related to net energy gain (e.g. Beauchamp et al. 1992; Thompson & Fedak 2001; Mori et al. 2002), but ignore predation risk effects on optimal dive cycle organization. However, risk of predation by a submerged predator can alter dive cycle organization such that energy gain is compromised to increase safety (Frid et al. in review).

A model recently co-authored by A. Frid, P.I. for our proposed study, expands the minimize $\mu/G$ rule (i.e. the probability of death divided by energy intake: Gilliam & Fraser 1987) to predict how foraging divers should modify their dive cycles when at risk from predators while at the surface. This model is summarized as follows (Heithaus & Frid in review). A diving forager faces risk of predation while breathing. It may alter its energy intake and predation risk by modifying surface interval duration and resulting time at the prey patch. The diver selects an optimal surface interval ($S_\star$) for minimizing $\mu/G$ over the course of a foraging bout. The net energy gain ($G$) for a single dive is determined by the amount of energy gained while at the food patch ($E$) and that which is expended during travel to and from the food patch. If $\tau$ is travel time (descent plus ascent), $b$ is time at the food patch, and $C_r, C_b$, and $C_s$ represent, respectively, the metabolic costs per unit time of travel, foraging, and resting at the surface,

$$G = E - \tau C_r - b C_b - s C_s$$

(1)

The model makes the simplifying assumptions that (a) the optimal surface interval does not change during the foraging bout, (b) travel time relates directly to diving depth, (c) travel and foraging costs per unit time are fixed, and (d) only one foraging depth is chosen for a particular foraging bout. A variety of different energy intake functions can be used to represent ($E$), but all depend to some degree on the time a forager spends at the food patch ($b$), which is expressed in terms of surface time ($s$) as:

$$b = K (1 - e^{-\alpha s}) - \tau$$

(2)

where $K$ is the maximum time at the food patch achievable with aerobic respiration and $\alpha$ is a scaling coefficient. Equation 2 makes the simplifying assumption that foragers will spend the maximum amount of time at the food patch for a given surface interval without shifting to anaerobic metabolism.

The cumulative risk of predation over a single surface interval ($\mu_t$) may increase with the time a diver spends at the surface as a linear, accelerating, or decelerating function, but in all cases cumulative risk of predation over the course of a foraging bout ($\mu_T$) is

$$\mu_T = 1 - (1 - \mu_t)^N$$

(3)

where $N$ is the number of dives made over the foraging bout. $N$ will be determined by the time available to forage ($T$), the surface time selected, and travel time to the prey patch.

Heithaus & Frid (in review) determined the surface time that optimized time at the foraging patch and safety ($S_\star$) over a variety of travel times and for all combinations of three energy intake functions and three predation risk regimes. Assuming that divers minimize the value of $\mu/G$ over the course of a foraging bout, the optimal surface time is represented by

$$S_\star = \min_s \left[ \frac{\mu_T}{N G_s} \right]$$

(4)

Comparing $S_\star$ to the predicted surface intervals that would maximize net energy gain when predation risk is ignored ($S$) provides testable predictions. The figure below shows the prediction when prey patches
deplete during the dive (i.e., energy gain is a decelerating function of time at the patch), and $\mu_t$ is a linear function of time at the surface. In the figure, $s_r^*$ is less than $s^*$, implying that surface interval is reduced under predation risk, and consequently dives are shorter and energy intake is lower on both a per dive and per bout basis.

The above assumption of patch depletion may apply to harbor seals if prey capture rate decreases due to prey density reduction or the prey’s antipredator response (e.g. Brown et al. 1999). The linear risk function may apply to seals under risk of attack by killer whales because the latter may approach either while submerged or while at the surface. Thus, even though a breathing seal cannot monitor its underwater environment, it can still scan for killer whales traveling at the surface. (When only subsurface predators are a threat, risk while breathing increases as an accelerating function and the difference between $s_r^*$ and $s^*$ is much greater: Heithaus & Frid in review). As detailed below, our proposed research will expand this theoretical structure by incorporating time and state-dependent decisions. This approach will greatly enhance our understanding of how predation risk and prey availability interact and influence a seal’s net energy intake and fitness.

4.2 The study system

In Prince William Sound, our proposed study system, the number of harbor seals declined by 63% between 1984 and 1997. The population is still diminishing and only a small portion of that decline can be attributed to the 1989 Exxon Valdez oil spill. In contrast, seal populations in adjacent regions have been either stable or increasing (Small et al. 2003; Blundell companion proposal).

Causes of the decline have been difficult to identify. An oceanographic regime shift in the 1970’s re-structured fish communities (Anderson & Platt 1999), and this change might have reduced carrying capacity for seals during early phases of the decline (R. J. Small, pers. comm.). Food limitation alone, however, cannot explain the current population trajectory because body condition of pups is presently good, suggesting that mothers are not nutritionally stressed (Trumble & Castellini 2001). The latter inference, however, applies only to individuals that succeeded in producing young and which might be inherently good foragers and competitors (see Sutherland 1996). The body condition of adult females without young and survival rates of juveniles are unknown. Further, how individual variation in foraging ability relates to fitness has not been addressed (Blundell companion proposal).

At the study site, diving behavior and movements of harbor seals have been studied with satellite transmitters (Frost et al. 2001; Lowry et al. 2001). These studies are very valuable for understanding broad patterns, but do not analyze individual dives—the cornerstone of some of our predictions. Thus, our proposed work will build on existing groundwork and address the functional significance of fine-scaled diving behavior. Notably, from data of Lowry et al. (2001) we can expect adult seals to forage...
relatively close to their haulout (average 5-10 km at-sea foraging distance), and thus know that boat-based manual tracking of individual seals is feasible. From data of Frost et al. (2001) we can expect nocturnal foraging, and also very frequent dives to depths below 50 m. While Frost et al. (2001) do not provide data on maximum dive depths, studies in Southeast Alaska and at Kodiak Island indicate that dives of 200-500 meters are common (Hastings et al. 2001).

Deep diving by seals is very relevant to our framework because satellite track data collected by NOAA personnel (Hulbert et al. in preparation) indicate that sleeper sharks spend most of their time deeper than 100 m. Thus, seals performing very deep dives likely do so at a higher risk of shark encounters. In 198 shark stomach contents analyzed by NOAA personnel (Hulbert et al. in preparation), various fish species and cephalopods were the main prey identified, and marine mammals were a small proportion of the diet (scavenged or hunted). These data, however, represent primarily sharks that were 1.5 to 2.5 m long (L. Hulbert pers. comm.). Sleeper sharks may grow much longer than 4 m, and success at capturing pinnipeds probably increases with size. Further, it is important to recognize that lack of direct mortality does not imply a lack of sublethal predation costs (Frid & Dill 2002). Consider, for instance, that tiger sharks (Galeocerdo cuvier) in Western Australia rarely kill bottlenose dolphins (Tursiops aduncus), but dolphins incur a substantial loss of access to prey to avoid shark encounters (Heithaus & Dill 2002). Thus, seals may be restricting their time at depth and incurring a functional loss of prey resources to reduce encounter rates with sleeper sharks. This possibility is important in the context of recent seal declines because sleeper shark numbers appear to be increasing (Courtney & Sigler 2002).

Why should seals spend time at depth? Main prey items in Prince William Sound include large herring (Clupeidae), pollock (Theragra chalcogramma), cephalopods, and flatfishes (Iverson et al. 1997). These species spend time in deep areas, at least during some life-stages, and deep diving by seals may relate to prey profitability. No study in Prince William Sound, however, has concurrently recorded prey availability and seal behavior, and this will be one major focus of our work.

Another characteristic of the study system relevant to our framework is that harbor seals are under risk from transient killer whales. Direct mortality caused by these predators is thoroughly documented, and danger appears to be highest at or near the surface (Saulitis et al. 2000).

4.3 Hypothesis, predictions, required data, and assumptions

We have two interrelated hypotheses. Below, greater emphasis is given to the first one because it provides the foundation for the second. Predictions and their empirical tests will address adult and subadult females. The rationale for addressing adult females is that the effect of risk-energy trade-offs on reproductive output is modeled and measured more easily for potential mothers than for other age-sex classes (i.e., individuals either produced young or did not). The rationale for addressing subadults is that they may be more vulnerable to predation and their survival might affect population growth strongly. These different age classes should also have different target energy levels, related to potential reproductive activity. Although male survival clearly affects population dynamics, in polygynous systems it may have a lesser role than that of female survival, and we do not consider males explicitly to avoid diluting sample sizes of field data.

4.3.1 Hypothesis 1: sublethal costs of predation risk

Our first hypothesis is that sleeper sharks and transient killer whales affect the survival and reproduction of seals not only through direct mortality, but also through sublethal costs due to seals compromising energy intake to reduce predation risk.

Preliminary predictions are presented below for heuristic purposes. Over the months following submission of this proposal, predictions will be refined and expressed mathematically with explicit assumptions in a dynamic state variable (DSV) model (Clark & Mangel 2000). This modeling technique is appropriate because seals forage during dives that have a time structure. Seals must decide on a continuous basis whether to dive deeper in search of prey based on a) remaining oxygen stores, b) prey
already captured, c) expected prey encounter with further search, d) depth-specific predation risk, and e) long term expected fitness based on current age and body condition (see Beauchamp et al. 1992; Clark & Mangel 2000).

Because danger from sleeper sharks might increase with descent depth, recent work by Mori et al. (2002) is relevant to our predictions. Briefly, Mori et al. (2002) argued that energy intake is a power function of time spent at the patch, and that the exponent defining this slope is an index of patch quality (i.e., larger exponents and steeper slopes imply higher quality). An empirical field test with Brünnich’s guillemots (Uria lomvia) suggested that the index was valid. Guillemots selected foraging depths that had higher exponent values and only single dives presumed to be exploratory (rather than actual foraging bouts) occurred to depths with low exponent values.

Our preliminary predictions are:

1) **Prediction**: Seals select foraging depths that are shallower than that which optimizes travel costs and access to high prey biomass if the latter is associated with a high encounter probability with sleeper sharks. Specifically,
   a. High quality prey patches (*sensu* Mori et al. 2002) will have a lower probability of being selected than shallower, lower quality patches if the probability of encountering sleeper sharks is lower at the latter.
   b. The cost of selecting shallower patches of lower quality is less prey biomass encountered. **Data required and source.** a) Encounter probabilities with sleeper sharks ≥2.5 m long will be estimated for different depth categories from existing satellite data collected by NOAA (Hulbert et al. in preparation). b) Depth-specific prey patches available and selected will be quantified through real time matching of seal behavior and acoustic prey measurements (see Sections 4.4.1 and 4.42). c) Dive cycle characteristics in relation to prey distribution (Section 4.4.1), and Mori et al.’s (2002) model will be used to estimate patch quality. **Assumptions:** a) Sleeper sharks are more likely to be predators at depth than near the surface (Hulbert et al. in preparation), while transient killer whales hunt mainly at or near the surface (e.g. Saulitis et al. 2000). b) Only sharks ≥2.5 m long are a substantial threat to seals. c) For dive patterns associated with foraging (e.g. Lesage et al. 1999), bottom time equals time at a prey patch. **Likely analytical approach:** The probability of a seal selecting a foraging depth will be analyzed as a function of the depth distributions of prey, Mori et al.’s (2002) index of patch quality, and predator encounter probabilities. Analysis will control for the probability of encountering a transient killer whale (see prediction 2). Observed descent depths and related parameters will be compared to theoretical predictions (Heithaus & Frid in review, and proposed DSV model).

2) **Prediction**: Relative to the surface interval that would maximize net energy intake in the absence of surface risk, seals will have shorter surface intervals when transient killer whales are likely to be encountered. The costs will be shorter dives, less time at a prey patch and reduced net energy intake (Heithaus & Frid in review). **Assumptions, data required and source:** Encounter probabilities with transient killer whales will be estimated from spatial data in Scheel et al. (2001) and ongoing work on killer whales (C. Matkin pers. comm.). Our own opportunistic observations will supplement these data. Other data requirements, sources, and assumptions are as in Prediction 1. **Likely analytical approach:** Observed surface intervals and related dive parameters will be compared a) to theoretical predictions (Heithaus & Frid in review, and proposed DSV model), and b) between places or times that differed in encounter probability with transient killer whales, while controlling statistically for prey availability.

3) **Prediction**: On average, diving behavior differs between seals in Prince William Sound and seals in adjacent regions with non-declining populations. A difference might reflect that PWS seals experience either similar prey availability and more risk, or similar risk and less prey; we will assess both possibilities a posteriori. **Data sources and likely analytical approach:** Diving and foraging parameters, as well as prey and predation risk distributions will be compared regionally by drawing from existing or ongoing studies.
in Kodiak and Southeast Alaska (see Hastings et al. 2001; Small & Ver Hoef 2001; Blundell companion proposal). We will use meta-analysis to analyze data collected with different methods and effort levels (Gurevitch & Hedges 1993).

4.3.2 Hypothesis 2: individual variation in foraging affects predation rates

Our second hypothesis is that individuals vary in their ability to match an optimal strategy that balances energetic and antipredator demands, and only individuals that follow the optimal strategy survive and reproduce. Following the Predation Sensitive Foraging Hypothesis (Sinclair & Arcese 1995), a proportion of the population might consist of poor foragers that initially compromise energy intake to avoid predation and—once energetically stressed—take larger risks to avoid starvation and consequently experience greater predation rates.

Some predictions of this hypothesis and their tests are outlined in Blundell (companion proposal). This study will test the following:

1) Prediction: Some individuals will behave consistently with the optimal strategy predicted by the DSV model (see Section 4.5), but a proportion of the sample population will not.
   - Data required and source: Diving parameters, as described for predictions of Hypothesis 1.
   - Likely analytical approach: For each individual, empirical data on diving behavior will be compared to the optimal policy predicted by the DSV model (see Section 4.5).

2) Prediction: Poor body conditions will correlate with diving behavior that is inconsistent with the optimal policy predicted by the DSV model.
   - Data required and source: a) Body condition measures as described in Blundell (companion proposal). b) Diving parameters, as described for predictions of Hypothesis 1.

3) Prediction: Individuals that already are energetically stressed follow a policy that puts them under a high probability of predation (Sinclair & Arcese 1995).
   - Likely analytical approach: The DSV model (see Section 4.5) will be used to estimate whether observed dive parameters of individuals in poor body condition are consistent with high risk-taking associated with a greater likelihood of death by predation.

4.4 Field methods

The first field season will be September-October 2003. Start dates are determined by a) the timing of the first seal capture cruise (see Blundell companion proposal) after NPRB money is released, b) when foraging by adult females is not disrupted by pupping, and c) when summer molt will not cause external transmitters to shed. End dates are based on the expected onset of poor weather for marine fieldwork.

A second field season will take place during April 2004. Transmitters (see below) attached during the previous fall will still be functional, and we expect that many seals instrumented the previous fall will not have died nor dispersed in the interim. The second field trip will broaden our seasonal interferences and enhance the value of having captured and instrumented seals during the previous fall.

4.4.1 Seal foraging behavior

During mid September 2003, seals will be captured at haulout sites and standard measurements and biopsies will be made as described by G. Blundell (companion proposal). Biopsies will include blubber samples for inferring diet from fatty acid signatures (Iversion et al. 1997), and data on body condition (morphometrics and blood chemistry profiles) will be collected as described in Blundell (companion proposal). Thirty five seals, 20 adult and 15 subadult females, will be instrumented with two external transmitters. The first is an ATS MM370 aerial transmitter that is glued with epoxy to the seal's head (minimum battery life at 40 pulses/min is 380 days; cylindrical shape with a 45° angle antenna, 7.2 cm long by 2.1 cm wide, weight = 90 grams). The second transmitter is a Sonotronics DT-97 depth tag (cylinder 18 mm wide by 86 mm long, weight = 14 gram, battery life 12 months). The latter's signal is decoded into depth information while manual tracking from a boat (signal range = 3 km). The DT-97 will
be attached to the seal’s back by tying it to mesh and gluing with epoxy as described in Lowry et al. (2001). Both transmitters will shed during the following molt (July).

Diving behavior and prey availability will be studied through boat based tracking. The aerial transmitter will be used to locate and track the seal at the surface. The DT-97 will provide the dependent variables that represent dive cycle organization (use of various depth strata, surface time, etc). Boat-based manual tracking is feasible because most seals forage relatively close to their haulout (Lowry et al. 2001) and successful manual tracking has been accomplished by similar studies (e.g. Bjørge et al. 1995). Tracking will cover both day and night, and GPS coordinates will document locations. Sampling will be spread as evenly as possible among the 35 tagged individuals.

We emphasize that the DT-97 is the best available choice for quantifying individual dive cycles under the circumstances of our study. The DT-97 is not archival; information is obtained in “real time” and tag recovery is unnecessary. While animal-borne digital cameras or other data loggers would add to the scope of the data, seals would have to be recaptured to use any commercially available system (e.g. Hooker et al. 2002). Recapture would be difficult in the rocky haulouts of our study site. Commercially available animal-borne data logging systems could be set up to be self-releasing, but not with sufficient predictability for time of release and thus risk of losing the equipment and data is high. Animal-borne cameras developed by National Geographic—which have provided excellent data on seals at Sable island (Bowen et al. 2002)—are the only ones that are currently self-releasing at predictable times (Marshall 1998), but these are not commercially available and our access to them could not be secured at the time of this writing. Finally, the DT-97 is substantially cheaper than other systems, and thus much greater sample sizes are possible for a given budget.

4.4.2 Matching prey distribution to foraging behavior

We will match prey availability to seal behavior by systematically making acoustic measurements on the seal’s track, as close to the foraging seal as possible while avoiding disturbance. Thus, the acoustic data will provide the real-time independent variables that will give a prey availability context to dive patterns by seals. Prey will also be sampled at random locations for comparison with seal foraging sites.

The acoustic prey surveys will be based on echointegration techniques (Thorne 1983a,b; MacLennan and Simmonds 1992; McClatchy and Thorne 2000). Details of the specific procedures for PWS are described in Thomas et al. (1997) and Thomas and Thorne (in press). Target strength characteristics of PWS herring (a primary prey species) are detailed in Thomas et al. (2002). The echointegration surveys are repeated several times to develop multiple, independent estimates of the biomass of specific fish concentrations. Historically, both 38 kHz and 120 kHz have been used for the surveys. More recently, 70 kHz systems have been added. Current systems in use include BioSonics DT4000 Digital Transducer Systems at 38 kHz, 70 kHz and 120 kHz and a BioSonics analog, preamp transducer scientific echosounder at 120 kHz. Transducers are mounted on a 2.5-m towing vehicle. All systems are routinely calibrated using procedures documented in Foote and MacLennan (1982). Transect locations for all systems were written on acoustic data files using GPS receivers. BioSonics Visual Analyzer software, Version 3.1.1, is used for basic analysis of data from the digital transducer systems, while the data from the analog system are analyzed using a BioSonics Model 221 Echo Signal Processor (ESP). The repeated survey estimates are used to determine the precision of the biomass estimates (Schaeffer et al. 1986). After the echointegration surveys, fish schools are subsampled to ground truth species identification and other biological information. The size composition of fish in the net catches is used to estimate target strengths for converting backscatter to biomass (Thomas et al. 2002).

4.5 Computer modeling: from dive cycles to population dynamics

Dynamic State Variable (DSV) models of optimal foraging assume that fitness (lifetime reproductive success) is a function of energy level discounted by mortality rate. Based on this function, they predict behavior from an initial period $t$ to a terminal time horizon $T$ (Clark & Mangel 2000). In the DSV application proposed in Section 3.3.1, $T$ represents the end of a foraging bout (series of dive cycles). Time, depth, oxygen stores, and energy level are the state variables, and prey availability and predation
risk are the factors varying with depth. The optimal policy tells the animal whether to dive deeper, remain at the current depth, or surface at each point during a dive; it also tells the animal when to leave the surface to initiate the next dive. The optimal policy is derived by backward induction such that fitness is maximized at the end of the foraging bout. A policy matrix is defined by the state variables, and assumes probability distributions for prey availability and risk. It is stochastic variation in prey availability and risk that causes individuals to differ in fitness during simulations. (see Alonzo & Mangel 2001). Season and age of the individual are additional variables defining the matrix.

To relate behavior to reproductive output and population dynamics, the fate of a population of seals of a specified age following the optimal policy is simulated from the onset of the first foraging bout of the season until pupping time. For the population of seals (e.g., n = 1000) with a given fitness at \( t \), multiple foraging bouts are modeled sequentially such that fitness at the end of a bout becomes the initial fitness for the next. At pupping time, the model estimates the proportion of individuals that survived (i.e., avoided predation and did not starve), and their likelihood of producing offspring based on accumulated energy level. These simulations provide the basic life table information from which population trajectories can be predicted (see Clark & Mangel 2000).

Seals and fisheries may compete for some of the same prey (e.g. Björge et al. 2002), and this relationship will be incorporated into our predictions. How a given fishery might alter the biomass of prey and the distribution of seal predators will first be elucidated using ECOPATH models of Prince William Sound (Okey & Pauly 1999). Subsequently, the new set of conditions will be incorporated into the DSV simulations to determine the new decision policies of seals and resulting fitness values. Fitness differences with and without the fishery estimate the potential costs to seals for the management policy (see Chapter 8 in Clark & Mangel 2000).

In addition to data collected during the proposed fieldwork, literature values from studies in Alaska (see Blundell companion proposal) and elsewhere will be used to broaden the range of parameters explored in the model.

4.6 Schedule of measurable milestones

**January-April 2003:** Though not part of the period of NPRB funding, DSV model development starts during this period.

**May-August 2003:** DSV model development, preliminary simulations of fisheries scenarios, and preparation for fieldwork.

**September - October 2003:** Fieldwork consisting of capture and instrumentation, and tracking/prey assessment.

**November 2003-March 2004:** Data analysis, computer modeling, and writing. Preparation for next field season.

**April 2004:** Second field season consisting of tracking/prey assessment for seals instrumented the previous fall.

**May 2004- April 2005:** Complete all analyses and final report to NPRB; submission of manuscripts to refereed journals. Interim reporting to NPRB will be done as stipulated in the RFP.

**Products that will ultimately measure our success:** Three manuscripts for submission to refereed journals will measure our success. 1) A DSV model predicting optimal diving by seals during foraging bouts. 2) An empirical analysis of diving behavior by seals in relation to prey availability and predation risk; this analysis is inextricably linked to the DSV model of #1, and will interpret data in the context of potential consequences to predation rates and reproductive output. 3) An expanded DSV model that builds on #1
and # 2 to predict survival and reproductive rates and population dynamics of seals in relation to changing prey, predation risk, and the possible influence of fisheries. Ultimately, our success will be measured by the extent to which our work contributes to management and conservation practices involving harbor seals and other ecosystem components of the Gulf of Alaska Region.

5. Project management, and experience and qualifications of personnel
Our project is a collaborative enterprise between the Alaska State Department of Fish and Game (ADF&G) and Simon Fraser University (SFU). We have brought together a strong interdisciplinary team and are confident that we will meet our goals. Our collective expertise includes strong analytical and theoretical skills, as well as field studies of marine mammals and their prey in Alaska, and studies of predator-prey systems in other parts of the world. Project management will be a collaboration between Dr. Gail Blundell and Alejandro Frid.

Alejandro Frid, PhD candidate at SFU and principal investigator, will oversee and participate in field data collection, and will be the lead data analyst, computer modeler, and writer. The work will form part of his doctoral research. A. Frid has already contributed substantially to the published literature on marine predator prey-interactions, and how predation risk theory can contribute to solving practical conservation problems.

Dr. Gail M. Blundell, co-principal investigator, leads the Harbor Seal Research Program for the ADF&G. Her program is in charge of addressing conservation and research issues for harbor seals in Alaska. Along with Alejandro Frid, she will co-supervise fieldwork and participate in the latter, and collaborate on analyses and reporting.

Dr. Larry Dill, co-principal investigator, is the academic supervisor of A. Frid at SFU. For almost 30 years, his research group has strongly influenced the study of risk energy trade-offs and other fields of behavioral ecology. His body of work covers a diversity of systems, including sharks and marine mammals.

Dr. Richard E. Thorne, contractor for prey assessments, is a senior scientist at the Prince William Sound Science Center and a leading expert on prey assessment and the fish populations of PWS.

6. Coordination and collaboration
Our project is based on coordination and collaboration between ADF&G and SFU. The proposal represents management concerns identified by ADF&G and the research framework developed by both ADF&G and SFU. ADF&G personnel will continue to ensure that all relevant management and conservation issues are addressed. Our work is built on seal research that is either currently being carried out or already published by ADF&G personnel. Further, communication with L. Hulbert, shark researcher from NOAA has been extensive, and our work builds on his existing data (currently being analyzed). Our research also will build on published and ongoing work on killer whales by the North Gulf Oceanic Society and the Prince William Sound Science Center. Our work does not duplicate any of these studies. Rather, it uses existing groundwork to address for the first time the functional significance (in terms of survival and reproduction) of diving patterns by seals relative to predator and prey distributions in Prince William Sound.

7. Possible peer reviewers
1) Don W. D. Bowen. Marine Fish Division, Bedford Institute of Oceanography, Department of Fisheries and Oceans, Dartmouth, Nova Scotia B2Y 4A2, Canada. Phone (902) 426-8909. Email: bowend@mar.dfo-mpo.gc.ca.
2) David Scheel. Environmental Science Department, Alaska Pacific University, 4101 University Drive, Anchorage, AK 99508, Phone: 907/ 564-8318; Email dscheel@alaskapacific.edu
3) Marc Mangel. Department of Environmental Studies. University of California. Santa Cruz, CA 95064 Email: msmangel@ams.ucsc.edu.

Effects of prey availability and predation risk on the foraging ecology and demography of harbor seals in Prince William Sound: Alaska Department of Fish & Game - Proposal to NPRB - page 9 of 11
4) Andrew Trites. Fisheries Centre, 2204 Main Mall, The University of British Columbia, Vancouver, BC, Canada V6T 1Z4. Phone (604) 822-2731, Email: a.trites@fisheries.ubc.ca.

9. Project costs and budget narratives

The proposed research is part of a bigger effort already supported to a large extent by funds from ADF&G. These funds imply that we already have secured substantial financial support, but are federal in-kind support that cannot be considered matching costs. They include a stipend to A. Frid for January-March 2003, travel and salaries for G. Blundell, and use of field equipment (e.g. VHF receivers). Below we itemize only requests to NPRB and matching costs.

10. Expenditure of Funds

ADF&G will develop and monitor a Cooperative Agreement with Simon Fraser University for the work described in this proposal. All expenditures for ADF&G are anticipated to be contractual. ADF&G has a negotiated indirect cost rate with the Department of Interior at a maximum level of 10.5%. The documentation is included with this application package. The ADF&G intends to assess this project at 6%.

The following budget narrative depicts the proposal budget for the Cooperative Agreement.

10.1 Personnel Salaries and Fringe Benefits

Costs requested from NPRB

The only salary being requested is for Alejandro Frid, the PI. For the two years of proposed work, he will dedicate directly to the project 90% of the standard work year. This time will be part of what is required to complete his PhD at Simon Fraser University, and will consist of further study design, data collection and analysis, computer modeling, reporting, and project managing and coordination. The remaining 10% of time per year will be dedicated to related academic activities. Fringe benefits are not requested.

Matching costs

Dr Larry Dill, co-PI supervising the computer modeling and analysis of AF, will dedicate 8% of the standard work year for each of the two years of this project. Simon Fraser University will provide his salary during this time (total $5,980/year). This includes fringe benefits (8% in Canada).

10.2 Travel

Costs requested from NPRB (there are no matching costs).

1) Travel for A. Frid includes:
   a) Access to field twice: $700 return flight Vancouver-Anchorage, $400 for extra baggage, lodging/sustenance in Anchorage during transitions to field and for taking ground transportation to Whittier ($1,100/year for 2 years).
   b) Travel to Juneau for 1-week for analysis meetings with L. Hulbert (NOAA shark data) and with G. Blundell. $600 return flight Vancouver-Juneau, and $300 for lodging/sustenance.
   c) NPRB meeting in Anchorage: $700 return flight Vancouver-Anchorage, $300 lodging/sustenance.

2) Travel to field site for L. Dill: $700 return flight Vancouver-Anchorage, $300 for lodging/sustenance during transitions in Anchorage.

10.3 Supplies

Costs requested from NPRB (there are no matching costs).

1) DT-97 depth tags: 35 @ $500 each ($17,500 total).

2) Sonotronics Mantrak Kit for tracking depth tags (hydrophone, receiver, case, cables, headphones, battery pack): $2,750.
3) ATS aerial transmitters: 35@ $150 each ($5,250 total)

10.4 Contractual/Consultants

Costs requested from NPRB (there are no matching costs).
1) Vessel for tracking of seals and simultaneous prey assessment: $30,000 (25 days @ $1,200/d) per year for two years.
2) Contract to Dr. D. Thorne (CV attached) for prey sampling: $12,500 (25 d @ $500/d ) per year for two years.
3) Float plane: $1000 (per year for two years) to fly in contractors for prey surveys and allowing extra flight time for emergencies during fieldwork.

10.5 Other

Total cost to NPRB (years 1 and 2 combined): $1500 for outreach and communication.

Total matching costs year 1 (SFU): $6,600 for campus facilities (computing, statistical consulting, library services) provided by SFU. Amount is based on 30 % of graduate student salary requested for A. Frid.

Total matching costs year 1 (SFU): $6,600 for use of campus facilities, as in year 1.

10.9 Total costs with overhead

Indirect is 6% for ADF&G

Requested from NPRB:

Year 1: $96,500 + 6% indirect = $102,290
Year 2: $66,000 + 6% indirect = $70,596
Total: $172,886

Match-Cost Sharing Funds

Year 1: $12,580
Year 2: $12,580
Total: $25,160
### NPRB BUDGET SUMMARY FORM

**PROJECT TITLE:** Effects of prey availability and predation risk on the foraging ecology and population processes of harbor seals in Prince William Sound  
**PRINCIPAL INVESTIGATOR:** Alejandro Frid

### FUNDING SOURCE

<table>
<thead>
<tr>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPRB Funding</td>
<td>102,290</td>
<td>70,596</td>
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<tr>
<td>Match/In Kind</td>
<td>12,580</td>
<td>12,580</td>
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<tr>
<td>TOTAL</td>
<td>114,870</td>
<td>83,176</td>
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Annual cost category breakdowns will be requested for matching funds only if project is funded.

### Cost Categories

<table>
<thead>
<tr>
<th>Cost Categories</th>
<th>NPRB Year 1</th>
<th>NPRB Year 2</th>
<th>NPRB Year 3</th>
<th>NPRB TOTAL</th>
<th>Match/In kind TOTAL (all years)</th>
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<tr>
<td>1. Personnel Salaries</td>
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<td>11,960</td>
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<td>2. Personnel Fringe Benefits</td>
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<td>3. Travel (include 1 trip to review meeting in Anchorage)</td>
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<td>0</td>
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<td>4. Equipment</td>
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<td>0</td>
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<td>0</td>
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<td>5. Supplies</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6. Contractual/Consultants</td>
<td>96,500</td>
<td>66,600</td>
<td>0</td>
<td>163,100</td>
<td>13,200</td>
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<td>7. Other (Include $1,500 for education and outreach)</td>
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<tr>
<td><strong>Total Direct Costs</strong></td>
<td>96,500</td>
<td>66,600</td>
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<td>163,100</td>
<td>25,160</td>
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<tr>
<td><strong>Indirect Costs</strong></td>
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<td>9,786</td>
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<td><strong>TOTAL PROJECT COSTS</strong></td>
<td>102,290</td>
<td>70,596</td>
<td>0</td>
<td>172,886</td>
<td>25,160</td>
</tr>
</tbody>
</table>
Bibliography


Hulbert, Lee (sleeper shark researcher). Personal Communication. Auk Bay Labs, NMFS, Juneau. lee.hulbert@noaa.gov.


Matkin, Craig (killer whale researcher). Personal Communication to GMB. North Gulf Oceanic Society, Homer, Alaska.


Small, R. J. (Statewide Coordinator, Marine Mammals Program, ADFG). Personal Communication.


C.V: ALEJANDRO FRID

Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, CANADA. Phone 604/291-4374. Email ilexp@yknet.yk.ca

Education:
Currently (since January 2000): Ph. D. Candidate, Simon Fraser University.
1994: M.Sc., Wildlife Ecology, University of British Columbia
1988: B.Sc., Biology, Evergreen State College, Washington State

Ongoing dissertation research.
I am conducting theoretical and field research on the behavioural ecology of air-breathing aquatic animals. Completed thesis chapters include empirical work on dive cycles of sea turtles under predation risk from sharks, and application of predation risk theory to solving practical conservation problems. Currently I am applying optimal diving and predation risk theory to systems in the North Pacific (as described in this proposal).

Other research
I have completed numerous research contracts or fellowships with Wildlife Conservation Society of New York’s Bronx Zoo, the Yukon Fish and Wildlife Branch, the Canadian Parks and Wilderness Society, and Kluane National Park Reserve, and other organizations.

Refereed publications
Frid, A. In press. Dall’s sheep responses to overflights by helicopter and fixed-wing aircraft. Biological Conservation.

Submitted manuscripts
Sample of consultant reports

Selected articles in the popular press

Research awards, fellowships, and scholarships
2001: Graduate fellowship, Simon Fraser University.
1999: National Science and Engineering Research Council (Canada) PGS-B graduate scholarship.
1995: Research Fellowship from Wildlife Conservation Society, Bronx, New York, for research on endangered huemul deer in southern Chile.
1993: Honourable mention from the Rolex Awards of Enterprise, for research on endangered huemul deer in southern Chile.
1992: Sisam forestry award (awarded by the University of Toronto).

Reviewing for refereed journals/funding agencies

Selected presentations
Frid, A. 2002. Beyond the gory wounds: sublethal effects of predation on animal populations. Department of Archaeology, Simon Fraser University.

General experience
My experience includes fieldwork in remote mountainous regions, capturing marine turtles at sea and instrumenting them, working on practical conservation problems in developing countries, and communicating my findings to both scientific audiences and the general public. In spite of no prior fieldwork in the north Pacific, 23 years of sea kayaking in exposed coasts of Alaska, British Columbia, and Patagonian Chile have given me a deep awareness of conditions to be encountered during the proposed study.
GAIL M. BLUNDELL, PH.D.
Alaska Department of Fish and Game
Division of Wildlife Conservation
P.O. Box 240020
Douglas, AK 99824-0020

Phone: (907) 465-4345
Fax: (907) 465-4272
gail_blundell@fishgame.state.ak.us

EDUCATION

EMPLOYMENT
Principal Investigator, Harbor Seal Research Program. Alaska Department of Fish and Game, Division of Wildlife Conservation/Marine Mammals. April 2002 to present. Overseer a large statewide research program tasked with the challenging objective of designing and implementing research to determine why some populations of harbor seals in Alaska are declining while others remain stable or are increasing. Supervise 2-3 biologists and various technical staff and college interns.

Post-Doctoral research, October 2001-April 2002. Institute of Marine Sciences and Institute of Arctic Biology, University of Alaska Fairbanks. Synthesis of spatial data from coastal river otters and marine fishes from several marine-ecosystem research projects; collaborated to construct a predator-prey spatial model and prepare a manuscript assessing dispersion of individuals relative to resources. Manuscript tests hypotheses of river otter social behavior (including prey acquisition and function of scent marking) and habitat associations of fish, incorporating empirical data for fishes and otters, along with terrestrial and marine habitat data.


Wildlife Biologist – Project Leader, “Nearshore Vertebrate Predator (NVP) Project” – Project leader for river otter component. January 1996 to September 2000. As part of a large ecosystem research project (~35 scientists), conducted research on ecology, demography, and toxicology of river otters in coastal environments of Prince William Sound, Alaska to address the question: Have river otters recovered from the effects of the Exxon Valdez oil spill? If not; is it oil or is it food? Study addressed this question for 2 mammals (sea otter and river otter) and 2 birds (harlequin duck and pigeon guillemot) — 1 invertebrate predator and 1 fish predator for each class – as a window to ecosystem-level dynamics in the nearshore environment.


MANUSCRIPTS REVIEWED: Behavioral Ecology; Mammalian Species; Wildlife Society Bulletin; Southeast Naturalist; Journal of Wildlife Management
PUBLICATIONS – PUBLISHED

PUBLICATIONS – IN PRESS

PUBLICATIONS – IN REVIEW

PROFESSIONAL PRESENTATIONS: 2001— As senior author presented 5 talks and 3 posters at national and international meetings, co-author on 4 talks and 1 poster. 1995-2000 – Presented 21 talks or posters at national and international meetings, co-author of 13 presentations.

OTHER PUBLICATIONS
DR. LAWRENCE M. DILL, FRSC,
Professor, Biological Sciences and Director, Behavioural Ecology Research Group, Simon Fraser
University, Burnaby, B.C. Email ldill@sfu.ca. Phone: 604/291-3664.

Educational Background
1972 Ph.D. Ecology, University of British Columbia

Current Research Interests
Behavioural Ecology. My major research interests are in the development and testing of optimality
models of foraging, predator avoidance and habitat selection behaviors, and laboratory and field study of
the decision rules used by animals to ensure adaptive behavioral responses in these contexts. Of
particular interest at the present time are situations in which animals must trade off foraging opportunity
and predation risk in the field, and the population and community consequences of their habitat choice
decisions. I also have an ongoing interest in social foraging behaviour, in fish and whales.

Sample of Publications (total 86 plus 5 in press)
interactions in marine communities and their importance to conservation and management.
Ecology.
Damsgard, B., and L.M. Dill. 1998. Risk-taking behaviour in weight compensating coho salmon,
(Oncorhynchus kisutch): ideal free distribution theory applied. Behav. Ecol. 8:437-447.
Ecol. Entomol. 16: 73-80.
Lima, S.L. and L.M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and
Ecology 79: 999-1007.

Postdoctoral fellows trained: (with current faculty positions, where applicable): P. F. Major, R.C.
Ydenberg (SFU), S.L. Lima (Indiana State), D. Soluk (U Illinois), A. Hedrick, B. Damsgaard (Tromso),
N. Hughes (U Alaska), B. Wilson, R. Rochette (U New Brunswick)

Graduate students supervised: PhD: L. Giguere, R. Dunbrack M. Abrahams P. Nonacs, R. Cartar, G.
Most significant research contributions

1. Application of economic logic to antipredator behavior of animals: A 1987 paper coauthored with RC Ydenberg (Adv. Study Behav. 16: 229-249) brought to the attention of many behavioral ecologists the idea that the performance of animal antipredator behavior is not maximized, but rather is optimized, because it has costs as well as benefits. We applied the sort of economic logic that had produced such important insights into foraging, reproductive and fighting behaviors, and this approach became incorporated into the textbooks. A number of my subsequent papers tested economic predictions about antipredator behavior, in a variety of systems, demonstrating its generality including a particularly convincing experimental demonstration of the fact that animals (hiding serpulid worms in this case) will take greater risks when the lost opportunity cost of avoiding risk (i.e., lost feeding opportunity) is increased.

2. Theoretical and empirical studies of the influence of predation risk on animal decision making: In Lima and Dill (1990) we summarized the information then available on the influence of predation risk on animal behavioral decisions, developed a theoretical framework, and laid out a prospectus for future research. The paper has been very extensively cited (over 1000 times), and has had a major impact on people's thinking. Subsequently, I have written another review paper on risk assessment through olfaction, and collaborated on research on foraging-risk tradeoffs. More recently, I have shown that predation risk also affects animal reproductive behavior, in crickets and in several fish species.

3. Use of ideal free distribution theory to study animal habitat choice in tradeoff situations: Starting with Abrahams and Dill (1989) much of the work in my lab has been concerned with predicting animal habitat use when they must tradeoff energy intake and mortality risk (i.e., when the best habitat is the riskiest one). The ideal free distribution turns out to be an extremely useful conceptual tool for thinking about this problem, and for quantifying the tradeoff. We have developed frequency-dependent models of habitat choice when the predator is also free to move, and extended the basic theory to situations in which competitors are unequal.

4. Application of behavioralecological concepts to the study of salmonid fishes and cetaceans: These two groups of animals are of great interest to the general public, for both cultural and economic reasons. Important species in both groups are threatened and both present opportunities for the application of behavioralecological theory in fields currently dominated by a descriptive approach. Some of our salmonid work has been discussed in point #3 above; in total, this work has led to new insights and approaches to old questions in stream salmon ecology. The cetacean work has been more wideranging, dealing with group size, foraging, and predation risk tradeoffs.

5. Applying behavioral ecology to important ecological and conservation problems: It is incumbent on behavioral ecologists to apply their rich conceptual and smallscale empirical results to important ecological questions in the "realworld". For instance, Remy Rochette, and I have shown that intertidal zonation in mobile marine invertebrates like gastropods is partly a behavioral response to predation risk, and cannot be fully understood without studying individual behaviors. Mike Heithaus and I are also using the theories and methods developed in my earlier work to understand habitat use of a community of animals in Shark Bay, West Australia (Heithaus and Dill, 2002). Most recently with Alejandro Frid I have been working on application of predation risk theory to conservation biology (Frid & Dill 2002).
CV: Richard E. Thorne, Ph.D.
P.O. Box 705, Cordova, Alaska 99574
(907) 424-5800 (work), -5820 (fax)

**Employment History**

Prince William Sound Science Center
Director of Research 2002
Senior Scientist 2000-present

BioSonics, Inc.
Vice President 1996-1999
4027 Leary Way NW
Manager Technical Services 1991-1999
Seattle, WA 98107
Senior Scientist 1988-1999
(206) 782-2211

University of Washington
Affiliate Research Professor 1991-2001
School of Fisheries
Fisheries Research Institute
Research Associate Professor 1976-1981
Seattle, WA
Senior Research Associate 1970-1976

Commercial Fisher (salmon and albacore) 1957-1968

**Academic Background**

Ph.D., Fisheries-1970, University of Washington, School of Fisheries
MS Degree-1968, University of Washington, Department of Oceanography
B.S. Degree-1965, University of Washington, Department of Oceanography

**Selected Publications**


Recently Completed Contract Reports:

Publications in review
Spatial and Numerical Relationships between Steller Sea Lions and Pacific Herring in Prince William Sound, Alaska
Thorne, R.E and G.L. Thomas
Canadian Journal of Fisheries & Aquatic Sciences

Density and Accessibility as Factors in the Foraging Behavior of Steller Sea Lions (Eumetopias jubatus) in Prince William Sound, Alaska
Thorne, R.E. and G.L. Thomas
Marine Mammal Journal

Acoustical-optical assessment of Pacific herring and their predator assemblage in Prince William Sound, Alaska
G.L. Thomas and Thorne, R.E.
Aquatic Living Resources

The Anatomy of a Population Collapse: the Prince William Sound Herring Stock
R.E. Thorne and G.L. Thomas
Biological Conservation