Optimal risk-taking theory applied to marine conservation: harbour seals in Prince William Sound

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Abstract

I sought theoretical insight on synergistic effects of resources and predators that are potentially relevant to the decline of harbour seals in Prince William Sound and to indirect effects of fisheries. Simulations predicted that compensatory foraging effort by seals will mitigate potential loss of energy reserves when resources decline, but only at the cost of higher predation rates, even if predator densities remain constant. A second study predicted net energy gain and predation risk per foraging dive, parameterising an analytical model with field data on seal behaviour, resource distributions, and use of depth by Pacific sleeper sharks and killer whales. Analyses suggested that risk of mortality from sharks and net energetic gain were greatest when seals foraged in deep strata, and empirical data showed individual variation in use of these strata. Plots of the individuals' predicted energy gain against predicted predation risk fit best when relative danger from sharks was assumed to be much greater than that from killer whales. The first two studies combined suggest that, theoretically, overfishing of near-surface fatty fishes might increase shark predation rates on seals. A third model predicted an asymmetric trophic cascade in which indirect effects of sleeper sharks on resources were mediated by seal avoidance of riskier strata. Risk management by seals is predicted to reduce mortality on the dangerous resource (deep pollock) while increasing mortality on the safer resource (shallow herring), and the bycatch of sharks altered this dynamic. Although empirical data are lacking to test most predictions and various assumptions, the three models derive from first principles of behavioural ecology and provide a rigorous basis for predicting indirect effects of fisheries. Further, overfishing of sharks and of resources used by marine mammals are pressing global problems which cannot be addressed by empirical studies alone; indirect interactions between species are too complex to be elucidated without theoretical guidance and rapid exploitation often outpaces the acquisition of data relevant to conservation. Thus, theory presented here is important for assessing the potential damage wrought by different fishery scenarios, informing decisions that attempt to optimise exploitation and conservation, and guiding empirical research.

Key words:

Dynamic state variable model, fisheries, Gulf of Alaska, harbour seal, predation risk

Dedication

…for…

…Twyla…her pulse… and that of the living ocean of her future…

…Gail…her pulse… and that of her pathways through space & time …

… My Parents…their pulse…and their awareness that without sea water there is no pulse…

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The expertise of Gail Blundell made the capture and instrumentation of seals possible. Lee Hulbert was incredibly generous with his sleeper shark data. Richard E. Thorne made essential contributions with herring and pollock data and general fish knowledge.

To those who participated in fieldwork—many, many thanks. They include Gail Blundell, Scott Wolfe, Randy Naylor, Richard E. Thorne , Jay Ver Hoef, the crews of the *Alexandra* and *Babkin*, Anne-Hoover Miller, Jennifer Burns, Bob Small, Steve Trumble, Steve Jeffries ...and apologies to others that I failed to include. Peter Olesiuk, designed and constructed the instrument packages and floatplane pilot Patrick Kearney recovered most of these instruments. The empirical data would be nonexistent without these contributions.

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As someone who finds a subtext for just about everything, I must acknowledge the deeper sources of the work. The music of Michael Franti, McCoy Tyner, The Flecktones and many others fuelled some key blasts. So did the following authors: Samantha Power (*A Problem From Hell: America and the Age Of Genocide*), Jared Diamond (*Collapse*), Ronald Wright (*A Scientific Romance* and *A Short History of Progress*), Joel Balkan (*The Corporation*), Hugh Brodie (*The Other Side of Eden*), Thomas King (*The Truth About Stories*), and Elie Wiesel (*The Night Trilogy*).

Gail Lotenberg, a true insider, contributed far beyond what I mentioned above. Suffice is to say that shortly after my defence she came to me and said, 'If you hit your head against the wall enough times, the wall will break'. Speaking of insiders, Twyla Bella Frid Lotenberg made me throw away all cynicism and actually believe in a living ocean for the future. These are, by far, the greatest of all contributions.

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Chapter 1. General introduction

It is tempting to introduce this body of work as a fresh look at an old problem but, truth is, that would not be quite right. What I *can* say is that this work highlights a not-so-new yet underutilised and potentially powerful tool for approaching a puzzle that is now over two decades old. I have no pretence that this tool will solve all mysteries and, in fact, it will be most useful when combined with complementary approaches. What a huge body of ecological work does tell us, however, is that this tool—more likely than not—can increase the speed and clarity with which plausible explanations for the 'old problem' are short-listed.

The 'old problem' is that of pinniped declines in the eastern North Pacific, although I focus on harbour seals *Phoca vitulina richardsi* in Prince William Sound (PWS), and inherent to it are questions about potential indirect effects of fisheries. The 'not-so-new tool' is optimal risk-taking theory, which can dissect synergistic effects of resources and predators on animal distributions and enhance predictions on the ensuing population and community processes. The 'complementary approaches' are long-term empirical field studies.

The outline of the story is as follows. Concurrent with other pinniped declines in the Gulf of Alaska and Bering Sea (National Research Council 2003, Springer et al. 2003; Trites & Donnelly 2003 and references within), the PWS population of harbour seals decreased 63% between 1984 and 1997 (Frost et al. 1999) and remains depressed (Ver Hoef & Frost 2003). Hypotheses on potential causes of pinniped declines have invoked dichotomous scenarios about 'bottom-up vs. top-down forcing' (e.g. National Research Council 2003; Trumble & Castellini 2002; Springer et al. 2003; Trites & Donnelly 2003). Yet even for the best studied species, the Steller sea lion *Eumetopias jubatus*, treating resources and predators as independent factors has brought limited resolution (National Research Council 2003; Dalton 2005).

Many ecologists would view this limited resolution as unsurprising. After all, it is a decades-old idea that population and community processes cannot be fully understood without invoking notions about optimal decision-making and synergistic effects of predators and resources (e.g. McNamara & Houston 1987; Mangel & Clark 1988; Abrahams & Dill 1989; Abrams 1993; Sinclair & Arcese 1995; Krebs et al. 1995; Lima 1998a,b; Werner & Peacor 2003). The underlying tenets are that (a) foraging decisions must optimize conflicting demands, including resource acquisition and predator avoidance (Lima & Dill 1990; Lima 1998a,b), and (b) antipredator behaviour has a cost—reduced net energy intake rate—which is less affordable to individuals in poor energy state because it might lead to starvation or net loss of reproductive potential (McNamara & Houston 1987; Clark 1994). Thus, poor energy state and resource scarcity synergistically promote greater risk-taking and higher predation rates (e.g. Anholt & Werner 1995; Sinclair & Arcese 1995; Sweitzer 1996). In an elegant experiment, for instance, Anholt & Werner (1995) exposed tadpoles to predatory dragonfly larvae and manipulated resource levels. A 22% decline in food density resulted in 1.5-fold increases in the tadpole's activity level and movement rate, and the increased exposure raised their predation rates by 60%, despite predator densities remaining constant. This experiment made it clear that (Anholt & Werner 1995:2230):

> *The dependence of predation mortality on resources available to prey underlines the futility of characterizing population regulation as being due to predation or resources. Adaptive variation in behaviour responds to both pressures simultaneously.*

From a second, more complex set of experiments, Anholt & Werner (1998:735), concluded that, 'If adaptive variation in prey behaviour is as widespread as it appears to be, then attempts to understand population and community dynamics without consideration of that variation may be doomed to failure.'

And the conclusions of Anholt & Werner do scale up. Recent field studies of vertebrate systems amenable to experimentation (e.g. Krebs et al. 1995; Biro et al. 2003; Zanette et al. 2003) or with access to long-term correlative data sets (Sinclair & Arcese 1995) clearly showed synergistic effects of resources and predators on population processes. For instance, the interactive effect on song bird reproductive success of relaxed predation risk and supplementary food was almost twice as large as the additive effect of the two factors (Zanette et al. 2003).

Until now, however, these concepts have not informed discussions on the possible causes of pinniped declines and related issues concerning indirect fishery effects. Part of the reason may be valid. Measuring individual reproductive rates, sequential changes in body condition, and cause and location of mortality is quite doable in some systems (e.g. Krebs et al. 1995; Zanette et al. 2003) but difficult or near-impossible for northeast Pacific pinnipeds.

Immeasurability, however, is unrelated to the potential importance of a process. Thus, I began my research by developing a dynamic state variable model (Mangel & Clark 1988; Clark & Mangel 2000) of foraging decisions that made mathematically-explicit links between behaviour and fitness (Chapter 2). Simulations predicted that compensatory foraging effort by seals will mitigate potential loss of energy reserves when resources decline, but only at the cost of higher predation rates, even if predator densities remain constant. I attempted to test behavioural predictions from this model, but failed to do so because data on seal diving behaviour was limited to 9 individuals spread over 5 age-sex classes and different levels of body condition. Thus, data representing individuals in a given category of residual reproductive value were unreplicated.

The data I did obtain, however, led to Chapter 3. Here I predicted net energy gain and predation risk per foraging dive, parameterising an analytical model with field data on seal behaviour, resource distributions, and use of depth by Pacific sleeper sharks *Somniosus pacificus* and killer whales *Orcinus orca*. Analyses suggested that risk of mortality from sharks and net energetic gain were greatest when seals foraged in deep strata, and empirical data showed individual variation in use of these strata. Plots of the individuals' predicted energy gain against predicted predation risk fit best when relative danger from sharks was assumed to be 50 times greater than the relative danger from killer whales. The first two studies combined suggest that, theoretically, overfishing of near-surface fatty fishes might increase shark predation rates on seals.

The results of Chapter 3, a growing concern for global shark declines (e.g. Stevens et al. 2000; Baum et al. 2003), and an apparent lack of discussion on the potential ecological consequences of the ongoing bycatch of Pacific sleeper sharks (see Courtney et al. 2004) led to Chapter 4. This chapter presents a dynamic state variable model that predicts an asymmetric trophic cascade in which indirect effects of sleeper sharks on resources are mediated by seal avoidance of riskier strata. Risk management by seals reduced mortality to the dangerous resource (walleye pollock *Theragra charcograma*) while increasing mortality to the safer resource (Pacific herring *Clupea pallasi*), and the bycatch of sharks altered this dynamic. This chapter ties together many theoretical strands by considering the potential indirect effects of directed and bycatch fisheries not only on seals themselves, but also on the resource species they use.

I emphasise from the outset that empirical tests of predictions and of some assumptions are lacking. The models, however, derive from first principles of behavioural ecology and thus can play an important role in the iterative process between empirical analyses and theory (e.g. Clark & Mangel 2000) and inform management decisions.

A note on formatting and style

The three main chapters of this dissertation (Chapters 2-4) were written as independent manuscripts intended for publication in refereed journals. Accordingly, each has a stand-alone introduction, discussion, list of references, and acknowledgements, which makes some redundancies inevitable (e.g. when introducing the general problem, caveats to conclusions, etc).

Also, each journal has its own guidelines, which leads to inconsistent spelling (U.S. vs. British) and formatting between chapters. Finally, I wrote Chapters 2-4 from a first-person plural perspective to reflect the collaborative nature of the work and, these chapters include a list of co-authors.

Literature cited

Abrahams M.V. & Dill L.M. (1989) A determination of the energetic equivalence of the risk of predation. Ecology 70, 999-1007

Abrams P.A. (1993) Why predation rate should not be proportional to predator density. Ecology 74, 726-733

Anholt B.R. & Werner E.E. (1995) Interactions between food availability and predation mortality mediated by adaptive behavior. Ecology 76, 2230-2234

Anholt B.R. & Werner E.E. (1998) Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. Evolutionary Ecology 12, 729-738

Baum J.K., Myers R.A., Kehler D.G., Worm B., Harley S.J. & Doherty P.A. (2003) Collapse and conservation of shark populations in the northwest Atlantic. Science 299, 389-392

Biro P.A., Post J.R. & Parkinson E.A. (2003) From individuals to populations: prey fish risk-taking mediates mortality in whole-system experiments. Ecology 84, 2419-2431

Clark C.W. (1994) Antipredator behavior and the asset-protection principle. Behavioral Ecology 5, 159-170

Clark C.W. & Mangel M. (2000) Dynamic state variable models in ecology. Oxford University Press, New York.

Courtney D.L., Gaichas S., Boldt J., Goldman K. & Tribuzio C. (2004) Sharks in the Gulf of Alaska, Eastern Bering Sea, and Aleutian Islands. In: Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 2005. North Pacific Fishery Management Council, 605 W 4th Ave. Suite 306, Anchorage, AK 99501.

Dalton R. (2005) Is this any was to save a species? Nature 436, 14-16

Frost K.J., Lowry L.F. & Ver Hoef J.M. (1999) Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Valdez Oil Spill. Marine Mammal Science 15, 494-506

Krebs C.J., Boutin S., Boonstra R., Sinclair A.R.E., Smith J.N.M., Dale M.R.T., Martin K. & Turkington R. (1995) Impact of food and predation on the snowshoe hare cycle. Science 269, 1112-1115

Lima S.L. (1998a) Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48, 25-34

Lima S.L. (1998b) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27, 215-290

Lima S.L. & Dill L.M. (1990) Behavioural decisions made under the risk of predation. Canadian Journal of Zoology 68, 619-640

Mangel M. & Clark C.W. (1988) Dynamic modeling in behavioral ecology. Princeton University Press, Princeton.

McNamara J.M. & Houston A.I. (1987) Starvation and predation as factors limiting population size. Ecology 68, 1515-1519

National Research Council (2003) Decline of the Steller sea lion in Alaskan waters. National Academy Press, Washington, D.C., USA.

Sinclair A.R.E. & Arcese P. (1995) Population consequences of predation-sensitive foraging: the Serengeti wildebeest. Ecology 76, 882-891

Springer A.M., Estes J.A., van Vliet G.B., Williams T.M., Doak D.F., Danner E.M., Forney K.A. & Pfister B. (2003) Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Science 100, 12223-12228

Stevens J.D., Bonfil R., Dulvy N.K. & Walker P.A. (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science 57, 476-494

Sweitzer R.A. (1996) Predation or starvation: consequences of foraging decisions by porcupines (*Erethizon dorsatum*). Journal of Mammalogy 77, 1068-1077

Trites A.W. & Donnelly C.P. (2003) The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. Mammal Review 33, 3-28

Trumble S.J. & Castellini M.A. (2002) Digestive efficiency of pollock and herring in harbor seals: Addressing the "is it food?" hypothesis. FASEB Journal 16, A47-A47

Ver Hoef J.M. & Frost K.J. (2003) A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. Environmental and Ecological Statistics 10, 201-209

Werner E.E. & Peacor S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84, 1083-1100

Zanette L., Smith J.N.M., van Oort H. & Clinchy M. (2003) Synergistic effects of food and predators on annual reproductive success in song sparrows. Proceedings of the Royal Society of London B. 270, 799-803

Chapter 2. Do resource declines increase predation rates on North Pacific harbor seals? A behaviour-based plausability model

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Abstract

Harbor seals and other pinnipeds in the Gulf of Alaska have declined since the 1980s. The search for causation has considered top-down and bottom-up influences as independent factors. Research on other systems, however, reveals that resource availability and predator densities synergistically determine the predation rates experienced by intermediate consumers. From this premise we developed a dynamic state variable model of behavior for the declining harbor seal population of Prince William Sound, Alaska. We modeled separate scenarios in which seals were prey to a) transient killer whales at and near the surface and Pacific sleeper sharks throughout the water column, or b) killer whales only. In both scenarios, resource decrements reduced the time spent by seals at the haulout (a refuge lacking food), increased the time spent at foraging areas, and lengthened surface intervals and dive durations. Due to this behavioral compensation, per capita fish consumption remained relatively constant but predation rates increased as resources declined, despite fixed predator densities. Foraging effort and predation rates increased further when energy stores were lower at the onset of simulation periods, but in all scenarios seals not killed by predators achieved a high level of energy stores by the reproductive season. These behavioral mechanisms proposed by the model potentially explain—at least partially—why the population has been declining while seals have maintained good energy stores throughout temporal shifts in resource availability. More generally, simulations suggest that overfishing and other factors that reduce fish populations indirectly increase predation rates on seals, but data are needed to test this hypothesis. Our model also encompasses a broader ecosystem perspective by predicting how resource level determines the relative strength of trait- and density-mediated interactions,

whereby predators of seals indirectly affect fish populations by influencing the foraging behavior and density of seals. The behavioral modeling approach presented here is an additional tool for resource managers attempting to optimize fisheries exploitation and pinniped conservation.

Introduction

Several pinniped populations of the eastern North Pacific have declined since the 1980s. The search for causation has considered top-down and bottom-up forces separately (e. g. Trumble & Castellini 2002a, National Research Council 2003, Springer et al. 2003). Research on other systems, however, reveals that resource availability and predator densities are inextricably linked in determining the predation rates experienced by intermediate consumers (e.g. Anholt & Werner 1995, Krebs et al. 1995, Sinclair & Arcese 1995, Biro et al. 2003). Thus, 'bottom-up versus top-down' questions likely over-simplify North Pacific pinniped declines.

This assertion builds on the behavioral ecological framework in which individuals optimize trade-offs between predator avoidance and resource acquisition (Lima & Dill 1990), and the optimal level of risk-taking (or conversely, of investment in antipredator behavior) depends on the individual's energetic state. Individuals in low energetic states must take greater risks to avoid either imminent starvation or loss of reproductive potential, and therefore incur higher predation rates than individuals in higher energetic states. Resource scarcity might reduce rates of energy gain and increase the frequency of poor energetic states in the population, indirectly increasing risk-taking and predation rates (e.g. McNamara & Houston 1987, Anholt & Werner 1995, Sinclair & Arcese 1995, Biro et al. 2003, Luttbeg et al. 2003).

The behavioral ecological framework extends to the community level through trait-mediated indirect interactions (TMII). Top predators might indirectly affect the population dynamics of a resource species by influencing the habitat selection and foraging rates of an intermediate consumer. These indirect effects could interact with density-mediated indirect interactions (DMII): predators not only affect the distribution and per capita foraging rates of consumers (the first step of a TMII), but also their overall density through direct mortality (the first step of a DMII) (Luttbeg et al. 2003, Werner & Peacor 2003).

These concepts have yet to be applied to the understanding of large-scale systems in the North Pacific. Consider our case study: harbor seals (*Phoca vitulina*) in Prince William Sound (PWS), Alaska. This population declined 63 % between 1984 and 1997 (Frost et al. 1999, Ver Hoef & Frost 2003) and its numbers are still depressed (G. M. Blundell unpublished data). Following a peak in 1988, the biomass of Pacific herring (*Clupea pallasi*), a near-surface resource important to seals (Iverson et al. 1997), dropped 95% to a low point in 2001 and its apparent recovery did not begin until 2003 (Thomas & Thorne 2003, R. E. Thorne unpublished data). The herring collapse stemmed from the combined effects of an oceanographic regime shift that began in the late 1970s and which affected the abundance of many fish species (Anderson & Piatt 1999), the 1989 Exxon Valdez oil spill, and overfishing (Thomas & Thorne 2003). Despite dramatic changes in resources, a conundrum surrounding the harbor seal decline is that individual seals studied in recent years have very good fat reserves (Fadely 1997, Trumble & Castellini 2002b, K. J. Frost unpublished data) and the pregnancy rates of adults (≥6 yr old) appear high (100 % of 11 adults females sampled in PWS between 2000 and 2002 were pregnant: A. Hoover-Miller unpublished data). A Leslie matrix projection model suggests that resource limitation may have initiated the decline in the mid 1980s—a period for which body condition data are unavailable to assess nutritional stress—but additional mortality was necessary to sustain the decline (R. J. Small unpublished data). Thus, interactions between energy state, predation risk, and resource levels require further examination. Transient killer whales (*Orcinus orca*) are well-known predators of seals at and near the surface (Saulitis et al. 2000). Pacific sleeper sharks (*Somniosus pacificus*), which use the entire water column (Hulbert et al. 2006), are another potential predator.

Herein we present a dynamic state variable model (Clark & Mangel 2000) that establishes the theoretical plausibility that declining resources elevate predation rates on seals, even if predator density does not increase. Our computer experiments contrasted seal behavior, survival and reproduction between three resource levels: a baseline level, twice the baseline, and half the baseline. This was done factorially for two levels of energy reserves at the onset of simulation periods: high (90% of maximum) and low (50% of maximum). Because the predatory role of killer whales is well established while that of sleeper sharks is assumed (see 'Methods-Model system and structure'), we modeled separate scenarios in which seals were threatened by a) killer whales and Pacific sleeper sharks, but with risk from sharks at a much lower level than risk from killer whales, or b) killer whales only.

Based on the body of theory discussed earlier, we expected declining resources and lower levels of initial energy reserves to elevate predation rates on seals by demanding more time exposed to risk in foraging areas and less time in the safety of the haulout. Along with these broad-scale time allocation decisions, which have counterparts in myriad other systems (Lima & Dill 1990), we needed to consider details of diving behavior. For seals and other aquatic foragers that breathe air (Boyd 1997), the time spent uploading oxygen at the surface is mutually exclusive with prey-searching while also influencing foraging depth and time (Kramer 1988). The optimal organization of a dive cycle is predicted to respond to ecological factors such as prey distribution (e.g. Thompson & Fedak 2001) and predation risk (Heithaus & Frid 2003). Not surprisingly, a recent empirical analysis demonstrated that the functional response of pinnipeds to prey density is best understood by applying optimal diving theory (Mori & Boyd 2004). Thus, we expected the greater risk-taking associated with resource scarcity to manifest at the scale of the dive cycle via longer surface intervals and dives (Heithaus & Frid 2003). Although a large theoretical literature predicts optimal dive cycles under many conditions (e.g. Kramer 1988, Mori 1998, Thompson & Fedak 2001, Heithaus & Frid 2003, Houston et al. 2003), it does not consider predation risk at multiple depth strata, as we do here. Further, ours is the first dynamic state variable model to explore how dive cycle organization contributes to survival and reproduction over multi-month periods.

Indirect interactions between top predators and resource species, as mediated by intermediate consumers such as seals, are inherent to marine communities (Dill et al. 2003). Single-species management is unlikely to solve marine conservation problems (Pauly et al. 2002, Alonzo et al. 2003). Thus, we placed our model in a broader ecosystem perspective by simulating the extent to which top predators influence fish populations by affecting the behavior and density of seals under different resource levels. We expected TMIIs to weaken and DMIIs to strengthen when energetic state and resource level were low because antipredator behavior is less affordable then than when energetic state and resource levels are higher (Luttbeg et al. 2003).

Methods

Model system and structure

This section describes the model and its assumptions. Appendix 2.1 details model derivation and Appendix 2.2 and Tables 2.1 & 2.2 describe parameterization.

Transient killer whales are the primary predator of seals at and near the surface, an assumption well supported by direct observations (Saulitis et al. 2000). We assume Pacific sleeper sharks to be predators at depth, but predation events involving them are unobservable from the surface and there is a dearth of data on pinniped-sleeper shark interactions. Stomach contents analyzed to date for sleeper sharks in the Gulf of Alaska do not provide compelling evidence of predation on seals. Only 1 of 36 samples of non-empty stomachs for sharks with pre-caudal lengths ≥2 m, the minimum size we assume capable of killing adult seals, contained seal tissues (data for 2001-2002: Sigler et al. 2006). Building an empirical understanding of seal-sleeper shark interactions will be a slow and expensive process, and it is the role of models to guide approaches to potentially relevant processes that have yet to measured (Clark & Mangel

2000). Thus, it is appropriate to consider danger from sleeper sharks in the model, particularly because in a sample of 429 PWS sharks, 25 % had precaudal lengths of 2.0–2.8 m (W. Bechtol unpublished data). Weight estimates for those lengths are approximately 100–200 kg (Sigler et al. 2006), or 1.3-2.5 times the weight of the average adult seal (80 kg: Frost 1997). Consistent with the notion that the larger size classes of sharks might kill seals opportunistically, time-at-depth data indicate spatial overlap between seals and sharks (Hulbert et al. 2006; Frost et al. 2001, Chapter 3).

Pacific herring and walleye pollock (*Theragra chalcogramma*) are the main resources sought by seals. Pollock are found deeper (Appendix 2.2) and contain about half the energy density of herring (Anthony et al. 2000), but can also be much larger. Based on prior surveys in the area (see Appendix 2.2), we assumed wet weights of 115 g for herring and 525 g for pollock for model parameterization. Ongoing studies with juvenile Steller sea lions (*Eumetopias jubatus*) suggest that adult harbor seals likely handle underwater the larger prey sizes of pollock assumed by the model (D. Tollit pers. comm.). Seals readily digest the extra biomass (Trumble et al. 2003), so the net energetic value per fish (independent of travel and search costs) is greater for pollock than for herring (Table 2.2, Appendix 2.2). Therefore, the model system has a vertical spatial structure in which choice of depth involves trade-offs between multiple predators and resource types, as well as oxygen-constrained travel and search times. Temporal trade-offs are created by day and night cycles; at night fish biomass can increase in shallower strata while killer whale hunting activity appears reduced (R. W. Baird unpublished data). This relative safety, however, is partly offset by the nocturnal use of shallow depths by sharks (Appendix 2.2).

The model is specific to adult female seals with the potential for 20 subsequent reproductive years. Here, seals optimize trade-offs for conditions encountered during late winter and spring (Appendix 2.2), the 120 days leading to reproduction in early June. In the model, decisions are made every 20 s time period. We used this small time step because, for many diving vertebrates, small differences in the duration of surface intervals between dives might have strong non-linear effects on energy gain and predation risk (Heithaus & Frid 2003).

The model uses two internal states, energy reserves and oxygen stores. An environmental state variable abstracts potential habitats and depths (Fig. 2.1), as suggested by preliminary data on seal locations and fish distributions (Appendix 2.2). These locations are a haulout or refuge from predation without food, a nearshore habitat 500 m from the haulout that includes a surface location for oxygen uploading and a 40 m-deep foraging patch, and an offshore habitat 3 km from the haulout that includes a surface location and foraging patches at depths of 20 and 100 m (Fig. 2.1).

The seal's choice of habitat and depth is unconstrained by time of day or night, an assumption supported by empirical data (Frost et al. 2001). We also 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).

Model tractability required the following simplifications. Travel speed between surface habitats and depths is fixed at 1 m s^{-1}. Although resource species in the wild might be schooling fishes, expected rate of resource acquisition is parameterized as an average rate of encounter with and capture of individual fish. There is no resource depletion, nor intra- or interspecific competition, and predator and resource species have fixed behaviors. Buoyancy upthrust due to fat stores and depth (e.g. Beck et al. 2000), and anaerobiosis (Ydenberg & Clark 1989) can affect optimal time allocation during diving, but these processes are not modeled.

Computer experiments

Solution to the dynamic programming equation 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. Initial energy state was treated as an experimental variable with two levels; low and high initial energy states representing 50 and 90% of the maximum value, respectively. These are the states at the start of forward iterations that send individuals onto different trajectories (Appendix 2.1). Resource level was a second experimental variable. High, medium and low resource levels were indexed, respectively, as 200, 100 and 50% of baseline values for the location-specific probabilities of encountering and capturing a fish each 20 s period (Table 2.2, Appendix 2.2). Location-specific probabilities of encountering a predator per 20-s period remained unchanged (Table 2.2). This is equivalent to maintaining a fixed predator density because in the model predator behavior is invariable and seal behavior does not change within a time period.

Treatment combinations were simulated 1000 times each and we interpret results as predicted responses by populations with initial sizes of 1000 individuals under the simplifying assumption of no density dependence (Clark & Mangel 2000). Following Luttbeg et al. (2003), we quantify the relative size of trait- and density-mediated indirect effects of top predators on fish as proportional reductions of the number of fish eaten by seals due to risk avoidance versus density reduction, respectively (Appendix 2.1).

Results

During all simulations, foraging occurred almost exclusively at night and at the 100 m foraging patch, where pollock were the only prey available. Refuge use was primarily diurnal. We first present results for the scenario in which both sharks and killer whales are assumed to be dangerous (Figs. 2.2-4), and follow with the main lessons from the scenario in which killer whales are assumed to be the only predator (Fig. 2.5).

The number of foraging trips (departures from the refuge) and dives made over the 120 d simulation period (Figs. 2.2a,b), and the average duration of each dive increased as resources became more scarce. Because travel time to the 100 m-deep foraging patch is fixed at 200 s (100 s spent for descent or ascent), increases in dive duration imply that more time per dive was spent at the foraging patch (Fig. 2.2c). Although longer periods of oxygen loading at the surface were needed to support the longer dives (Fig. 2.2d), the proportion of the dive cycle spent at the foraging patch increased slightly with declining resources (Fig. 2.2e). These correlated sets of responses combined into an overall response whereby decrements in resource levels led to an increase and decrease, respectively, in the overall proportions of time at the 100 m foraging patch and at the refuge (Figs. 2.2f,g). Due to this behavioral compensation, the total number of fish eaten was similar across resource levels (Fig. 2.2h). At a given resource level, foraging effort and per capita fish consumption generally were greater and time at the refuge was smaller for the low than for the high initial energy state. However, at high resource levels the effect of state was smallest, and even absent in the case of dive cycle organization (Fig. 2.2).

Despite fixed predator densities, predation rates increased with declining resources and, at a given resource level, were higher when initial energy state was low (Fig. 2.3a). Nearly all survivors, however, were near the maximum energy state at the end of the simulation, regardless of initial state and resource level, except when resource level was lowest (Fig. 2.3b).

For both initial energy states, TMIIs strongly dominated and DMIIs were weak at high resource levels, whereas DMIIs dominated and TMIIs were very weak at mid- and low resource levels (Fig. 2.4). At high resource levels, TMIIs were stronger for high than for low initial energy state (the net reduction in fish eaten was ~4% greater: Fig. 2.4).

When killer whales were assumed to be the only predator, behavioral responses to resource decrements were undistinguishable from the scenario with both predator types. Within a resource level, there were no differences in foraging effort and success (Figs. 2.5a-c), and therefore on TMIIs. These results indicate that killer whale risk alone determined diving behavior and other time allocation in simulations where both sharks and killer whales were assumed to be dangerous. However, due solely to predator density effects, mortality rates within a resource level were higher in the scenario that included both predator types. Mortality rates at mid- and low resource levels in the killer whale scenario, however, are approximately equal to mortality rates at high and mid-resource levels, respectively, in the scenario that included both predator types (Fig 2.5d). Thus, doubling resource level in the latter scenario decreased mortality rates to a similar degree as removing shark risk.

Discussion

Our model formally establishes the theoretical plausibility that declining resources and lower energy states increase predation rates on harbor seals when predator density is assumed to remain constant. Our results are consistent with the principle that fewer resources and poor energy reserves demand a greater level of foraging effort that is attainable only by relaxing antipredator behavior (McNamara & Houston 1987, Anholt & Werner 1995, Sinclair & Arcese 1995, Biro et al. 2003, Luttbeg et al. 2003).

Simulations indicate that synergistic effects of resources and predators might contribute to harbor seal declines via behavioral decisions occurring at two scales. At the scale of broad habitat selection, resource scarcity and lower energy state reduced the amount of time spent in the safety of the haulout and increased the time spent at risk in foraging areas. At the scale of dive cycle organization, declining resources and lower energy state led to longer surface intervals and dives. These responses increased the proportion of the dive cycle spent at the foraging patch and resource gain per dive. The cost was more time spent where encounters with killer whales (the surface) and sleeper sharks (the 100 m patch) were most likely. Existing theory predicts that trade-offs between increased risk at the surface and energy gain are optimized by shortening surface intervals, despite the resulting decrease in proportion of the dive cycle at the foraging patch (unless a shallower patch is selected) and the lower rates of energy gain (Heithaus & Frid 2003). Our simulations indicate, however, that the foraging costs of safer and shorter surface intervals become less affordable as resources decline or when initial energy state is lower.

The most relevant theoretical insight for the population decline of PWS seals is two-fold. First, under model assumptions, individual seals can maintain a constant rate of foraging success through periods of resource scarcity if they invoke compensatory foraging effort, but only at the cost of increased predation rates. Second, foraging effort and predation rates increase further if energy stores are lower at the onset of simulation periods, but in all scenarios seals not killed by predators achieve a high level of energy stores by the reproductive season. These behavioral mechanisms proposed by our application of the state-dependent optimal foraging paradigm potentially explain—at least partially—why the seal population has been declining while individuals have maintained good energy stores (Fadely 1997, Trumble & Castellini 2002b, Trumble et al. 2003, b, K. J. Frost unpublished data, A. Hoover-Miller unpublished data) throughout temporal shifts in resource availability (Anderson & Piatt 1999, Thomas & Thorne 2003).

Our general conclusions are robust even if sleeper sharks are assumed not to be dangerous to seals. In our model, killer whale predation increases with declining resources largely because resource decrements demand more dives, as well as longer periods at the surface for meeting the oxygen requirements of longer dive durations. Thus, cumulative surface time increases (Fig. 2.5c) raising encounter rates with killer whales. In addition, more foraging effort correlates with less time in the safety of the haulout.

Our model also expands the concept of resource- and state-dependent TMIIs to intermediate consumers whose internal state depends not only on energy, but also on the level of oxygen available to seek resources. It reinforces the theoretical prediction that TMIIs strengthen and DMIIs weaken when resource level and energy state are high (Luttbeg et al. 2003). Thus, our model can inform conservation approaches not only for pinnipeds but also for broader ecosystem issues. For instance, resource managers strive to estimate the extent to which fisheries compete with pinnipeds, and the latter's effect on fish populations. Considering the distribution of energy states in the pinniped population and the indirect effects of top predators might improve these estimates. Our model's output could effectively become the input for existing ecosystem models where all players are behaviorally inert (e.g. Okey & Wright 2004). Whether dissecting responses to resources and risk into components of the dive cycle is relevant to understanding TMIIs or DMIIs could depend on the extent to which predators use the surface rather than deeper strata.

Our simulation results are consistent with some empirical studies. For example, at Sable Island, Nova Scotia, there is dietary overlap between sympatric harbor seals and grey seals (*Halichoerus gryphus*). The harbor seal population has declined since the early 1990s, while grey seals have been increasing exponentially (Bowen et al. 2003 and references within). As suggested by Bowen et al. (2003), interspecific competition may have functionally reduced resource availability for harbor seals. During their population decline, harbor seals have experienced elevated rates of shark predation (Lucas & Stobo 2000, Bowen et al. 2003), while maternal post-partum mass and most other resource-sensitive life-history parameters have remained constant (Bowen et al. 2003). These data are consistent with our prediction that seals can cope with declining resources via compensatory foraging effort (Fig. 2.2), thus maintaining high energy reserves but at the cost of increased encounters with predators (Fig. 2.3). If real, greater risk-taking by Sable Island harbor seals may have resulted from behavioral mechanisms similar to those elucidated by simulations (see Fig. 2.2), but long-term trends in foraging behavior have yet to be analyzed in the context of competition-induced resource declines. Consistent with our state-dependent risk-taking predictions (see Fig. 2.2), however, dive effort (measured as vertical meters traveled per hour) was inversely related to maternal post-partum mass during mid- and late-lactation (Bowen et al. 2001). Thus, it could well be that shark predation is the proximate cause of the Sable Island harbor seal decline, but resource scarcity leading to greater risk-taking is the ultimate cause.

Unfortunately, our predictions cannot be assessed by published studies on the behavior of Alaskan harbor seals during 1992-1997 (Frost et al. 2001, Lowry et al. 2001, Hastings et al. 2004), as these lack the requisite data on individual energy states and on resource and predator distributions. However, unpublished data on the behavior of harbour seal pups in PWS during 1997-1999 are consistent with the general results of our simulations. Pups were heavier and spent more time hauled and less time at sea during a year of abundant resources (1997) than during other years (K. J. Frost unpublished data). Also, decreases in foraging effort in response to more abundant resources are well-documented for other pinnipeds (e.g. *Arctocephalus gazelle*: Mori & Boyd 2004).

Is our model relevant to the recent and notorious population decline of the western stock of the Steller sea lion in Alaska (National Research Council 2003)? Hypotheses on the underlying causes of the sea lion decline have followed a dichotomous 'bottom-up vs. top-down forcing' approach, with the apparent weight of the evidence leaning towards 'top-down forcing' (e.g. National Research Council 2003). Observed rises in predation rate and good body condition of adult females and pups, currently interpreted as indicating top-down forcing (Table 6.2 of National Research Council 2003), suggest that interactions between resource level and predation rate, as elucidated by our model, should be considered among the alternative hypotheses. Admittedly, foraging effort by adult females during summer has decreased during the period of population decline (Table 6.2 of National Research Council 2003), which does not support our predictions, but a broader seasonal scope is needed for assessing the behavioral mechanisms influencing mortality rate.

Caveats and conclusions

The significance of our behavioural modeling approach is that it provides a rigorous way of thinking about pinniped declines that transcends the 'top-down vs. bottom-up' dichotomy. Its mathematical explicitness and consideration of micro-behaviour eliminate mechanistic black boxes, and lead to more realistic, testable predictions. All models, however, require simplifications that do not always satisfy the natural historian. Ours is no different, and we offer the following caveats.

First, we considered only two resources, 115 g herring and 525 g pollock, whereas seals use additional resources (Iverson et al. 1997). Also, parameterization did not consider seasonal variation in resources within the February–early June period considered. Nonetheless, herring and pollock appear to dominate the diet of seals (Iverson et al. 1997) and comprise the dominant biomass in PWS during late winter and early spring (R. E. Thorne unpublished data). While we acknowledge that future studies should consider finer scale seasonality and a wider range of fish species and size classes, our parameterization is adequate for initial hypothesis development. Another simplifying assumption was that patches do not deplete, and thus energy intake rate is a linear function of patch residence time, which might be unrealistic. A decelerating intake rate function might amplify the indirect effect of resource decrements on predation rate and should be considered by future studies.

Second, although there were no differences in seal behavior and foraging success between the scenarios with and without risk from sharks, simulations were not designed explicitly to compare the influence of a surface versus an at-depth predator. Killer whale risk at the surface during the night (when foraging occurred) was 6 times greater than shark risk at the foraging patch (Table 2.2). At the time of model development there was no information with which to evaluate the realism of that scenario. Subsequent analyses suggest that we greatly underestimated the relative abundance of sharks in the current parameterization, and that sharks may actually influence the risk-energy trade-off experienced by seals more strongly than do killer whales (Chapter 3).

Third, in our simulations seals used only the 100 m deep patch, and did not forage in shallower strata, which contradicts empirical data showing that harbor seals in PWS and elsewhere in Alaska forage throughout the water column (Hastings et al. 2004). This inconsistency likely arose from the underestimated shark risk discussed above, which would increase the security of deep strata relative to shallow ones. Also, resource encounter probabilities were based on median values for depth-specific fish biomass (Appendix 2.2). Consequently, parameterization did not adequately capture large ephemeral aggregations of herring near the surface, exaggerating the low expected energy gain of foraging in shallow strata. Thus, the conditions discouraging shallow foraging in the model may not represent those experienced by seals in recent studies (see Hastings et al. 2004). Future simulation studies should experimentally vary the relative abundance of predators and resources in deep versus shallow strata.

A final caveat is that although haulouts are refuges from sharks and killer whales, Alaska native subsistence hunting activities focus on these locations. While risk from hunters is beyond the scope of this model, it could well be that subsistence hunters not only inflict direct mortality, but also indirectly increase predation rates from sharks and killer whales by discounting the expected benefit and reducing the actual use of haulouts for safety from these predators (see Dill et al. 2003). It would be interesting for future simulation studies to vary the levels of human hunting and of resources factorially and predict shark and killer whale predation rates for these scenarios.

The above caveats qualify our inferences on seal behavior without diminishing our general conclusion. Our model suggests, as a theoretically plausible hypothesis, that overfishing and other factors that reduce fish populations indirectly increase predation rates on pinnipeds. This hypothesis could be quite relevant to analyses of the harbor seal decline in Prince William Sound. Pacific herring collapsed (Thomas & Thorne 2003) and other resources shifted availability (Anderson & Piatt 1999) concurrent with the decline, yet evidence for nutritional limitation is lacking (Fadely 1997, Trumble & Castellini 2002b, Trumble et al. 2003, b, K. J. Frost unpublished data, A. Hoover-Miller unpublished data). Similar mechanisms may be inherent to other pinniped declines (e.g. Bowen et al. 2003). By explicitly considering behavior and addressing indirect interactions between species, our model contributes towards a more diverse tool box for resource managers attempting to optimize fisheries exploitation and focal species conservation (Alonzo et al. 2003, Okey & Wright 2004).

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Appendix 2.1. Derivation of the dynamic state variable model

The model's terminal horizon, T, is when condition-dependent reproduction occurs. The time span preceding T is divided into 20 s periods, t, and decisions are made every t. The model has two 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 2.2) are 0–45 and 0–11, respectively.

An environmental state, $H(t) = h$, represents location at t (Fig. 2.1). 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 two further qualified as foraging habitats, and locations 1, 2 and 5 as *depths* or *patches* (Fig. 2.1).

The decision variable is $D(x,y,h,t) = d$, where d is the future location (at either $t + 1$ or $t +$ *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 m s^{-1} between habitats and depths. The notation $time(h,d)$ will indicate the travel time (in 20 s time units) from location 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 $1\text{-}p$ probability of predation during the behavior in question. See Appendix 2.2 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, $D(x, y, h, t) = d$, with $h = d$ and

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

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 2.2) determining the shape of the oxygen gain curve as a decelerating function of $Y(t) = y$ (see Kramer 1988); $\mu_{shark}(h,d)$ and $\mu_{orca}(h,d)$ are the probabilities of predation by sleeper sharks and killer whales, 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

$$\begin{aligned} &X(t + time(h,d)) = x - time(h,d)\alpha_{h,d} \\ &Y(t + time(h,d)) = y_k \\ &H(t + time(h,d)) = d \\ &\Pr\{h,d\} = (1 - \mu_{shark}(h,d) - \mu_{orca}(h,d) + \mu_{shark}(h,d)\mu_{orca}(h,d))^{time(h,d)} \end{aligned} \tag{2}$$

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

$$\begin{aligned} &X(t + time(h,d)) = x - time(h,d)\alpha_{h,d} \\ &Y(t + time(h,d)) = y - time(h,d)u_{h,d} \\ &H(t + time(h,d)) = d \\ &\Pr\{h,d\} = (1 - \mu_{shark}(h,d) - \mu_{orca}(h,d) + \mu_{shark}(h,d)\mu_{orca}(h,d))^{time(h,d)} \end{aligned} \tag{3}$$

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 two possible outcomes. First, the seal may encounter and capture prey with probability λ_h and then

$$
\begin{aligned}
&X(t+1) = x + g_h - c\alpha_{h,d} \\
&Y(t+1) = y - cu_{h,d} \\
&H(t+1) = d \\
&\Pr\{h,d\} = 1 - \mu_{shark}(h,d) - \mu_{orca}(h,d) + \mu_{shark}(h,d)\mu_{orca}(h,d)
\end{aligned}
\tag{4}
$$

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

$$
\begin{aligned}
&X(t+1) = x - \alpha_{h,d} \\
&Y(t+1) = y - u_{h,d} \\
&H(t+1) = d \\
&\Pr\{h,d\} = 1 - \mu_{shark}(h,d) - \mu_{orca}(h,d) + \mu_{shark}(h,d)\mu_{orca}(h,d)
\end{aligned}
\tag{5}
$$

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 animal behaves optimally from $t + 1$ until T. Let $V_d(x,y,h,t)$ be the fitness value of decision d, as determined by equations 1–5, 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:

$$
\begin{aligned}
F(x,y,0,t) &= \max\{V_0(x,y,0,t), V_{25}(x,y,0,t), V_{150}(x,y,0,t)\} \\
F(x,y,25,t) &= \max\{V_0(x,y,25,t), V_2(x,y,25,t), V_{25}(x,y,25,t), V_{150}(x,y,25,t)\} \\
F(x,y,150,t) &= \max\{V_0(x,y,150,t), V_1(x,y,150,t), V_5(x,y,1,50,t) \\
&\qquad V_{25}(x,y,150,t), V_{150}(x,y,150,t)\} \\
F(x,y,2,t) &= \max\{V_2(x,y,2,t), V_{25}(x,y,2,t)\} \\
F(x,y,1,t) &= \max\{V_1(x,y,1,t), V_{150}(x,y,1,t)\} \\
F(x,y,5,t) &= \max\{V_5(x,y,5,t), V_{150}(x,y,5,t)\}
\end{aligned}
\tag{6}
$$

Terminal fitness function

Next, we assume that ψ and σ 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 years is given by φ. Then, the terminal fitness function becomes:

$$F(x,y,h,T) = \psi + \sigma\varphi \tag{7}$$

where ψ and σ depend on $X(T) = x$ such that

$$
\psi = \begin{cases} 0 & \text{if } X(T) < 8 \text{ or } H(t) \neq 0 \\ -0.00002x^3 + 0.00161x^2 - 001134x & \text{if } X(T) \geq 8 \text{ and } H(t) = 0 \end{cases}
\tag{8}
$$

and

$$\sigma = 0.77x^{0.041} \tag{9}$$

Equation 8 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, Equation 8 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 $X(T)$. Equation 9 was constructed by running a preliminary model with baseline parameters values (Tables 2.1, 2.2) and using equation 8 as the terminal fitness function. We ran nine 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 $0.11x_{max}$ and x_{max}. Equation 9 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.

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

$$\varphi = \sum_{y=1}^{20} l_x{}^y m_x \tag{10}$$

where y represents years after T. Survival probability from y-1 to y, $l_x = 0.87$, is the average σ (from Equation 9) for all values of $X(0)=x$. Fecundity at y, $m_x = 0.92$, was calculated as the average ψ (from Equation 8) for all seals that survived to T during forward iterations described above. Our simplifying assumption is that the seal's performance in one year does not predict future performance. We solved Equation set 6 through backward iteration from Equation 7 (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 days, computer memory limited the decision matrix to the last 20 days 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 twentieth 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 day season based on baseline parameter values and two decision matrices (1000 replicates/matrix). The first matrix was generated with a run of 86400 periods, or 20 d; the second with run of 82080 periods, or 19 d. The time spent at any location during forward iterations was nearly identical when using either matrix.

Experimental treatments (see 'Methods-Computer experiments') 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 vs. density reduction, respectively. Following Luttbeg et al. (2003).

$$TMII = 1 - \frac{\textit{fish eaten (risk manipulation)}}{\textit{fish eaten (no manipulation)}} \tag{11}$$

and

$$DMII = 1 - \frac{\textit{fish eaten (predator manipulation)}}{\textit{fish eaten (risk manipulation)}} \tag{12}$$

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 one 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 2.2 Parameterizing the model

Internal state variables.

For energy state $X(t)$, we assumed an energy density of 15923.53 kJ kg^{-1} (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 equation 2.3 of Clark and 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 period and that oxygen level can rise from y_{min} = 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 equation 2.3 of Clark & Mangel (2000), we created the 11 computer values (0-10) of $Y(t)$. The oxygen gain function in Equation 1 was constructed so that the resulting surface and dive durations were consistent with the range recorded during preliminary observations (A. Frid unpublished data). Activity-specific energy and oxygen costs are detailed in Table 2.1.

Resource-related parameters

In SW Prince William Sound during February and March of 2004, nine harbor seals instrumented with VHF headmounts were tracked from a moving vessel during day and night (Chapter 3). While lagging approximately 0.5–2 km behind the seal, depth-specific fish biomass was estimated every second and averaged every minute 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 two habitats according to bottom depth (which correlates with distance from the refuge): a) 35–45 m deep, and b) 90–120 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 unpublished 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, λ_h, (Table 2.2) were calculated as λ_h = S(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 2.2) were assumed based on previous surveys in the area at similar times of year (Thomas & Thorne 2003, R. E. Thorne unpublished data). For walleye pollock, length was converted to weight (525 g) with equations from www.fishbase.org. For herring, weight (115 g) was taken from spring data in the area (R. E. Thorne unpublished data). Energy gain per fish caught (Table 2.2) 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 2.1–2.5 m-long sleeper sharks instrumented with recording devices in Prince William Sound (a subset of data in Hulbert et al. 2006). Data were available for 6 months (January through June) for one shark, 2 months (January and February) for the second, and 1 month (May) for the third. Location-specific risk from sharks $\mu_{shark}(h,d)$ when $d = h$ (Table 2.2) was calculated as $\mu_{shark}(h,d)$ = S(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 = 1.00E-7.

For risk from killer whales, $\mu_{orca}(h,d)$ when $d = h$ (Table 2.2), relative differences between depths were assumed based on limited data suggesting that mammal-eating transient killer whales generally use depths ≤20 m, use 20–40 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 unpublished 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 Prince William Sounds 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 *personal communication.*)

Diurnal vs. 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 diurnal cycle, respectively (means for February through May at Prince William Sound). Specifically, let *day_len* = 4320, the number of 20-s time periods *t* in a day. Daytime parameter values are used if $(day\_len - t \bmod day\_len) \geq \frac{9}{24} day\_len$, otherwise nighttime values are used.

Limited seasonality

One of the model's simplifications is lack of seasonality during the 120 days considered in forward simulations. For this period, February through 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.

Literature cited

Alonzo SH, Switzer PV, Mangel M (2003) An ecosystem-based approach to management: using individual behaviour to predict the indirect effects of Antarctic krill fisheries on penguin foraging. J Appl Ecol 40:692-702

Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117-123

Anholt, BR, Werner, E E (1995) Interactions between food availability and predation mortality mediated by adaptive behavior. Ecology 76: 2230-2234

Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J Exp Mar Biol Ecol 248:53-78

Baird RW (1994) Foraging behaviour and ecology of transient killer whales. PhD thesis Simon Fraser University, Burnaby, BC

Beck CA, Bowen WD, Iverson SJ (2000) Seasonal changes in buoyancy and diving behaviour of adult grey seals. J Exp Biol 203:2323-2330

Biro PA, Post JR, Parkinson (2003) From individuals to populations: Prey fish risk-taking mediates mortality in whole-system experiments. Ecology 84:2419-2431

Bowen WD, Iverson SJ, Boness DJ, Oftedal OT (2001) Foraging effort, food intake, and lactation performance depend on maternal mass in a small phocid seal. Funct Eco 15:325-332

Bowen WD, Ellis SL, Iverson SJ, Boness DJ (2003) Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. J Zool 261: 55-163

Boyd IL (1997) The behavioural and physiological ecology of diving. Trends Ecol Evol 12:213-217

Boyd IL (2000) State-dependent fertility in pinnipeds: contrasting capital and income breeders. Funct Ecol 14:623-630

Clark CW, Mangel M (2000) Dynamic state variable models in ecology. Oxford University Press, New York

Davis RW, Williams TM, Kooyman GL (1985) Swimming metabolism of yearling and adult harbor seals *Phoca vitulina.* Physiol Zool 58:590-596

Dill LM, Heithaus MR, Walters C (2003) Behaviorally-mediated indirect interactions in marine communities and their conservation implications. Ecology 84:1151-1157

Fadely BS (1997) Investigations of harbor seal (*Phoca vitulina*) health status and body condition in the Gulf of Alaska. PhD thesis, University of Alaska at Fairbanks, Fairbanks, Alaska

Frost KJ (1997) Harbor seal Restoration Notebook, Exxon Valdez Oil Spill Trustee Council , http://www.evostc.state.ak.us/Habitat/Downloadables/RN_seals.pdf, 8 pp.

Frost KJ, Lowry LF, Ver Hoef JM (1999) Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Valdez Oil Spill. Mar Mamm Sci 15:494-506

Frost KJ, Simpkins MA, Lowry LF (2001) Diving behavior of subadult and adult harbor seals in Prince William Sound, Alaska. Mar Mamm Sci 17:813-834

Hastings KK, Frost KJ, Simpkins MA, Pendleton GW, Swain UG, Small RJ (2004) Regional differences in diving behaviour of harbor seals in the Gulf of Alaska. Can J Zool 82:1755-1773

Heithaus MR, Frid A (2003) Optimal diving under the risk of predation . J Theor Biol 223:79-92

Houston AI, McNamara JM, Heron JE, Barta Z (2003) The effect of foraging parameters on the probability that a dive is successful. Proc R Soc Lond B Biol Sci 2451-2455

Hulbert L., Sigler M. & Lunsford CR (2006) Depth and movement behaviour of the Pacific sleeper shark in the northeast Pacific Ocean. *Journal of Fish Biology* (in press)

Iverson SJ, Frost KJ, Lowry LF (1997) Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Mar Ecol Prog Ser 151:255-271

Kramer DL (1988) The behavioral ecology of air breathing by aquatic animals. Can J Zool 66:89-94

Krebs CJ, Boutin S, Boonstra R, Sinclair ARE, Smith JNM, Dale M.R.T., Martin K, Turkington R (1995) Impact of food and predation on the snowshoe hare cycle. Science 269:1112-1115

Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation. Can J Zool 68:619-640

Lowry LF, Frost KJ, Ver Hoef JM, DeLong RA (2001) Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. Mar Mamm Sci 17:835-861

Lucas Z, Stobo WT (2000) Shark-inflicted mortality on a population of harbour seals(*Phoca vitulina*) at Sable Island, Nova Scotia. J Zool 252:405-414

Luttbeg B, Rowe L, Mangel M (2003) Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. Ecology 84:1140-1150

McNamara JM, Houston AI (1987) Starvation and predation as factors limiting population size. Ecology 68:1515-1519

Mori Y (1998) The optimal patch use in divers: optimal time budget and the number of dive cycles during bout. J Theor Biol 190:187-199

Mori Y, Boyd IL (2004) The behavioral basis for nonlinear functional responses and optimal foraging in Antarctic fur seals. Ecology 85:398-410

National Research Council (2003) Decline of the Steller sea lion in Alaskan waters. National Academy Press, Washington, D.C.

Okey TA, Wright B (2004) Toward ecosystem-based extraction policies for Prince William Sound, Alaska: Integrating conflicting objectives and rebuilding pinnipeds. Bulletin of Marine Science 74:727-747

Pauly D, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, Zeller D (2002) Towards sustainability in world fisheries. Nature 418:689-695

Saulitis E, Matkin C, Heise K, Barrett-Lennard L, Ellis GM (2000) Foraging strategies of sympatric killer whale (Orcinus orca) populations in Prince William Sound, Alaska. Mar Mamm Sci 16:94-109

Scheel D, Matkin C, Saulitis E (2001) Distribution of killer whale pods in Prince William Sound, Alaska over a thirteen-year period, 1984-1996. Mar Mamm Sci 17:555-569

Sigler M.F., Hulbert L.B., Lunsford C.R., Thompson N., Burek K., Hirons A. & Corry-Crowe G.M. (2006) Diet of Pacific sleeper shark, a potential Steller sea lion predator, in the northeast Pacific Ocean. Journal of Fish Biology. In press.

Simpkins MA, Kelly BP, Wartzok D (2001) Three-dimensional analysis of search behaviour by ringed seals. Anim Behav 62:67-72

Sinclair ARE, Arcese P (1995) Population consequences of predation-sensitive foraging: the Serengeti wildebeest. Ecology 76:882-891

Springer AM, Estes JA, van Vliet GB, Williams TM, Doak DF, Danner EM, Forney KA, Pfister B (2003) Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? PNAS 100:12223-12228

Thomas GL, Thorne RE (2003) Acoustical-optical assessment of Pacific herring and their predator assemblage in Prince William Sound, Alaska. Aquat Living Resour 6:247-253

Thompson D, Fedak MA (2001) How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. Anim Behav 61:287-296

Trumble SJ, Castellini MA (2002a) Digestive efficiency of pollock and herring in harbor seals: Addressing the "is it food?" hypothesis. FASEB Journal 16:A47-A47

Trumble SJ, Castellini MA (2002b) Blood chemistry, hematology, and morphology of wild harbor seal pups in Alaska. J Wildl Manage 66:1197-1207

Trumble SJ, Barboza PS, Castellini MA (2003) Digestive constraints on an aquatic carnivore: effects of feeding frequency and prey consumption on harbor seals. J Comp Physiol B 173:501-509

Ver Hoef JM, Frost KJ (2003) A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. Environ Ecol Stat 10:201-209

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083-1100

Williams TM, Davies RW, Fuiman LA, Francis J, Le Boeuf BJ, Horning M, Calambokidis J, Croll DA (2000) Sink or swim: strategies for cost-efficient diving by marine mammals. Science 288:133-136

Wilson RP (2003) Penguins predict their performance. Mar Ecol Prog Ser 249:305-310

Ydenberg RC, Clark CW (1989) Aerobiosis and anaerobiosis during diving by Western Grebes: an optimal foraging approach. J Theor Biol 139:437-439

Table 2.1: Activity-specific energy and oxygen costs per 20 s time period. See Appendix 2.1 for notation regarding location and decisions.

Description of activity	Location $H(t) = h$	Decision $D(x,y,h,t) = d$	Energetic cost (kJ) $a_{h,d}$	Oxygen cost (ml) $u_{h,d}$
Remain at refuge or surface	0, 25, 150	$d = h$	1.94	--
Travel between habitats	0, 25, 150	$d \neq h$ and $d \neq 1, 2, 5$	3.25	--
Travel between surface and depth	25, 150, 1, 2, 5	$d \neq h$ and $d>0$	2.11	105.11
Resource search at depth	1, 2, 5	$d = h$	2.44	121.27

Notes: Energetic costs were calculated from oxygen consumption during surface travel at 1 m s^{-1} and during resting at the surface by a 63 kg harbor seal (Davis et al. 1985) using standard conversion factors. However, data were unavailable for travel between and resource search within a depth stratum, and these activities were assumed to be 65 and 75% as costly as surface swimming (see Williams et al. 2000), respectively. Similarly, energetic cost of remaining at the refuge was assumed to equal that of surface resting.

Table 2.2: Baseline parameter values (10^{-6}) for probabilities of encountering and capturing a resource (λ_h) or of being killed by predators per 20 s time period when decision $D(x,y,h,t) = h$.

Locations and decisions are defined in Appendix 2.1 and Fig. 2.1.

Location *H(t)*	λ_h for Pacific herring (gross gain = 604.4 kJ fish^{-1})		λ_h for walleye pollock (gross gain = 1531 kJ fish^{-1})		Sleeper shark predation probability $\mu_{shark}(h,d)$		Killer whale predation probability $\mu_{orca}(h,d)$	
	Day	*Night*	*Day*	*Night*	*Day*	*Night*	*Day*	*Night*
–								
0	0	0	0	0	0	0	0	0
25	0	0	0	0	0.0182	0.169	10	6.6
2	7.48	3330			0.127	0.271	1.3	3.3
150	0	0	0	0	0.0182	0.169	5	0.858
1	365	71.4	0	0	0.0357	0.155	2	1.32
5	0	0	1650	17300	1.16	1.14	0	0

Notes: If $D(x,y,h,t) \neq h$, then (a) risk while traveling between surface habitats is 50% of that when remaining at the more dangerous endpoint (e.g. $\mu_{shark}(0,150) = 0.5\mu_{shark}(150,150)$), and (b) risk while traveling between the surface and a depth stratum is 25% of that while searching for resources at that depth (e.g. $\mu_{shark}(5,150) = 0.25\mu_{shark}(5,5) = \mu_{shark}(150,5)$).

Figure 2.1: Spatial structure of the model.

Locations are represented by boxes that contain descriptive names and mathematical designation (see Appendix 2.1) in which values of $H(t)$ 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). Arrows depict allowable decisions at each location, and numbers over arrow indicate travel distances inherent to decisions. See 'Methods' for details.

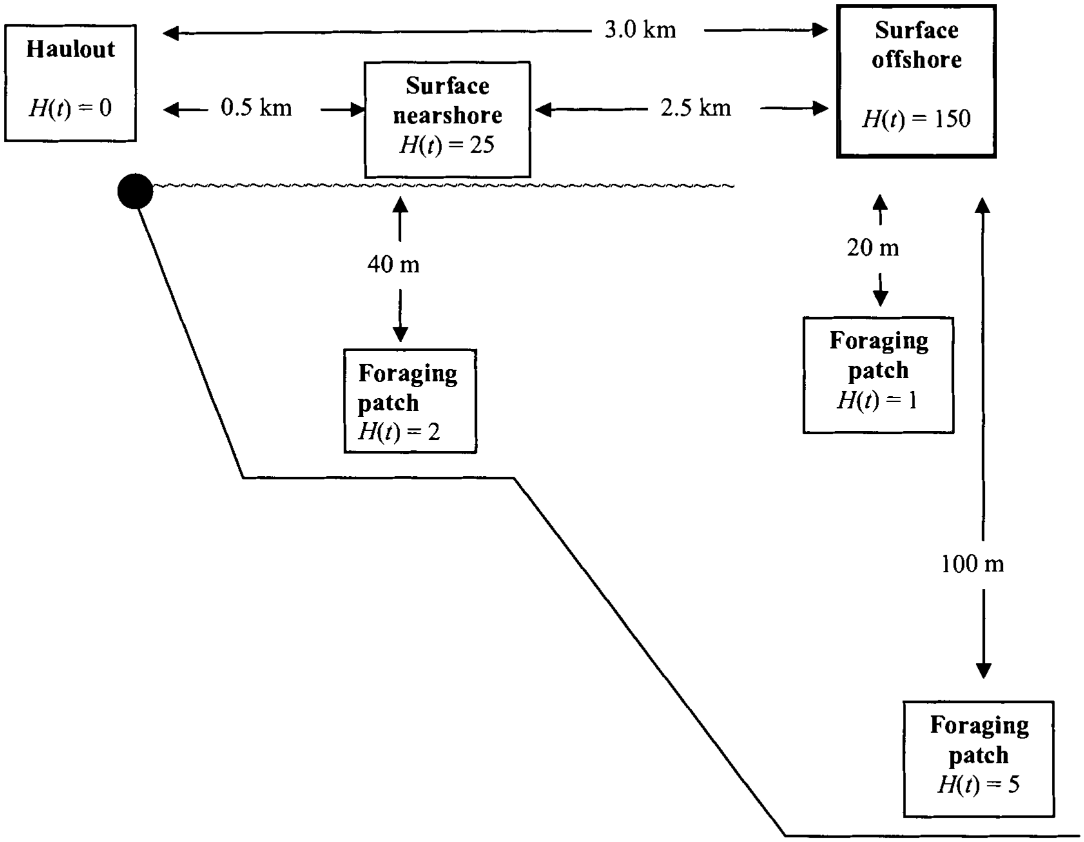


Figure 2.2: Effect of resource level and initial energy state on behavioral responses by individual seals during the 120 d period simulated by forward iterations when killer whales and sharks are dangerous.

Data are mean (±SD) for individuals that avoided predation and starvation, surviving to the terminal horizon (N = 1000 replicates per treatment, but only simulations in which seals survived to the terminal horizon are shown). Low and high initial energy state treatments correspond to 50 and 90% of maximum energy state at the start of the simulation. High, medium, and low resource levels were indexed, respectively, as 200, 100, and 50% of baseline values for the location-specific probabilities of encountering and capturing a fish (see Table 2.2, Appendix 2.2).

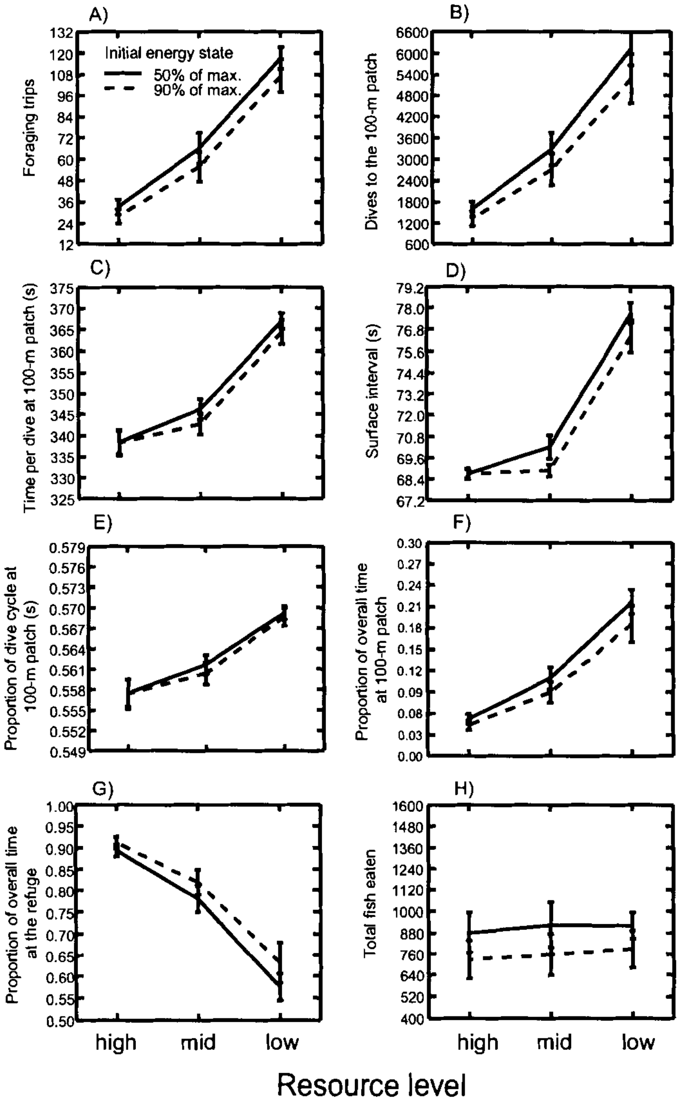


Figure 2.3: (A) Proportion of the population killed by predators and (B) energy state of survivors. in relation to resource level and initial energy state when killer whales and sharks are dangerous.

In addition to mortalities shown in panel A, 15 individuals of low initial energy state starved when at low resource level. Further details as in Fig. 2.2 legend.

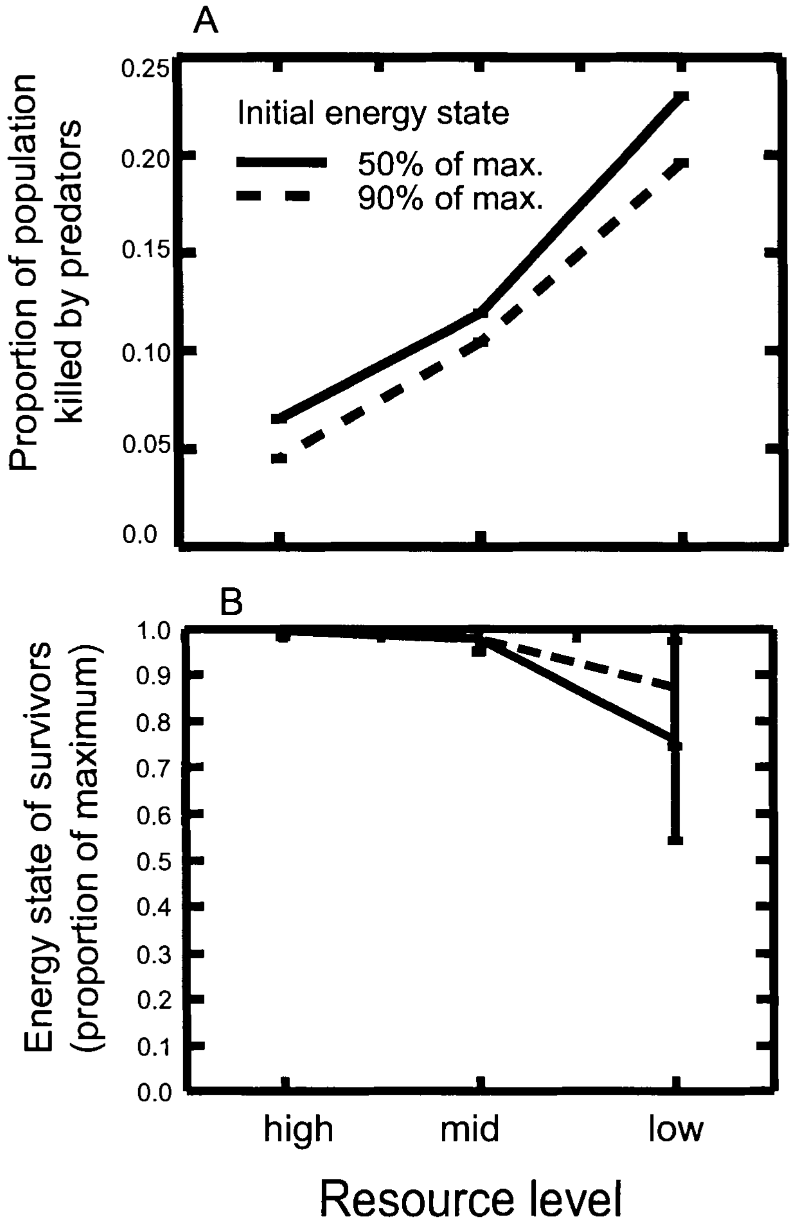


Figure 2.4: Relative strength of TMII and DMII in relation to resource level when killer whales and sharks are dangerous

Note that TMIIs were slightly negative at mid to low resource levels. This occurred because in the predator-free reference case (see Appendix 2.1) seals rested at the surface of the foraging area and did not use the refuge between foraging bouts. Thus, overall energy consumption and prey capture requirements were lower than in simulations with predation risk, which required that seals travel to the refuge for safety between foraging bouts.

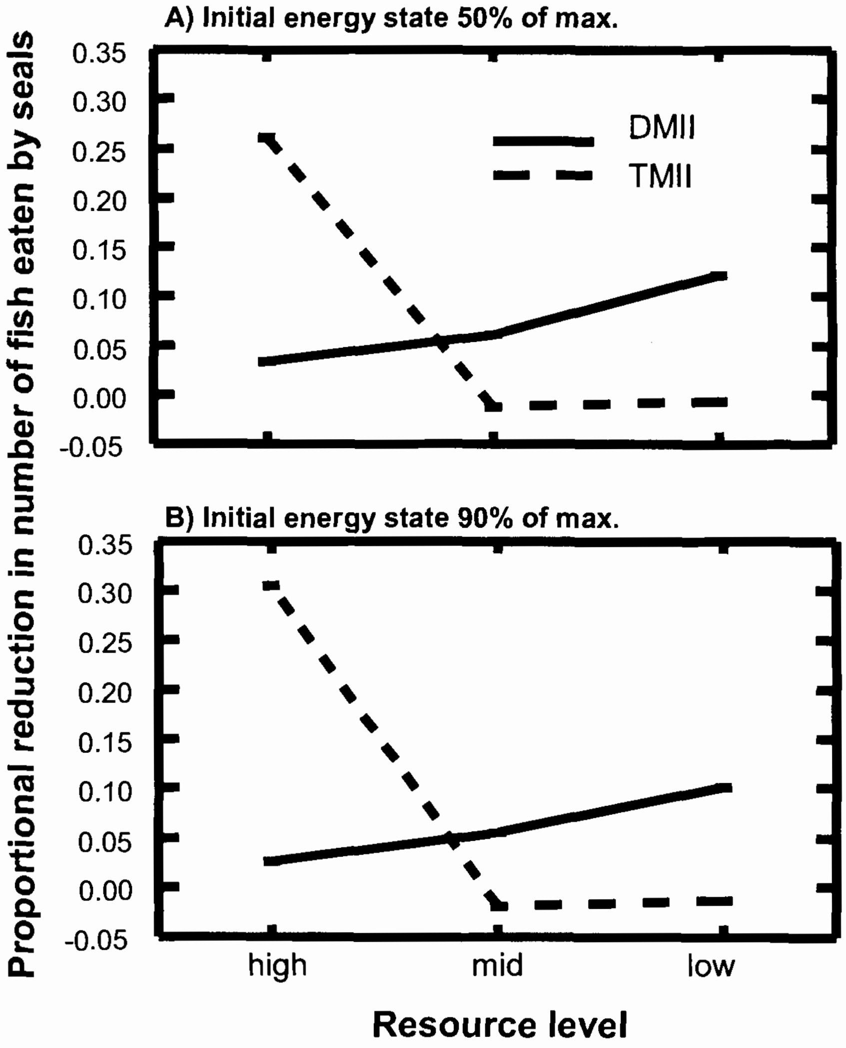
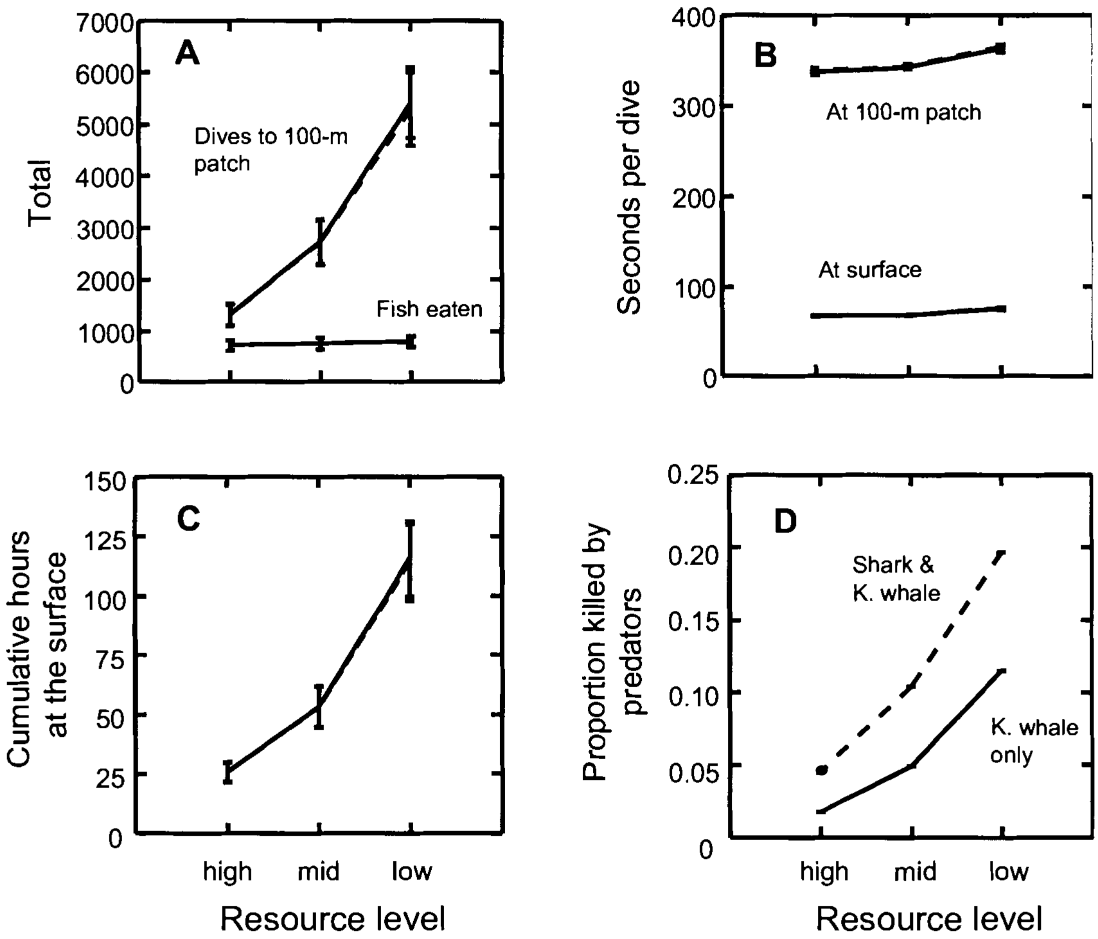


Figure 2.5: Sample output comparing responses to resource declines between simulations in which both predator types are assumed to be dangerous (dashed line) and simulations in which only killer whales are assumed to prey on seals (solid line).

Results are shown only for simulations in which initial energy state was high (results were similar when initial energy state was low). Because behavior did not respond to the removal of shark risk, lines overlap for both predator scenarios in panels A–C. Panel D illustrates increases in predation rates during resource declines, with differences between predator treatments reflecting predator density effects. Further details as in Fig. 2.2 legend.



Chapter 3: A behavioural approach for inferring relative danger from killer whales and deep-water sharks to pinnipeds

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Summary

1. Evidence of killer whale predation on pinnipeds is readily observable from surface platforms while interactions between pinnipeds and deep-water predators, such as Pacific sleeper shark, are not. This observational bias could limit understanding of how each predator type influences pinniped fitness and potentially of the causes of ongoing pinniped declines, including that of harbour seals in Prince William Sound (PWS), Alaska.
2. Relative danger was defined as the aggregate contribution to seal mortality risk of a predator's abundance, hunting efficiency, and probability of attack given an encounter. We used individual variation in seal foraging tactics to infer the relative danger from sleeper sharks and killer whales that is theoretically most plausible in PWS. We predicted net energy gain and predation risk per foraging dive, parameterising the model with field data on seal behaviour and the spatial distributions of predators and resources. Assumptions about relative danger and the influence of rare bonanzas—huge but ephemeral herring schools—on expected foraging success were used as treatments in a factorial computer experiment. According to first principles, individuals that risk more should gain more. We sought the treatment combination best supporting this tenet by plotting the individual seals' predicted cumulative energy gain against cumulative predation risk, whereby improved statistical fit for a positive and monotonic relationship implied greater support.
3. Individual seals differed in their observed use of deep strata (>70 m), where sleeper sharks spent most of their time. Plots of predicted cumulative energy gain against cumulative predation risk fit best when assuming that relative danger from sleeper sharks is much greater

than that from killer whales and that rare bonanzas have a weak influence on expected foraging success.

4. Some seals used shallow strata almost exclusively. Shallow foraging options, however, may have been more limited during the preceding 15 years. During that period human impacts had depressed the abundance of Pacific herring, a near-surface resource, possibly increasing shark predation rates indirectly.
5. *Synthesis and applications*. Our method infers the relative danger from different predator types that is theoretically most plausible according to intermediate consumer behaviour. Its general framework might apply to many large-scale marine systems where the ecological influence of deep-water predators is impractical to measure directly.

Introduction

Current pinniped declines in the Gulf of Alaska are a poorly understood conservation problem (Ver Hoef & Frost 2003; National Research Council 2003). Predation appears to be an important contributor to the declines (e.g. Springer et al. 2003), but its influence relative to that of bottom-up forces remains unclear (National Research Council 2003). Further, recent theory highlights behavioural mechanisms that may generate synergistic, rather than independent, effects of resources and predators on pinniped mortality rates (Frid et al. 2006).

Clearly, underlying causes of pinniped declines will remain elusive unless the relative risk of mortality from different predator types is better understood. Observational biases exacerbate this problem. Evidence of predation by killer whales (*Orcinus orca* Linnaeus 1758) is readily observable from surface platforms (e.g. Saulitis et al. 2000). In contrast, interactions between pinnipeds and another potential predator—the Pacific sleeper shark (*Somniosus pacificus* Bigelow & Schroeder 1944)—likely occur at the deeper strata preferred by the sharks (Hulbert et al. 2006), where human observation is impractical. Thus, researchers have assumed that killer whales are *the* main predator and that risk from sharks has a minor influence, if any, on the ecology of North Pacific pinnipeds (Loughlin & York 2000; Springer et al. 2003; Williams et al. 2004). Is this perception justified or an artifact of observational biases?

Pinniped research in other systems faces similar uncertainties about the ecological influence of subsurface predators (e.g. Lucas & Stobo 2000). Can we, in cases like this, use the known to get a better understanding of the unknown? More explicitly, can we use the observed behaviour of pinnipeds or other marine intermediate consumers to infer the relative risk of mortality from different top predators?

These questions might be relevant to the study of harbour seals (*Phoca vitulina richardsi* Gray 1864) in Prince William Sound (PWS), Alaska. The population declined 63% between 1984 and 1997 (Frost et al. 1999) and remains depressed (Ver Hoef & Frost 2003). Resources have fluctuated widely during the decline period due to combined oceanographic and human influences (Anderson & Piatt 1999; Thomas & Thorne 2003) yet data collected since the 1990s shows that seals have good fat reserves (Fadely 1997; Trumble & Castellini 2002; K. J. Frost unpublished data) and pregnancy rates of adults (≥6 years old) appear high (all 11 adults sampled between 2000 and 2002 were pregnant: A. Hoover-Miller unpublished data). Thus, resource scarcity alone cannot explain the current decline of harbour seals in PWS (-3.1%/yr 1990-2004: Alaska Department of Fish and Game unpublished data). Killer whales (*Orcinus orca* Linnaeus 1758) are a well-recognised predator of seals (Saulitis et al. 2000), but declined from 22 to 8 individuals in PWS between 1989 and 2004 (C. Matkin unpublished data). Consistent with the observational biases discussed earlier, direct evidence for sleeper shark predation on seals is much weaker (Sigler et al. 2006). Time-at-depth data, however, indicate that sleeper sharks prefer strata deeper than 100 m while using the upper water column to a lesser extent (Hulbert et al. 2006), and that harbour seals overlap spatially with them (see Frost et al. 2001). The biomass of Pacific herring (*Clupea pallasi* Valenciennes 1847), a near-surface resource important to seals (Iverson et al. 1997), dropped 95 % between 1989 and 2001 and its apparent recovery did not begin until 2003 (Thomas & Thorne 2003; R. E. Thorne unpublished data). Concurrent declines of herring and killer whales might have increased the influence of sleeper sharks on seal behaviour and fitness (see Frid et al. 2006). While this hypothesis might be near-impossible to test directly, the relative danger from sharks and killer whales can be examined from the perspective of behavioural optimisation.

Consider the framework of risk-sensitive and state-dependent foraging models that is available to infer predation risk. Myriad experimental, theoretical, and field studies on the behavioural ecology of intermediate consumers support the hypothesis that resource acquisition demands exposure to predators, and conversely risk avoidance entails a functional loss of resources (reviews in Lima & Dill 1990; Lima 1998; Brown & Kotler 2004). Energy state, age, body size and other factors affecting residual reproductive value determine the optimal trade-off between safety and resource gain that an individual should choose (Clark 1994; Lima 1998; Clark & Mangel 2000). Further, 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. Gilliam & Fraser 1987; Abrahams & Dill

1989). This 'hazardous duty pay' paradigm (*sensu* Brown & Kotler 2004) has been widely tested in the field and laboratory (reviews in Lima & Dill 1990; Lima 1998; Brown & Kotler 2004).

Accordingly, we developed a model for inferring the relative danger from sharks and killer whales faced by seals that is theoretically most plausible from the perspective of intermediate consumer behaviour. 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. Abrams 1993; Lima 2002). In our model, (a) and (e) are empirical inputs while (b), (c) and (d) are unknown. Given this context, we defined 'relative danger' as the aggregate contribution to seal mortality risk of a predator's abundance, hunting efficiency and probability of attack given an encounter.

We used the model to predict net energy gain and predation risk per foraging dive for each individual seal. It was parameterised with field data on semi-concurrent empirical measures of seal behaviour and resource distributions, and with the available data on use of the water column by sharks and killer whales. Assumptions about the relative danger from sharks and killer whales were used as treatments in a computer experiment. These treatments were combined 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 then sought the treatment combination best supporting the hazardous duty pay paradigm (Brown & Kotler 2004) by plotting the individual seals' predicted cumulative energy gain against their predicted cumulative predation risk, whereby a better statistical fit to a positive and monotonic relationship implied greater support. This novel application of predation risk theory to marine field studies suggested ecological dynamics that have been impractical to measure directly but which are potentially relevant to the seal decline.

Methods

We conducted a theoretical search for the danger from sharks and killer whales faced by seals that would give the best fit to a positive relationship between the individuals' exposure to predation risk and energy gain while foraging. As detailed below, this was done by modeling risk-energy trade-offs under different assumptions on a per dive basis, and then summing the cumulative risks and energetic gains incurred by individuals over the thousands of dives performed.

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 defined patch residence as time spent within 90% of the dive's maximum depth, and travel time as the difference between total dive duration and patch residence time. The distribution of predators and resources is influenced by diel period (night vs. day) and depth (Fig. 3.1, see also Figs. S3.1 and S3.2 in Supplementary Material), and time spent at a stratum affects predation risk and energy gain. There is no density-dependence in the model and thus we do 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 at 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, 1.2 % of depth-specific fish biomass measurements (N=956, see next section) were >10 times greater than the mean, and the largest value was 280 times greater (Fig. S3.1). Nine of these extreme outliers represented herring schools in shallow strata, and only two of the smallest outliers represented pollock aggregations at greater depth. The same sampling regime also found that pollock in the deep were more evenly distributed than herring in the shallows (Fig. S3.1). Limited data suggest that PWS seals do exploit—in the short term—rare herring bonanzas if they happen to come upon them (A. Frid unpublished data). It is unclear, however, to what extent these events influence expected foraging success during winter, when herring aggregations are found predictably only within a few bays (Thomas & Thorne 2001; 2003). Further, while the larger and more aggressive Steller sea lion (*Eumetopias jubatus* Schreber, 1776) aggregates to exploit wintering herring in these bays (Thomas & 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] show few satellite tag locations within these bays.) Given the empirical gaps, the function was designed to explore two theoretical scenarios. In the first, herring bonanzas are targeted and predictably found by seals, and therefore 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 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 [Fig S3.1] 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 [see Table 3.2]). 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 on the expected number of fish caught during $t = 1$ 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 kJ kg$^{-0.75}$ d^{-1} for captive seals fed a mixed diet of pollock and herring at high frequency [Trumble & Castellini 2005]), we contrasted strong (ε=100, $a_{100} = 0.13$) vs. weak influence (ε=10000, $a_{10000} = 0.008$) scenarios in computer experiments (Table 3.3; Fig. 3.1; see Fig S3.2). We point out that $P_{l,s,d}$ always was <1.

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

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

where parameter k represents the proportion of resources available at t relative to t-1. We assumed $k = 0.99$ (see sensitivity analyses in Supplementary Material). Based on the energy content (kJ) of exploitable fish at a given depth (Table 3.2), $\psi_{l,s}$, 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 r_m=0.00154 kJ.kg^{-1}.s^{-1} if $m \geq 48$ kg or r_m=0.00170 kJ.kg^{-1}.s^{-1} if $m \leq 40$ kg. These values were converted from oxygen consumption rates when resting at the surface by a 63 kg and a 33 kg harbour seal, respectively (Williams 1999). Thus, 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, calculated as vertical distance traveled divided by the total time spent ascending and descending, represented vertical travel speed (an underestimate because travel angles are not necessarily vertical). Surface swimming is energetically more expensive than vertical travel (see Williams 1999; Williams et al. 2000), but data on vertical swimming costs are lacking for harbour seals. Thus, we assumed that the metabolic cost of vertical travel at rate ρ for a seal of mass m, $v_{p,m}$, was 65% of the cost of surface swimming at the same rate. To obtain $v_{p,m}$, we first estimated oxygen consumption rates (V_{O2} in mL O_2 min^{-1} kg^{-1}) as $V_{O2} = 4.6 + 3.1\rho^{1.42}$ if $m \geq 48$ kg, or $V_{O2} = 5.1 + 6.25\rho^{1.42}$ if $m \leq 40$ kg. These equations were derived for a 63 kg 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 kJ kg^{-1} s^{-1}. We assumed also that seals glide passively through a depth-dependent proportion of descent and ascent (Williams et al. 2000), and that the metabolic cost of this activity was equal to r_m. Total travel cost (kJ) per dive, τ_m, is

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

where ϕ is total travel time, and γ is seconds spent in passive gliding rather than active stroking (Williams et al. 2000). While ρ and ϕ were measured empirically (see Fig. S3.3 in Supplementary Material), γ was estimated from Williams et al.'s (2000) Fig. 2. (Negative estimates for shallow dives were treated as zero values.)

Energetic cost at the foraging patch was estimated from Davis et al.'s (1985) equations described above for surface swimming costs, and by assuming ρ = 1 m.s^{-1}. Here we multiplied V_{O2} estimates by 0.75 to account for lesser energy costs below the surface before converting to kJ.kg^{-1}.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:

$$E = G_l - R_m - \tau_m - B_m \qquad (5)$$

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

$$\mu_{\omega,s,d} = h_\omega(1 - (1 - \mu_{shark}\mathrm{T}_{sharks,d} - \mu_{orca}\mathrm{T}_{orcas,d} + \mu_{shark}\mathrm{T}_{sharks,d}\mu_{orca}\mathrm{T}_{orcas,d})^{\zeta}) \qquad (6)$$

where μ_{shark} and μ_{orca} are instantaneous predation risk constants (Table 3.3) representing relative danger to seals from the given predator type. Variable $T_{sharks,d}$ is the empirical estimate for the mean proportion of time sharks spent at s during d, $T_{orcas,d}$ is an assumed value for the proportion of subsurface time killer whales spent at s during d (Fig. 3.1), and ζ is the duration (s) of ω (Fig. S3.3). Variable h_ω represents the assumption that vertical travel is safer than remaining within a stratum, such that h_ω=1 if ω denotes foraging or surface interval, while h_ω=0.25 if ω denotes vertical travel. If dives were deeper than maximum killer whale depths (see Fig. 3.1), we substituted $\frac{70}{s}T_{orca70,night}$ or $\frac{80}{s}T_{orca80,day}$ into Equation 6. Background risk from killer whales at the surface, $T_{orca0,d}$, equalled the value of μ_{orca}. Total predation risk per dive, μ_{dive}, is

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

Parameterisation

Time allocation by harbour seals

Data on time allocation by seals were used as empirical inputs for the model's behavioural parameters. During late February of 2004 in southwestern Prince William Sound, Alaska, 28 harbour seals were caught by entanglement in a seine net set near their haulout and transferred to a large vessel where standard morphometrics were recorded. Capture and handling procedures followed those described in Lowry et al. (2001). A subset of 13 harbour seals (Table 3.1) were instrumented with time-at-depth recorders (TDRs: model Mk9 Wildlife Computers, Redmond, WA) programmed to record depth every 2 seconds with 0.5 m resolution. TDRs were embedded in a flotation package of syntactic foam glued to the seal's back, which released when seals moulted in early summer. Nine TDRs were subsequently recovered by tracking the signal of a VHF transmitter also embedded in the syntactic foam. TDRs archived data from late winter to early summer, but analyses presented here are for the late winter period for which we collected detailed data on resource distribution (late February and March). Seals were also instrumented with headmount VHF transmitters for locating them at the surface.

Time-at-depth data were filtered for analyses as follows. Minimum diving depth was 6 m because shallower dives often have disproportionately long surface intervals and short submergences (A. Frid unpublished data), possibly representing social behaviour near the haulout rather than foraging. Also, substantial aggregations of pelagic fish almost always are deeper than 5 m during winter (R. E. Thorne unpublished data) and our methods for quantifying fish biomass were optimized for >5-m depths. We excluded data for 24 hours after releasing seals, when handling stress might have influenced behaviour. The maximum surface interval considered to be part of a dive cycle was 5 min; longer surfacings likely represented foraging interruptions.

Resource distribution

To estimate $\delta_{l,s,d}$, we collected data on depth-specific fish biomass (Fig S3.1) during late February and early March of 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 echosounder at 70 kHz (see Thomas & 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 excluded, yielding effective sampling period durations of 2–22 min (mean ± SD = 6.9 ± 3.5 min, N = 86 sampling periods). Depending on weather and navigation hazards, we collected multiple samples on the foraging tracks of individual seals during 1.5 to 10-hour focal follows (gaps between samples were <15 min). Effort was spread over 9 individuals over 2 weeks. Seals remained in <120-m deep habitats during focal follows. TDR data, however, later showed use of much deeper strata and data for habitats with maximum depths of 400 m were obtained from walleye pollock (*Theragra chalcogramma* Pallas 1814) surveys conducted in the same area during March 2003 (R. E. Thorne unpublished data). 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 ± SD duration of 24.8 ± 5.6 min). Data from focal follows and pollock surveys were pooled. Mean fish biomass values (kg/m^3) at each sampling period, stratified by 10-m depth bins, were the units of analyses (N = 956, Fig. S3.1).

Based on surveys conducted during March and April of 2000-2004 by the Prince William Sound Science Center (Thomas & Thorne 2001, 2003; R. E. Thorne Unpublished data) and the Alaska Department of Fish & Game (W. Bechtol unpublished data; S. Moffitt unpublished data), 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 dominate the diet of seals in southern PWS (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 & Game test fishery surveys for eastern PWS: 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 & Game 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 (see Table 3.1). Under this assumptions, 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.). Table 3.2 describes average size and energy content of fish under these assumptions (also see sensitivity analyses in Supplementary Material).

Empirical data on time-at-depth by sleeper sharks

To parameterize $T_{sharks,\,d}$ we used time-at-depth data for sleeper sharks provided by the Auke Bay Laboratory of the National Marine Fisheries Service (a subset of data in Hulbert et al. 2006). Depths recorded every min were available for three sharks instrumented in PWS or the adjacent Gulf of Alaska between 2001 and 2002. Archived depth data encompassed multiple months, but for each shark we used a 4-week subset approximating seasonal conditions for the winter period for which we analyzed seal behaviour. For sharks identified as 2, 11, and 21 (Table 3.1), these periods were March 2002, 15 Jan–15 Feb 2002, and 3 November–3 December 2002, respectively. 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 >200 m were pooled into a maximum depth bin (Hulbert et al. 2006) which we excluded from analyses. From these data we estimated proportions of time spent at 10-m depth bins (Fig 3.1).

Assumed use of depth by killer whales

Time-at-depth data for transient killer whales are almost non-existent due to the difficulty of attaching recording devices to free-ranging whales. We parameterized $T_{orcas,\,d}$ (Fig. 3.1) from a 19-h record of time-at-depth by one individual in Southeast Alaska (R. W. Baird unpublished data). These data also show night-time travel speed to be only two thirds of day-time travel speed, perhaps reflecting reduced activity at night (R. W. Baird pers. comm.); thus, in the model $T_{orcas,\,night} = 0.66\,T_{orcas,\,day}$ (see also sensitivity analyses in Supplementary Material).

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. We clarify that the term 'experiment' does not imply stochasticity, as in Monte Carlo simulations (e.g. Clark & 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 8 treatment combinations: 2 levels of ε, and 4 levels of μ_{shark} to μ_{orca} ratios (Table 3.3). 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 scrutinised eight parameters whose values had little or no empirical support and which potentially could produce suspect conclusions. We changed these values one at the time and re-ran computer experiments as described in Supplementary Material, testing whether the relative fit of plots derived from each treatment combination (Table 3.3) was robust to re-parameterisation.

Results

We first outline the main spatial trade-offs faced by seals under model assumptions. If rare bonanzas are assumed to weakly influence long term foraging success ($\varepsilon = 10000$), 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 <200 m are greatest during the night. If rare bonanzas are assumed to strongly influence long term 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. 3.1, see Fig S3.2). The model also accounts for other trade-offs not captured by this description, e.g. killer whale risk at the surface and depth-specific energy content of resources.

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. 3.2). Possibly influenced by an increase in expected fish captures nearer to the surface at night (Figs. 3.1, S3.2), dives were shallower and individual difference 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. 3.2). As predicted by theory (e.g. Houston & Carbone 1992), the duration of surface intervals, travel durations and patch residence time generally increased with depth (Fig 3.3; but notice exceptions and the relative invariance of nocturnal surface intervals in Figs. S3.3). In addition, travel rate (average descent and ascent rates combined) was greater for deeper dives (Figs. 3.3; S3.3). There were no apparent effects of body mass or age-class on the individuals' depth preferences (Fig. 3.2), which is surprising given that mass limits maximum dive capacity (e.g. Schreer & Kovacs 1997) and has been found to influence harbour seal diving characteristics in other systems (Eguchi & Harvey 2005). Our results and similar findings by others (e.g. Costa & Gales 2000) suggest that interactions between ecological conditions and the individual's state may, in some contexts, influence average dive characteristics more strongly than body mass alone.

We now summarize the outcome of the computer experiments. Given that individuals differed in their diving behaviour, so did their predicted predation risk and energy gain, both per dive (Fig. 3.4) and cumulatively (Fig. 3.5). The regression model for plots of the 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 μ_{shark} to μ_{orca} and $\varepsilon = 10000$ (Experiment 8 in Table 3.3 and Fig. 3.5). 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 μ_{shark} to μ_{orca} (Fig. 3.5). These results were robust to sensitivity analyses (see Supplementary Material).

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 & 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 (>70 m), where sleeper sharks spent most of their time and net energy gain is predicted to be highest under 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 (e.g. Gilliam & Fraser 1987; Abrahams & Dill 1989; Brown & Kotler 2004). Accordingly, plots of the individuals' 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 that of killer whales and the worst fit when sharks were assumed to not be dangerous or only as dangerous as killer whales. While these results are not be taken literally, they do suggest that, theoretically, the system has many more large sharks (i.e. that have reached the size class capable of killing seals) than killer whales and that sharks are the greater threat to seals. During *a posteriori* analyses statistical fit improved slightly with even greater shark abundance ($R^2 = 0.95$ for a μ_{shark} to μ_{orca} ratio of 75:1 and ε=10000, vs. $R^2 = 0.94$ 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.

Our theoretical results also suggest that rare bonanzas have a weak influence on expected foraging success by PWS 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.

The above conclusions were robust to sensitivity analyses of eight parameters. The relative support for the hazardous duty pay paradigm provided by the original treatment combinations remained unchanged through each step of re-parameterisation (see Supplementary Material).

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 cryptic snow leopards (*Uncia uncia* Schreber 1758) from the vigilance of their ungulate prey. Alonzo et al. (2003a: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 and more data are needed to parameterise the spatial distributions of top predators. Such data, however, may require great expense and time to collect in large-scale marine systems. Meanwhile, 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. 2003a:1598).

A limitation of our method is that it can suggest relative danger from multiple predators only if these are largely segregated in the water column. Salmon sharks (*Lamna ditropis* Hubbs & Follet 1947), for instance, are abundant in PWS 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.

The analyses we present here, combined with insight from dynamic state variable (DSV) models (Clark & Mangel 2000), can help build hypotheses about the causes of the seal decline. DSV models predicts optimal risk-taking to be greater for individuals in poorer energetic state because imminent loss of reproductive potential makes caution less affordable (e.g. Clark 1994; reviews in Lima 1998; see also McNamara & Houston 1987). Theoretically, we expect seals that prefer the relative safety of shallow strata to have superior energy stores than seals preferring greater depths. (Unfortunately, our data is limited to nine individuals spread over five age-sex classes [Table 3.1] and cannot test this prediction.) Resource declines in shallow strata, however, may limit safe foraging options and force a greater proportion of seals to exploit deeper, more dangerous strata. It is through these behavioural mechanisms that resource scarcity might have indirectly elevated predation rates on PWS seals during portions of the seal decline. Supporting this view, a DSV model predicts that compensatory foraging effort by PWS seals will mitigate potential loss of energy reserves when resources decline, but only at the cost of higher predation rates (Frid et al. 2006). Consistent with this prediction, PWS seals have good fat stores (Fadely 1997; Trumble & Castellini 2002; K. J. Frost unpublished data) and appear to have high pregnancy rates (A. Hoover-Miller unpublished data). This is notable, given that the seal population decline began in 1984 (Frost et al. 1999), shortly after an oceanographic regime shift diminished the abundance of near-surface fatty fishes (Anderson & Piatt 1999). Further, the PWS population of herring collapsed in 1989 due to the combined effects of the Exxon Valdez oil spill and subsequent overfishing (Thomas & Thorne 2003), and did not show recovery signs until 2003 (R. Thorne unpublished data). Thus, resource scarcity induced by overfishing or other factors may not necessarily starve seals, but instead might increase predation rates (Frid et al. 2006). The model we presented here suggests that, theoretically, sleeper sharks would be the dominant mortality agent for PWS seals if the affected resource were herring or other near-surface fatty fishes.

Our case study develops a general methodology for inferring the relative risk of mortality from different top predators that is theoretically most plausible according to intermediate consumer behaviour. Our general framework might apply to many large-scale marine systems where the ecological influence of deep-water predators is impractical to measure directly. Resulting insights can inform hypotheses on how different predators influence the population trajectories of pinnipeds or other intermediate consumers. In the case of declining populations, such as harbour seals in PWS, these inferences might suggest approaches to the conservation problem (see Frid et al. 2006).

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Literature cited

Abrahams, M.V. & Dill, L. M. (1989) A determination of the energetic equivalence of the risk of predation. *Ecology,* **70**, 999-1007.

Abrams P.A. (1993) Why predation rate should not be proportional to predator density. Ecology 74, 726-733

Alonzo S.H., Switzer P.V. & Mangel M. (2003a) Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology* 84, 1598-1607

Anderson, P.J. & Piatt, J. F. (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series,***189**, 117-123.

Anholt, B.R. & Werner, E. E. (1995) Interactions between food availability and predation mortality mediated by adaptive behavior. *Ecology,* **76**, 2230-2234.

Anthony, J.A., Roby, D. D., & Turco, K. R. (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology*, **248**, 53-78.

Brown, J.S. & Kotler, B. P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecology Letters,* 7, 999-1014.

Clark, C.W. (1994) Antipredator behavior and the asset-protection principle. *Behavioral Ecology,* **5**, 159-170.

Clark, C.W. & Mangel, M. (2000) *Dynamic state variable models in ecology.* Oxford University Press, New York.

Costa, D.P. & Gales, N. J. (2000) Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phococarctos hookeri. The Journal of Experimental Biology,* **203**, 3655-3665.

Dalton, R. (2005) Is this any was to save a species? *Nature,* **436**, 14-16.

Davis, R.W., Williams, T. M., & Kooyman, G. L. (1985) Swimming metabolism of yearling and adult harbor seals *Phoca vitulina.* Physiological Zoology, **58**, 590-596.

Dill, L.M., Heithaus, M. R., & Walters, C. (2003) Behaviorally-mediated indirect interactions in marine communities and their conservation implications. *Ecology,* **84**, 1151-1157.

Eguchi, T. & Harvey, J. T. (2005) Diving behavior of the Pacific harbor seal (*Phoca vitulina richardsi*) in Monterey Bay, California. *Marine Mammal Science,* **21**, 283-295.

Fadely, B.S. (1997) *Investigations of harbor seal* (*Phoca vitulina*) *health status and body condition in the Gulf of Alaska.* PhD thesis, University of Alaska at Fairbanks.

Frid A., Baker G.G. & Dill L.M. (2006) Do resource declines increase predation rates on North Pacific harbor seals? A behavior-based plausibility model. Marine Ecology Progress Series 312, 265-275.

Frost, K.J., Lowry, L. F., & Ver Hoef, J. M. (1999) Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Valdez Oil Spill. *Marine Mammal Science,* **15**, 494-506.

Frost, K.J., Simpkins, M. A., & Lowry, L. F. (2001) Diving behavior of subadult and adult harbor seals in Prince William Sound, Alaska. *Marine Mammal Science,* **17**, 813-834.

Gilliam J.F. & Fraser D.F. (1987) Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68, 1856-1862

Heithaus, M.R. & Frid, A. (2003) Optimal diving under the risk of predation . *Journal of Theoretical Biology,* **223**, 79-92.

Houston, A.I. & Carbone, C. (1992) The optimal allocation of time during the dive cycle. *Behavioral Ecology,* **3**, 255-265.

Hulbert, L.B., Da-Silva A, M., Gallucci, V. F., & Rice, J. S. (2005) Seasonal foraging movements and migratory patterns of female Lamna ditropis tagged in Prince William Sound, Alaska. *Journal of Fish Biology,* **67**, 490-509.

Hulbert L., Sigler M. & Lunsford CR (2006) Depth and movement behaviour of the Pacific sleeper shark in the northeast Pacific Ocean. *Journal of Fish Biology* (in press).

Hugie, D.M. & Dill, L. M. (1994) Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology,* **45**, 151-169.

Iverson, S.J., Frost, K. J., & Lowry, L. F. (1997) Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Marine Ecology Progress Series,* **151**, 255-271.

Lima, S.L. (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior,* **27**, 215-290.

Lima, S.L. & Dill, L. M. (1990) Behavioural decisions made under the risk of predation. *Canadian Journal of Zoology,* **68**, 619-640.

Lima S.L. (2002) Putting predators back into behavioral predator-prey interactions. *Trends in Ecology and Evolution* **17**, 70-75.

Lowry, L.F., Frost, K. J., Ver Hoef, J. M., & DeLong, R. A. (2001) Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. *Marine Mammal Science*, **17**, 835-861.

McNamara, J.M. & Houston, A. I. (1987) Starvation and predation as factors limiting population size. *Ecology,* **68**, 1515-1519.

National Research Council (2003) *Decline of the Steller sea lion in Alaskan waters.* National Academy Press, Washington, D.C., USA

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R., & Zeller, D. (2002) Towards sustainability in world fisheries. *Nature,* **418**, 689-695.

Pitcher, K.W. & Calkins D.G. (1979) Biology of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Final report to OCSEAP, U.S. Department of Interior,BLM. Res. Unit 229. Contract 03-5-002-69. pp. 72pp

Saulitis, E., Matkin, C., Heise, K., Barrett-Lennard, L., & Ellis, G. M. (2000) Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science*, **16**, 94-109.

Schreer, J.F. & Kovacs, K. M. (1997) Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology,* **75**, 339-358.

Shepherd T. & Myers R.A. (2005) Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecology Letters* 8, 1095-1104

Sinclair, A.R.E. & Arcese, P. (1995) Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology*, 76, 882-891.

Sigler M.F., Hulbert L., Lunsford C., Thompson N., Burek K., Hirons A. & Corry-Crowe G. (2006) Diet of Pacific sleeper shark, a potential Steller sea lion predator, in the northeast Pacific Ocean. Journal of Fish Biology. In press.

Springer, A.M., Estes, J. A., van Vliet, G. B., Williams, T. M., Doak, D. F., Danner, E. M., Forney, K. A., & Pfister, B. (2003) Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Science*, **100**, 12223-12228.

Thomas, G.L. & Thorne, R. E. (2001) Night -time predation by Steller sea lions. *Nature,* **411**, 1013.

Thomas, G.L. & Thorne, R. E. (2003) Acoustical-optical assessment of Pacific herring and their predator assemblage in Prince William Sound, Alaska. *Aquatic Living Resources,* **6**, 247-253.

Trumble, S.J. & Castellini, M. A. (2002) Blood chemistry, hematology, and morphology of wild harbor seal pups in Alaska. *Journal of Wildlife Management,* **66**, 1197-1207.

Trumble S.J. & Castellini M.A. (2005) Diet mixing in an aquatic carnivore, the harbour seal. *Canadian Journal of Zoology* 83, 851-859

Ver Hoef J.M. & Frost K.J. (2003) A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. *Environmental and Ecological Statistics* 10, 201-209

Vollenweider J.J. Variability in Steller sea lion (*Eumetopias jubatus*) prey quality in southeastern Alaska. 2004. MS Thesis. University of Alaska, Fairbanks. Fairbanks, Alaska.

Wilkinson, L. (2004) Smoothing. *SYSTAT 11 Statistics* (ed SYSTAT Software Inc.), pp. 391-422. SYSTAT Sotware Inc., CA.

Williams, T.M. (1999) The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society of London B*, **354**, 193-201.

Williams, T.M., Davies, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J., & Croll, D. A. (2000) Sink or swim: strategies for cost-efficient diving by marine mammals. *Science,* **288**, 133-136.

Werner, E.E. & Peacor, S. D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology,* **84,** 1083-1100.

Table 3.1: Characteristics of instrumented harbour seals and sleeper sharks at time of capture. Likely age classes of seal are estimated from length-age plots in Pitcher & Calkins (1979).

Species and identification	*Sex class	*Weight (kg).	┼Length (cm)	Likely age class of seals (years)
seal af3	female	74.5	139	adult (>3)
seal af17	female	48.9	132	adult (≥3)
seal jf12	female	33.7	111	juvenile (1–2)
seal jf24	female	40.3	115	juvenile (1–2)
seal yf22	female	33.0	99	yearling (<1)
seal yf27	female	34.6	105	yearling (<1)
seal am1	male	157	101.0	adult (>3)
seal am8	male	86.4	149	adult (>3)
seal jm9	male	59.4	130	juvenile (1–2)
shark 2	unknown	231.4	250	-
shark 11	unknown	138.9	210	-
shark 21	unknown	120.4	200	-

*Seals were handled aboard a vessel and sexed and weighed directly. Sharks were handled in the water alongside the vessel and could not be sexed; their weights were estimated from the equation $W = 2.18 \times 10^{-5} PCL^{2.93}$ (Sigler et al. 2006), were W is weight and PCL is precaudal length.

┼ Precaudal length for sharks (Hulbert et al. 2006); standard length for seals.

Table 3.2: Assumptions about resources available to seals of length l (see Table 3.1). Fish species compositions for strata ≤55 m, 56-95 m, and >95 m were, respectively, herring only, equal proportions of herring and walleye pollock, and walleye pollock only.

Seal standard length *l* (cm)	Depth (m)	*Exploitable proportion of fish	Mean values for characteristics of exploitable fish		
			Fork tail length (cm)	**Mass (g)	Energy content (kJ)†
All seals	≤55	1.0	21.1	121.57	638.97
≤115	56-95	0.83	28.3	240.02	842.13
≤115	>95	0.66	35.5	358.46	1045.28
≥130	56-95	0.90	28.9	272.78	937.65
≥130	>95	0.80	36.7	423.98	1236.33

*Assumes maximum exploitable lengths of fish were 40 and 45 cm, respectively, for $l \leq 115$ and ≥130 cm.

**When including all fish sizes, mean mass at >95 m and 56-95 m is 711.35 g and 416.46 grams, respectively.

†Estimated energy densities in Anthony et al. (2000) multiplied by an assumed assimilation efficiency of 0.9.

Table 3.3: Experimental treatment combinations.

Experiment ID	Levels of each treatment		
	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	10000	0	5.00×10^{-9}
6	10000	5.00×10^{-9}	5.00×10^{-9}
7	10000	2.5×10^{-7}	5.00×10^{-9}
8	10000	2.5×10^{-7}	5.00×10^{-9}

* $a_{100} = 0.13$ and , $a_{10000} = 0.008$ (see Equation 1).

†Killer whales were assumed to be primarily diurnal and we used 66% of this value for night.

Figure 3.1: Ecological parameters influencing predicted energy gain and predation risk per dive during day (open symbols) and night (filled symbols).

See Fig. S3.2 in supplementary material for $P_{\leq 115,s,d}$.

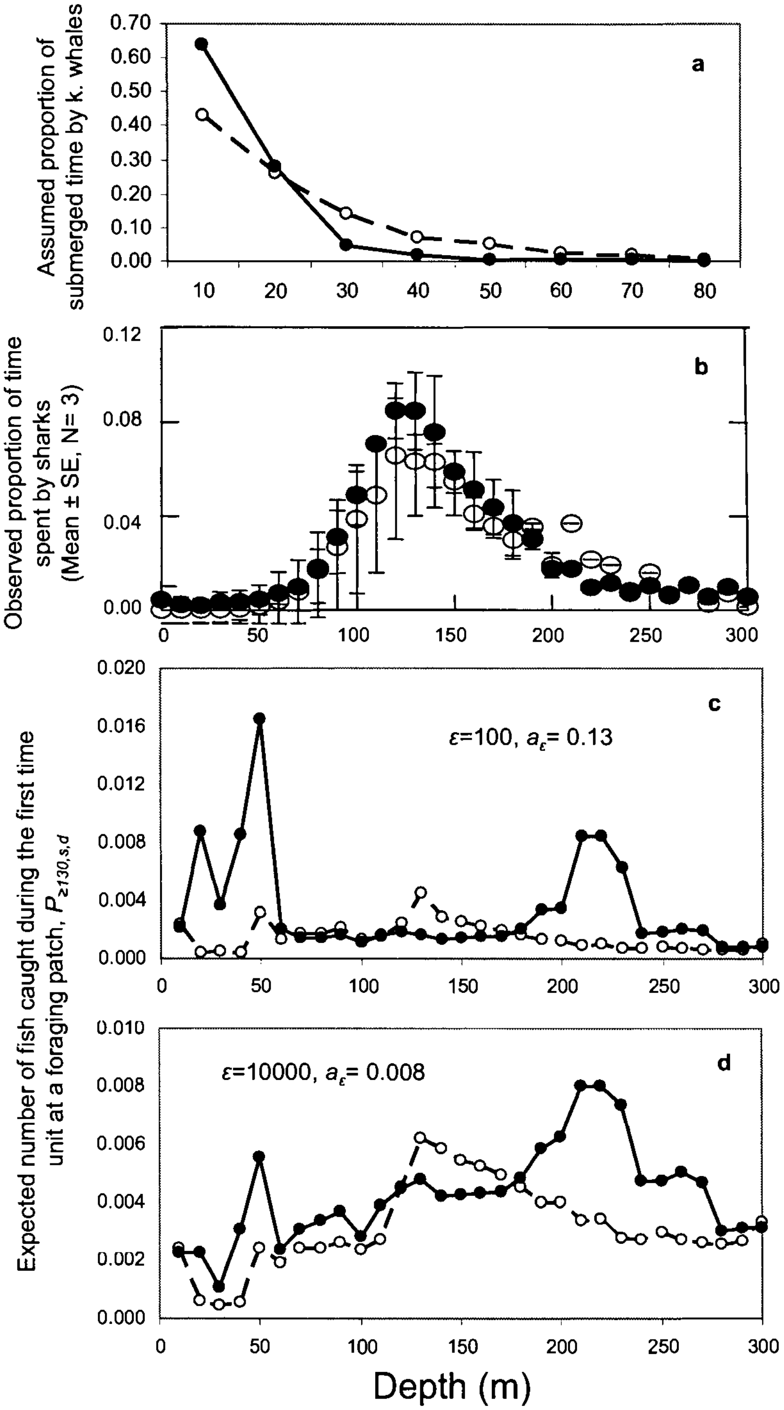


Figure 3.2: Individual variation in depth, diel period, and total number of dives by harbour seals in PWS during late February–31 March 2004.

Letters in the legend indicate likely age class (a = adult ≥3 years, j = juvenile 1–2 years, y = yearling <1 year; see Table 3.1) and gender (f = female, m = male). Frequency polygons are for 10-m depth bins and y-axis scales differ between panels. To enhance visual clarity, the few dives made to depth >240 m are not shown. Note that Y-axis scales differ between panels.

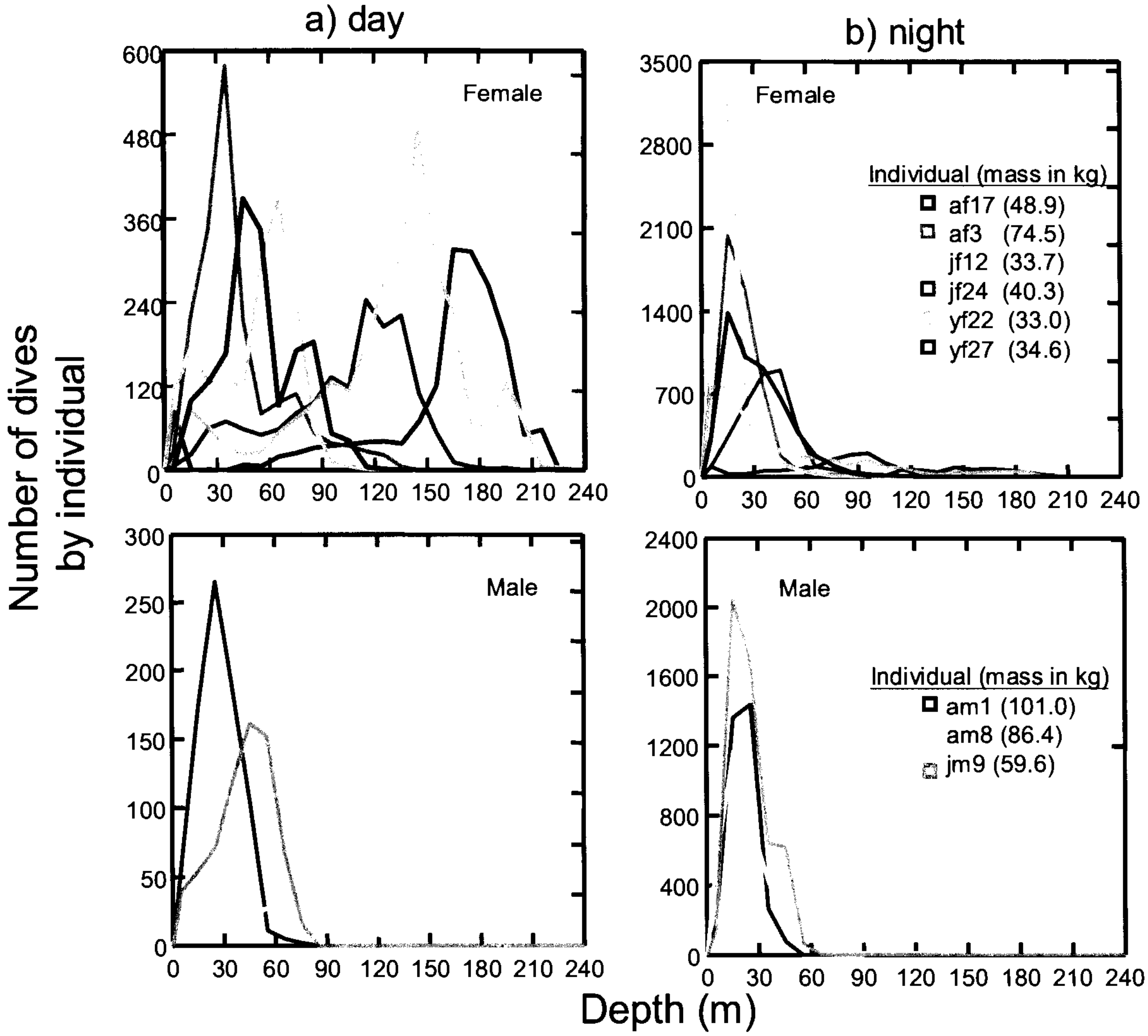


Figure 3.3: Example of dive cycle characteristics by depth and diel period (day = red, night = blue) used as empirical inputs for estimating risk-energy trade-offs.

Data are for adult female af17. Histogram above upper left panel displays the relative frequency of diving depths by diel period. Regression lines are not stratified by diel period and are drawn with a locally weighted smoother at tension = 0.5 (Wilkinson 2004), except for travel rate which is a linear smoother. Y-axes are $\log_{10}$-scaled except for travel rate. See Figures S3.2 in Supplementary Material for dive characteristics of all seals.

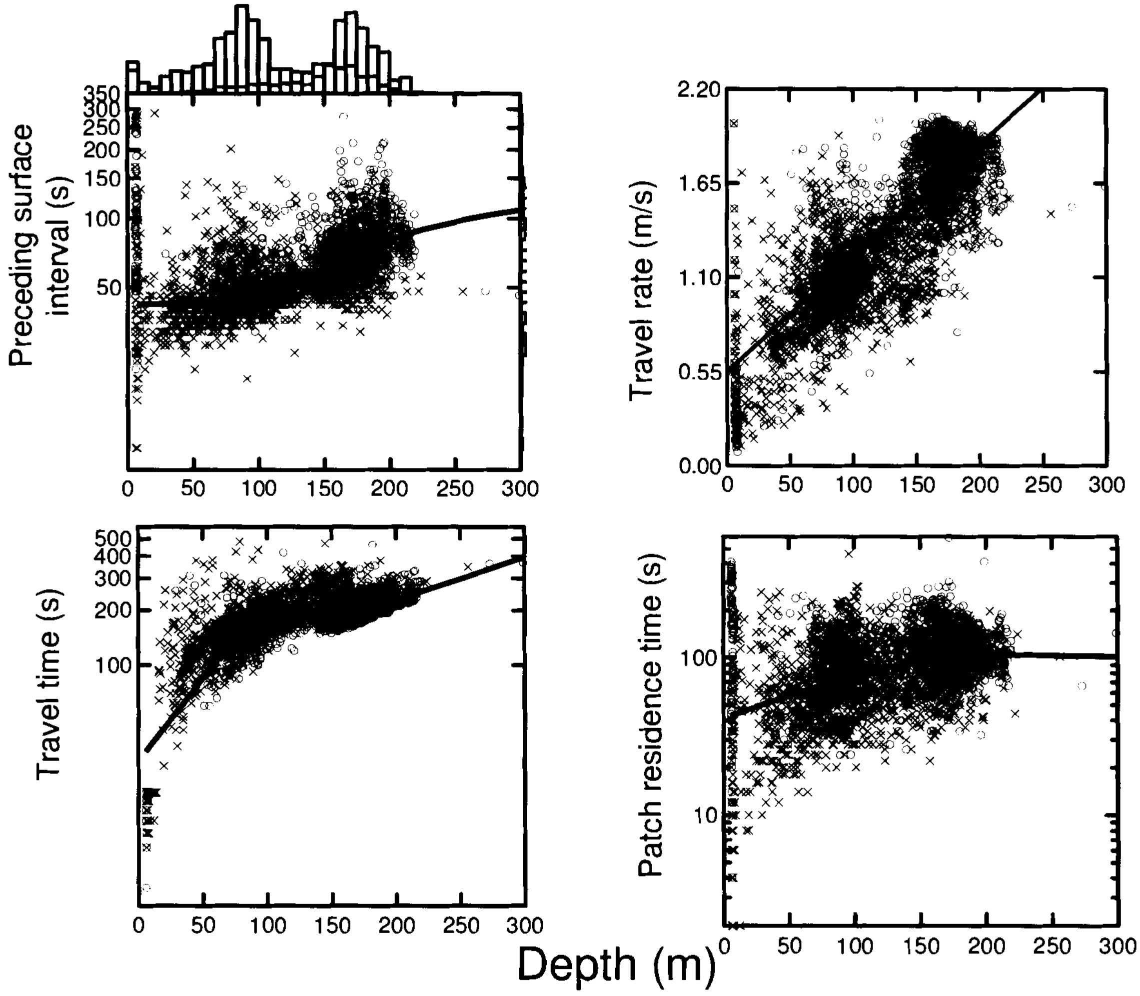


Figure 3.4: Examples of per dive net energy gain and predation risk predicted when assuming conditions of Experiment 8 in Table 3.3 (i.e. ε=10000, a_{10000} = 0.008, and a 50:1 ratio of μ_{shark} to μ_{orca}).

Figure contrasts a deep and a shallow diving adult female (af17 and af3, respectively). Red symbols represent day, and blue symbols represent night.

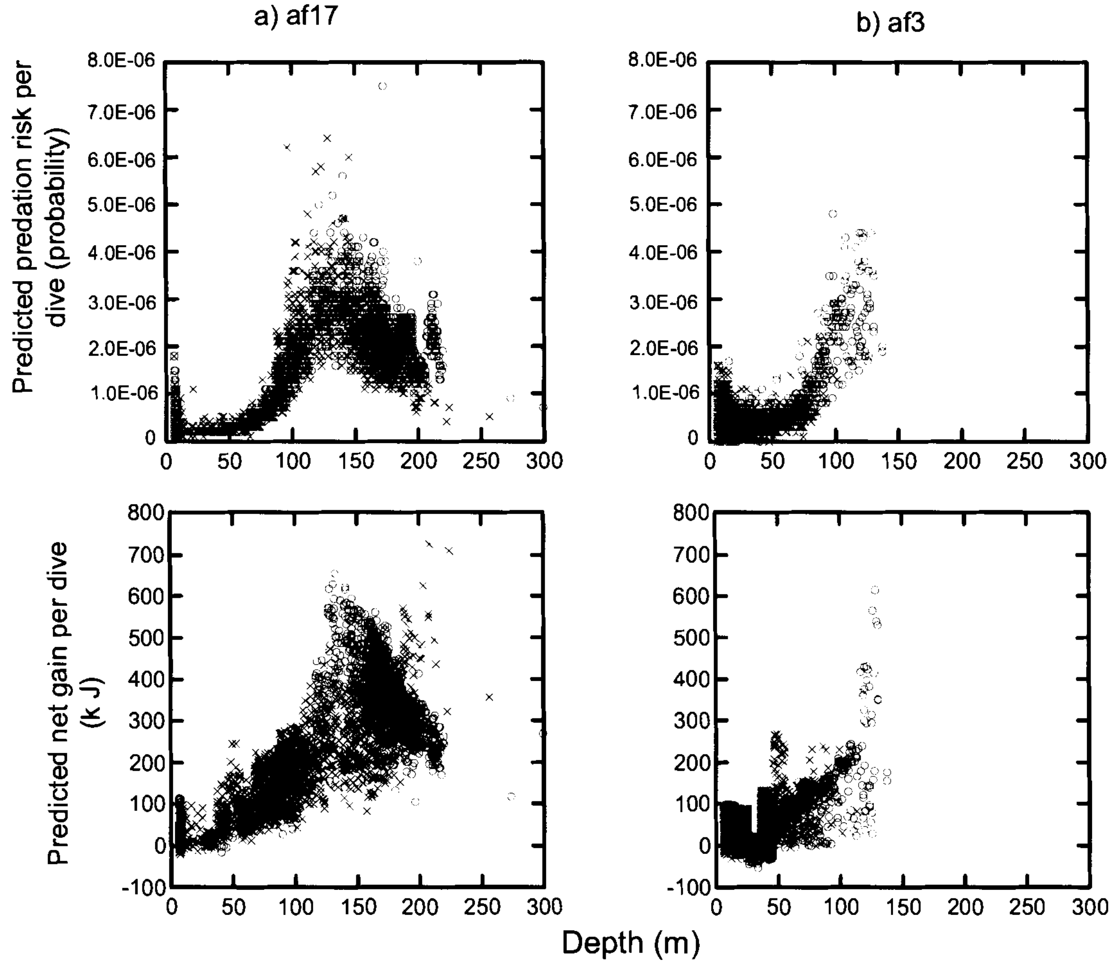
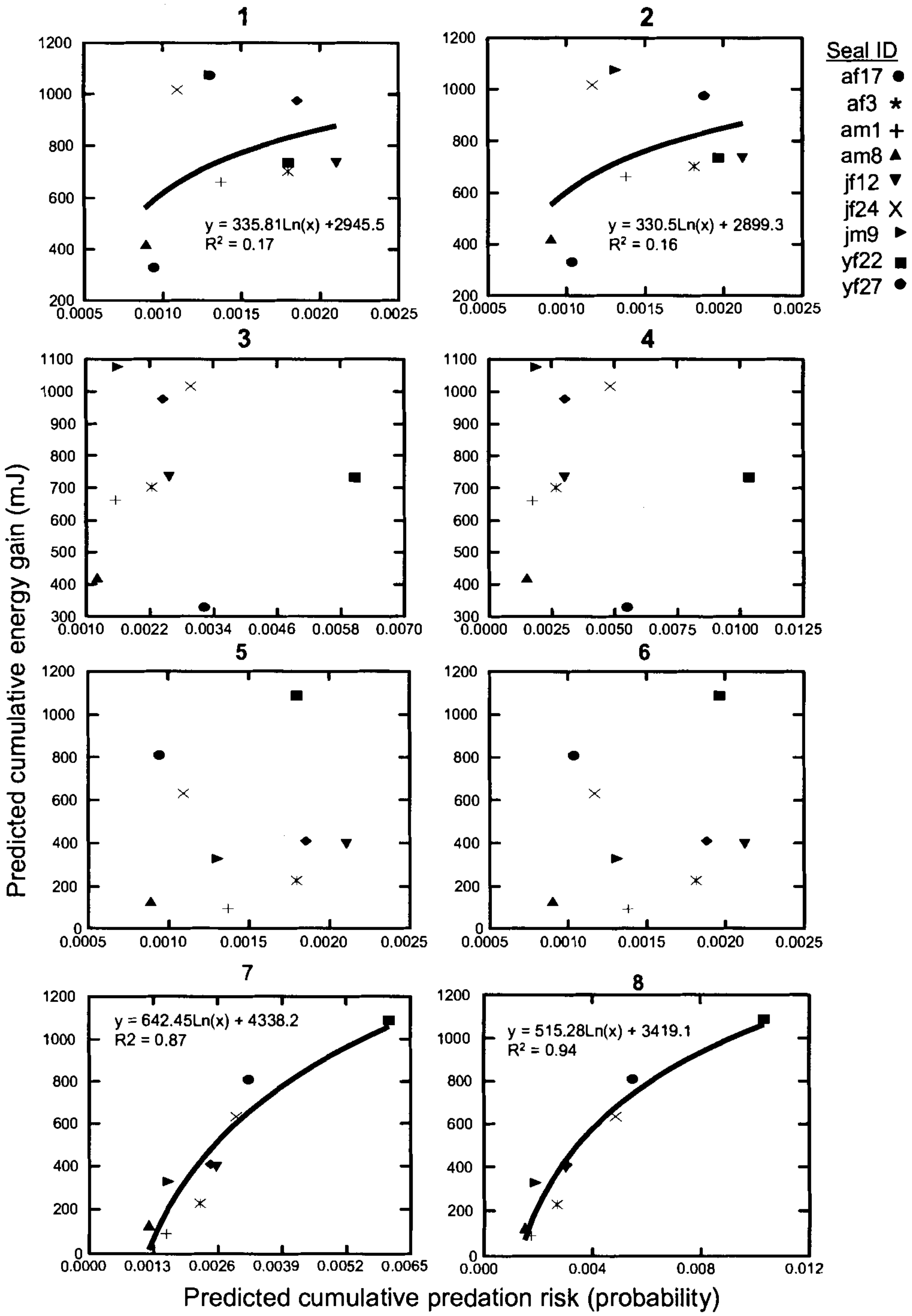


Figure 3.5: Plots of the individuals' predicted cumulative net energy gain against predicted cumulative predation risk for the 8 theoretical scenarios.

Panel numbers correspond to computer experiments described in Table 3.3. Note overlap of two data points (seals yf27 and jf12) in Experiment 8.



Supplementary material for Chapter 3

This section presents the print version of supplementary material for Chapter 3 that would appear as electronic appendices in the journal's website (contingent on the manuscript's acceptance for publication).

Figure S3.1: Empirical measures of fish biomass during day (red) and night (blue) used to predict resource encounter probabilities.

Data were collected during March 2003 and 2004 in Prince William Sound (years pooled, see Methods). Panel A shows extreme outliers (11-280 X the mean) and Panel B shows values ≤10 X the mean. Regression lines are drawn with a distance weighted least square smother at tension = 1 (Wilkinson 2004).

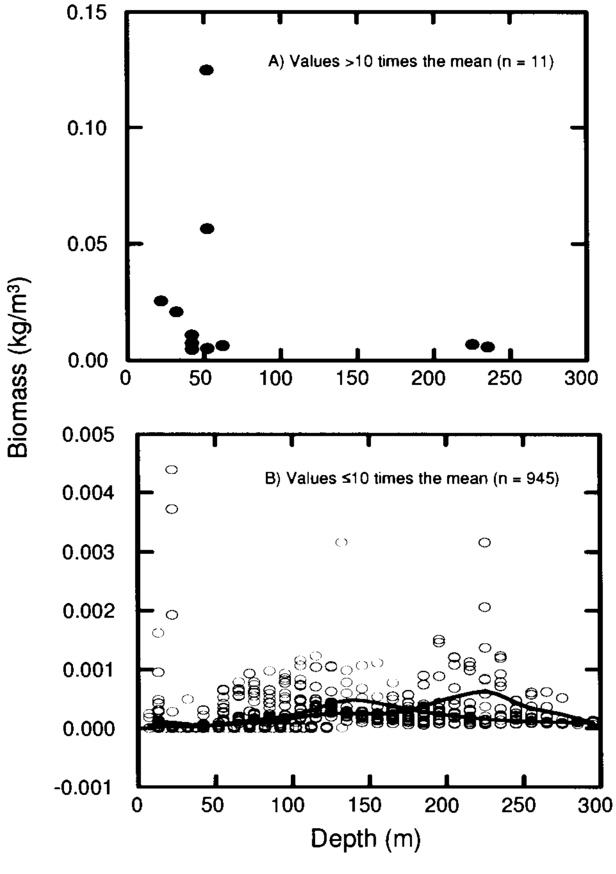


Figure S3.2: Expected number of fish caught upon arriving to a depth stratum during day (red) and night (blue) by seals of length ≤115 cm (see Table 3.1).

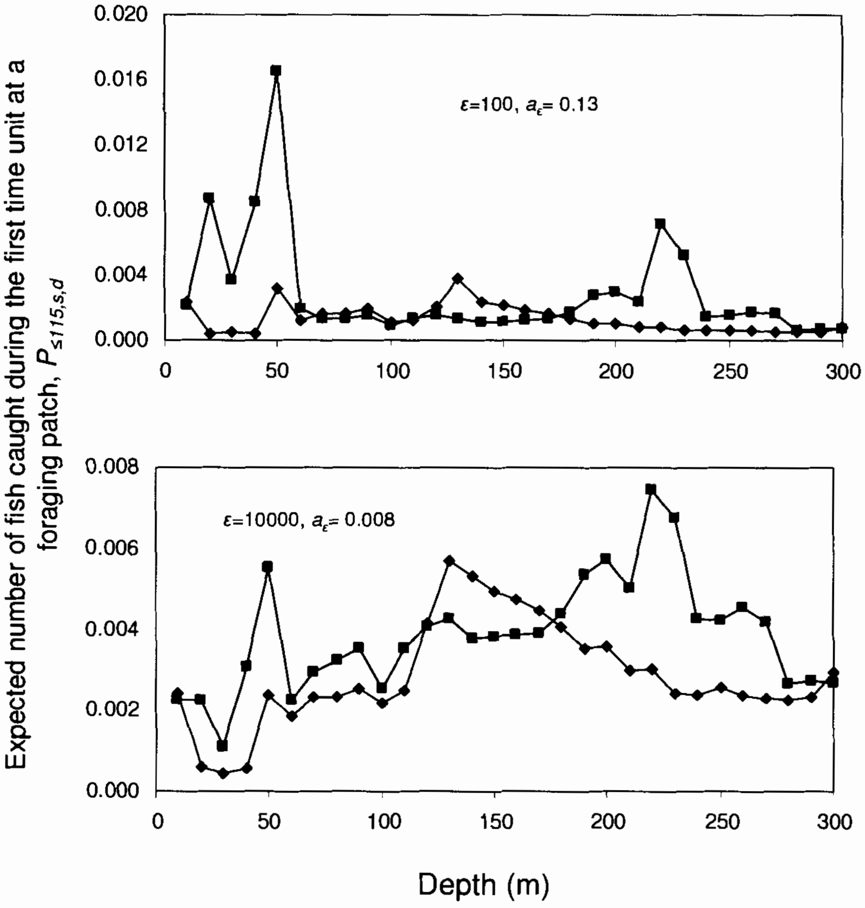
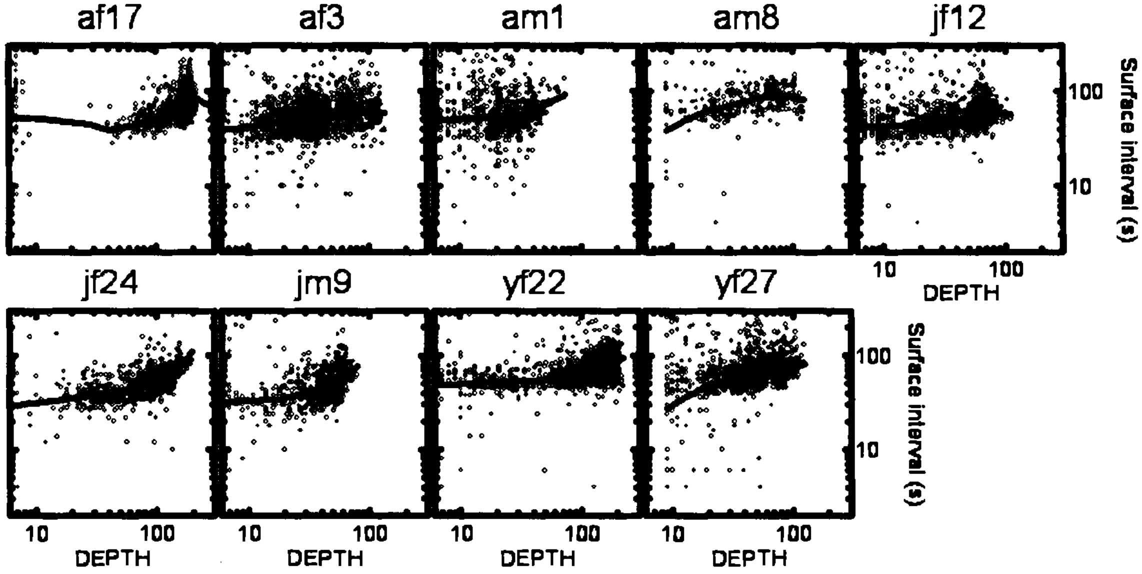


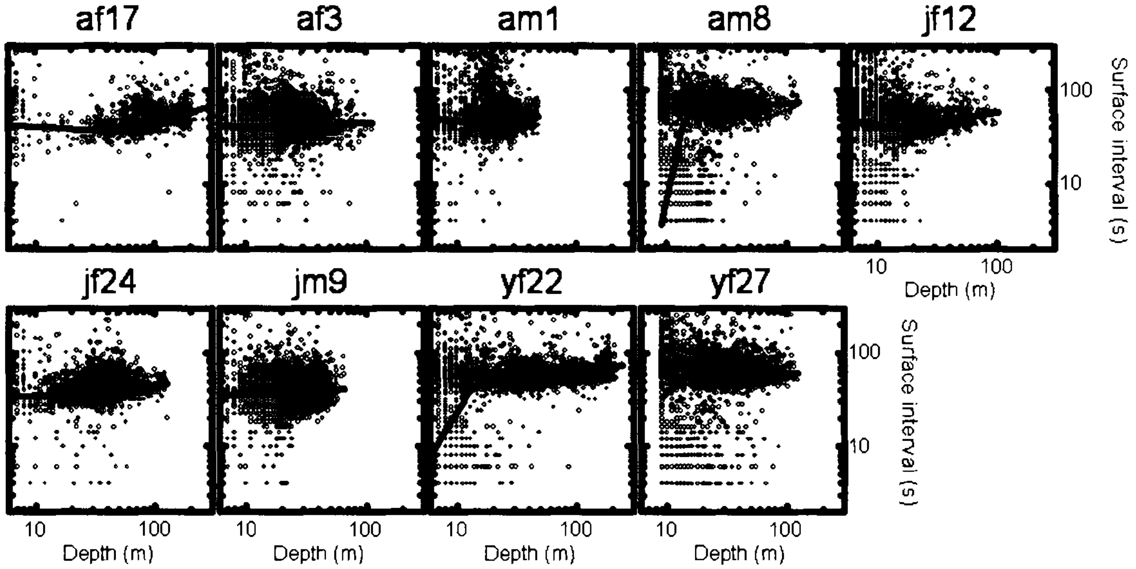
Figure S3.3: Dive data used as empirical inputs into the model.

Panel sets A-H are identified by diel period and dive cycle component. Individual panels within a set are identified by individual (see Table 3.1). Regression lines are drawn with a locally weighted smoother at tension = 0.5 (Wilkinson 2004); axes are $\log_{10}$ scaled.

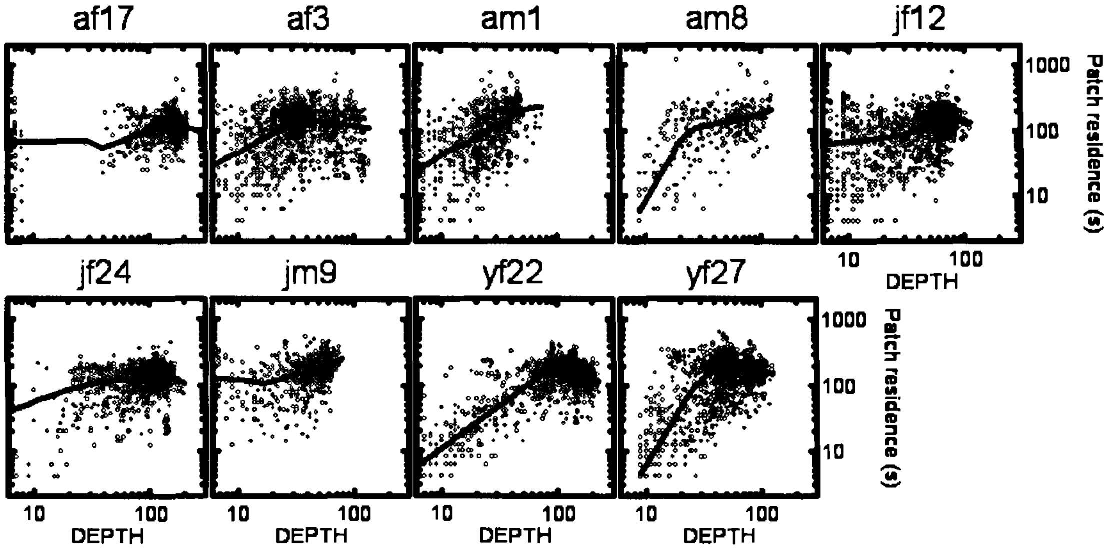
A) Preceding surface interval during day.



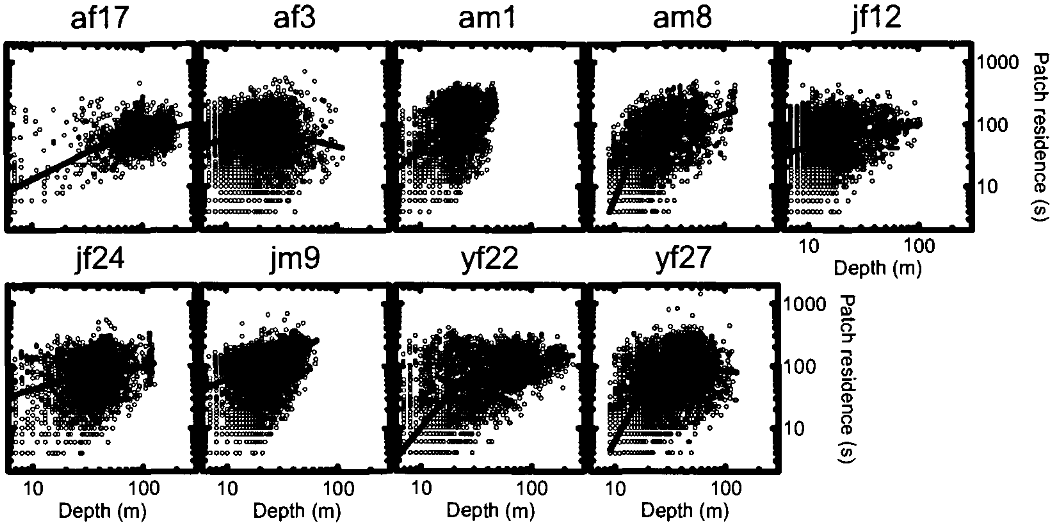
B). Preceding surface interval during night.



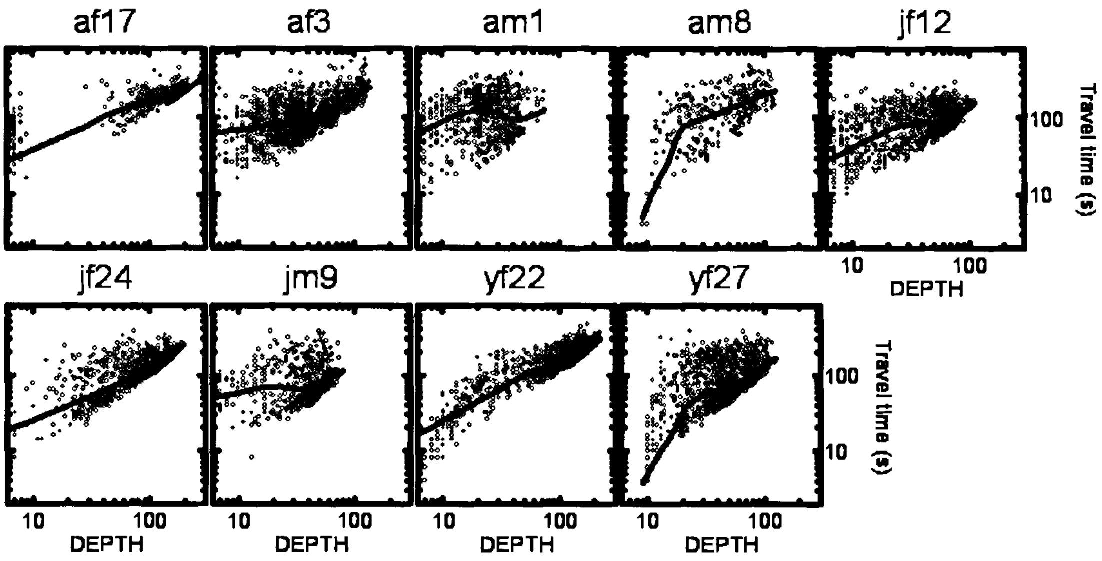
C). Patch residence during day.



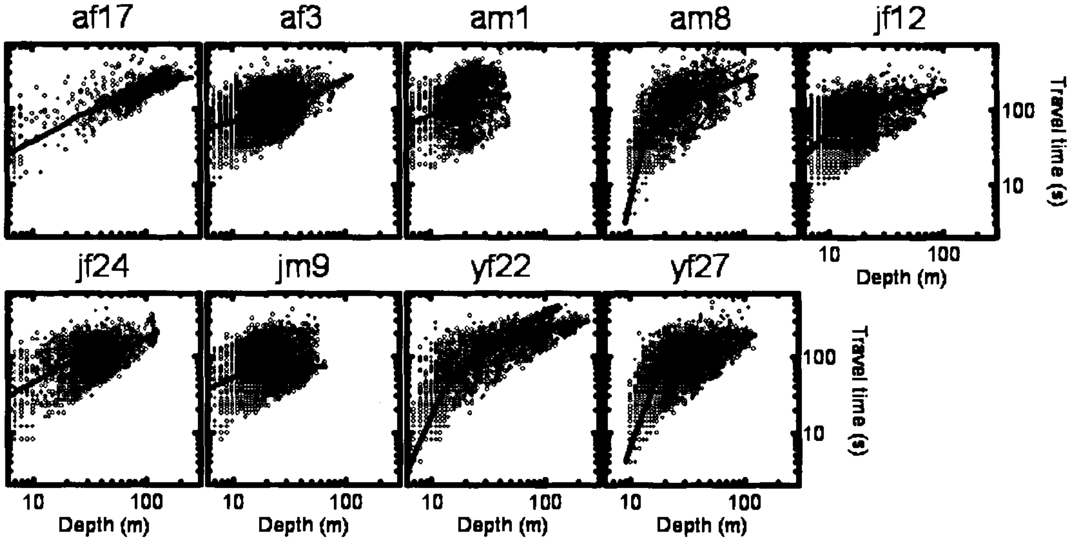
D). Patch residence during night.



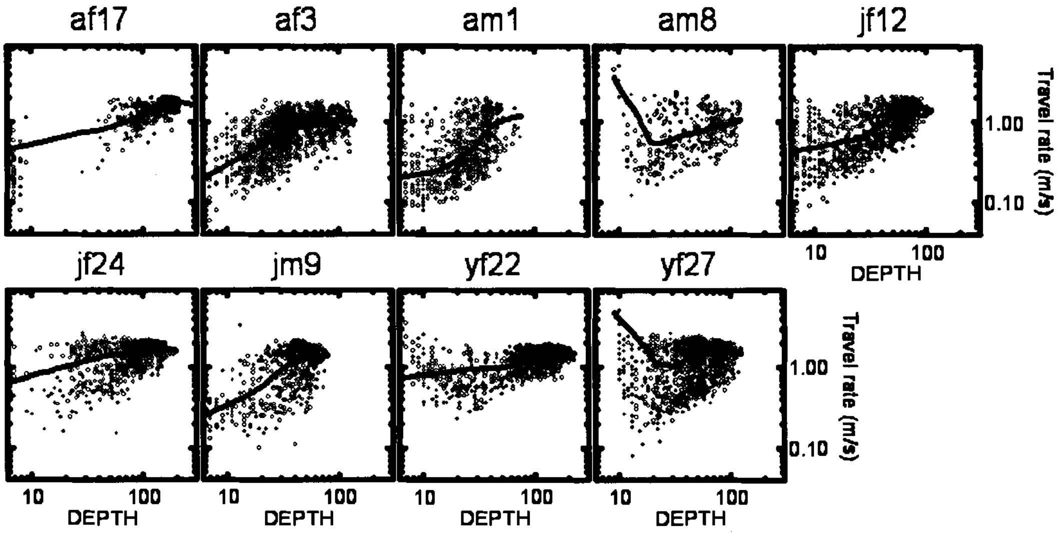
E) Travel time during day.



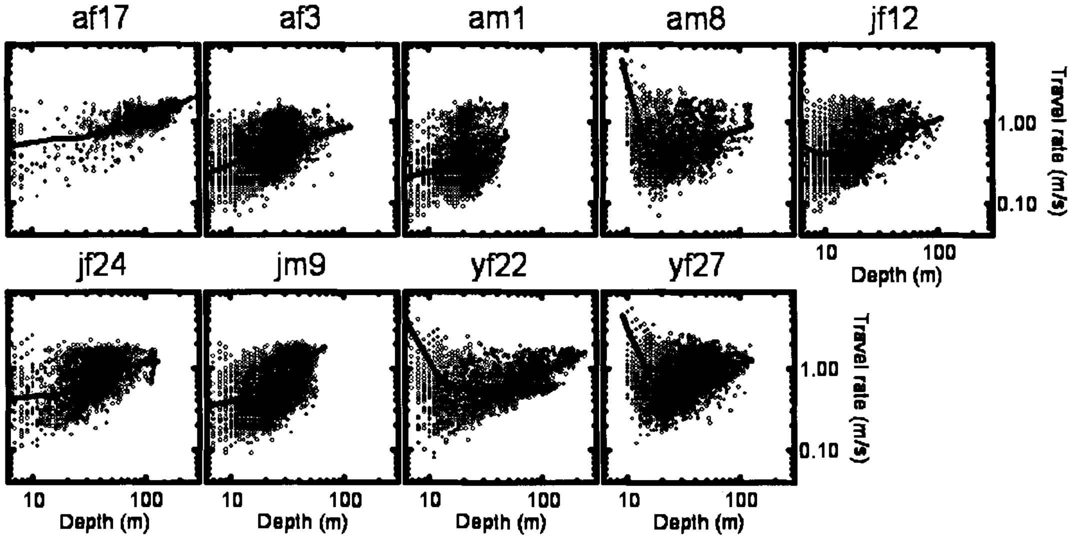
F) Travel time during night.



G) Travel rate during day.



H) Travel rate during night.

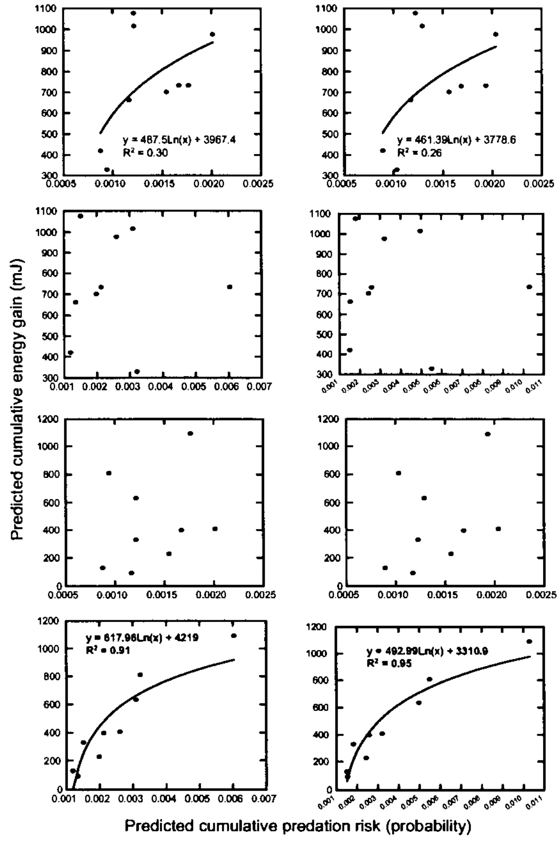


Sensitivity analyses

We conducted sensitivity analyses for eight parameters whose values were based on either limited or no empirical data (details in text). Values were changed one at the time, as described below. For all figures shown below, the panels represent computer experiments in the same order as Fig. 3.5.

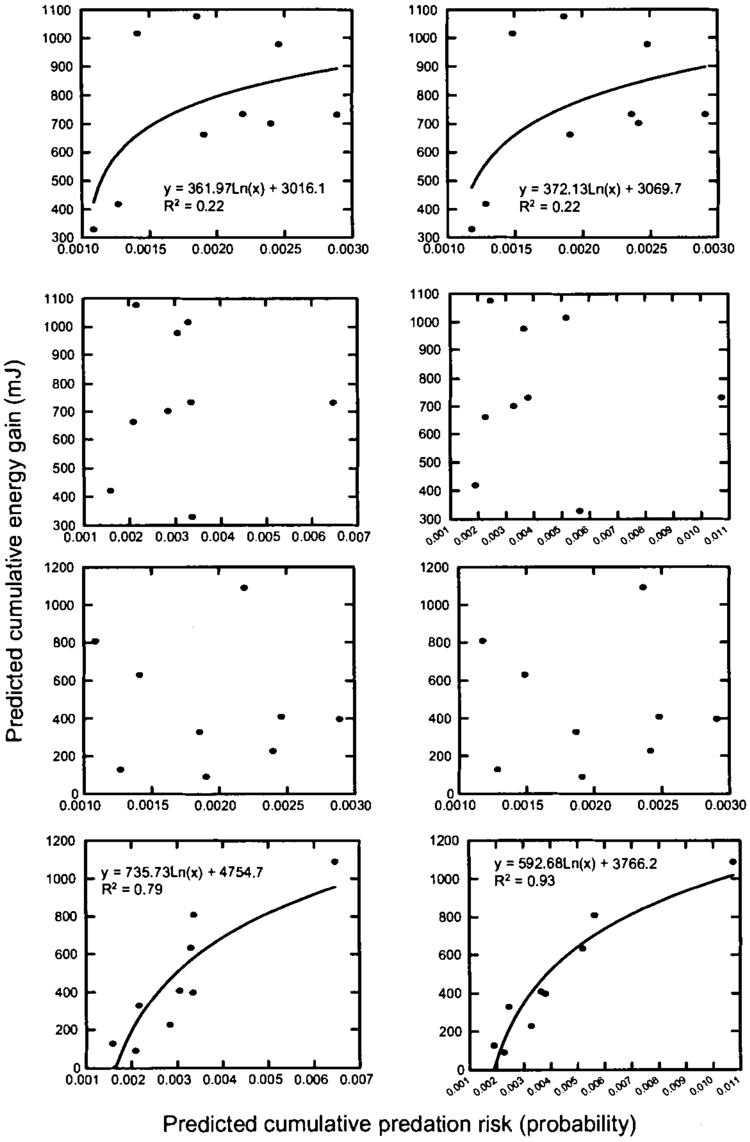
Killer whale use of depth

Based on game theory (Hugie & Dill 1994), we re-parameterised time at depth by killer whales as proportional to expected resource encounter rates (as plotted by depth, diel period and ε scenario in Fig. 3.1). We considered only the $P_{\geq 130,s,d}$ scenario and assumed that killer whales did not dive below 50 m; i.e., proportions of submerged time at 10 m, 20 m, 30 m, 40 m and 50 m were, respectively, 0.373, 0.094, 0.071, 0.090, 0.372 during day vs. 0.158, 0.159, 0.077, 0.217, and 0.389 at night. As shown below, conclusions derived from the original experiments (Fig. 3.5) were robust to the re-parameterization.



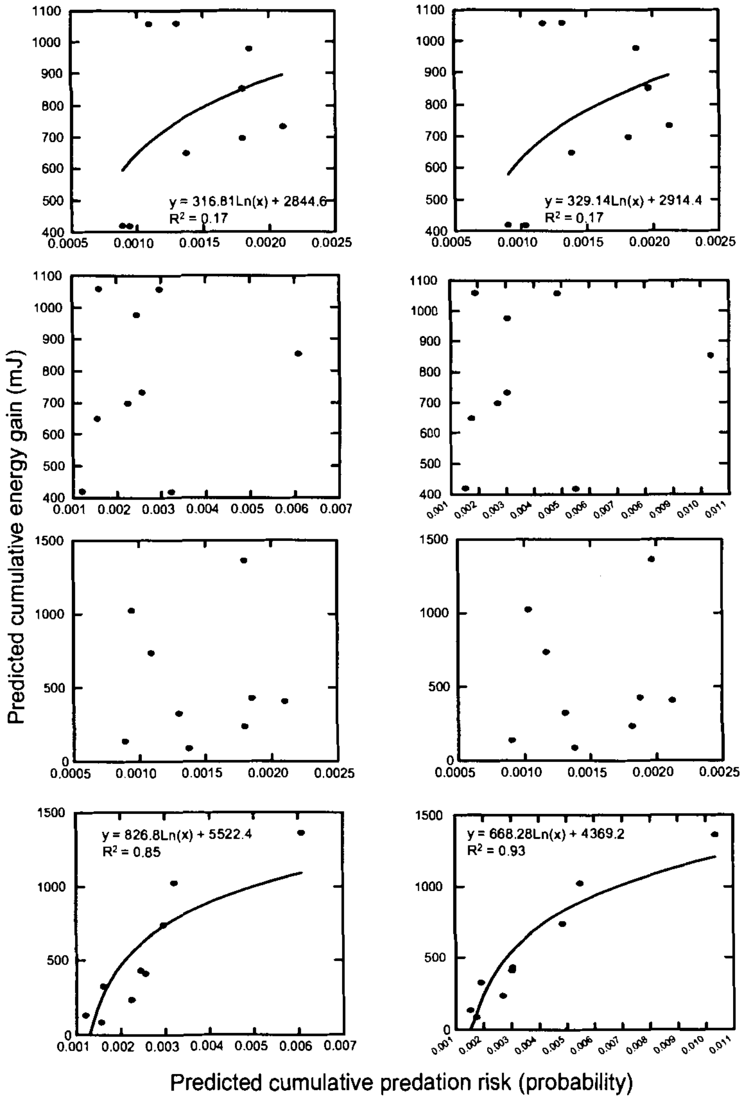
Diel activity level by killer whales

Rather than decreasing killer whale activity (and therefore killer whale risk to seals) by one third at night, here we assumed equal activity during day and night. As shown in the figure below, the re-parameterization did not change conclusions derived from the original experiments (Fig. 3.5).



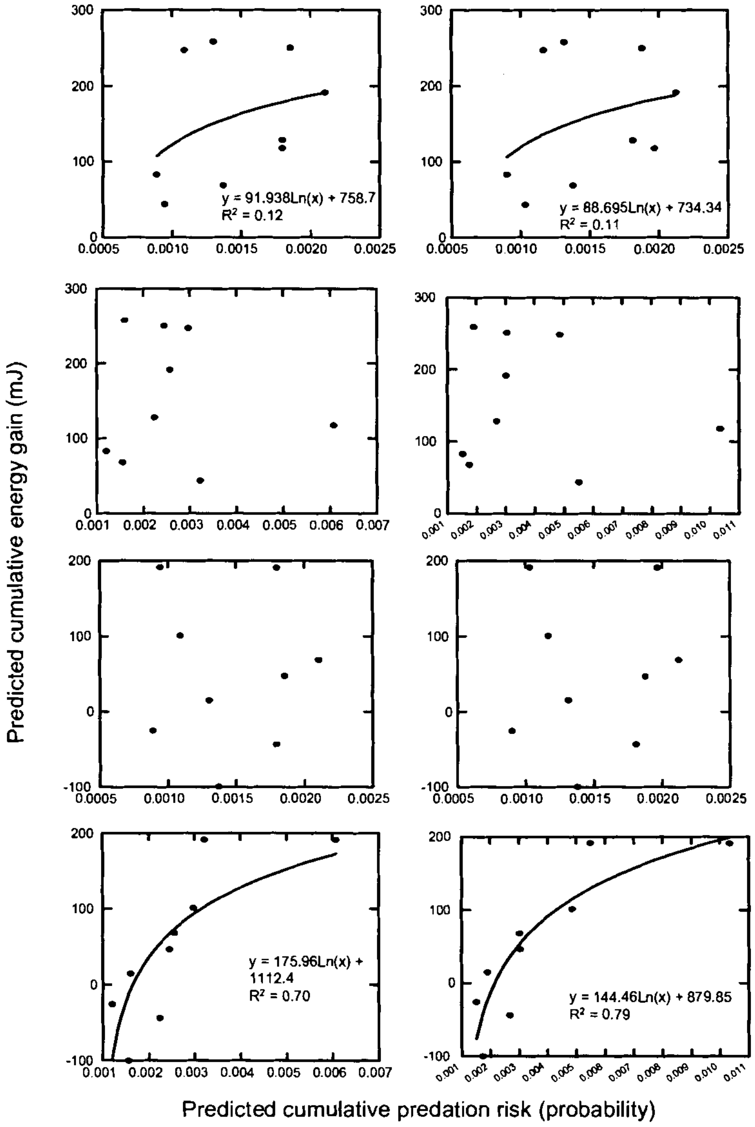
Energy densities of herring and pollock

At the time of model development, Anthony et al. (2000) contained the best data available to us for parameterising energy densities of pollock and herring, which—though specific to Prince William Sound—represented values for May-August. Recently, we became aware of Vollenweider (2004) which, though based on fish collected in Southeast Alaska, provides mean energy densities during March for adult pollock (4.08 kJ/g) and herring (5.74 kJ/g), which are seasonally appropriate to our model. As shown in the figure below, the re-parameterisation with the March values did not change conclusions derived from the original experiments (Fig. 3.5).



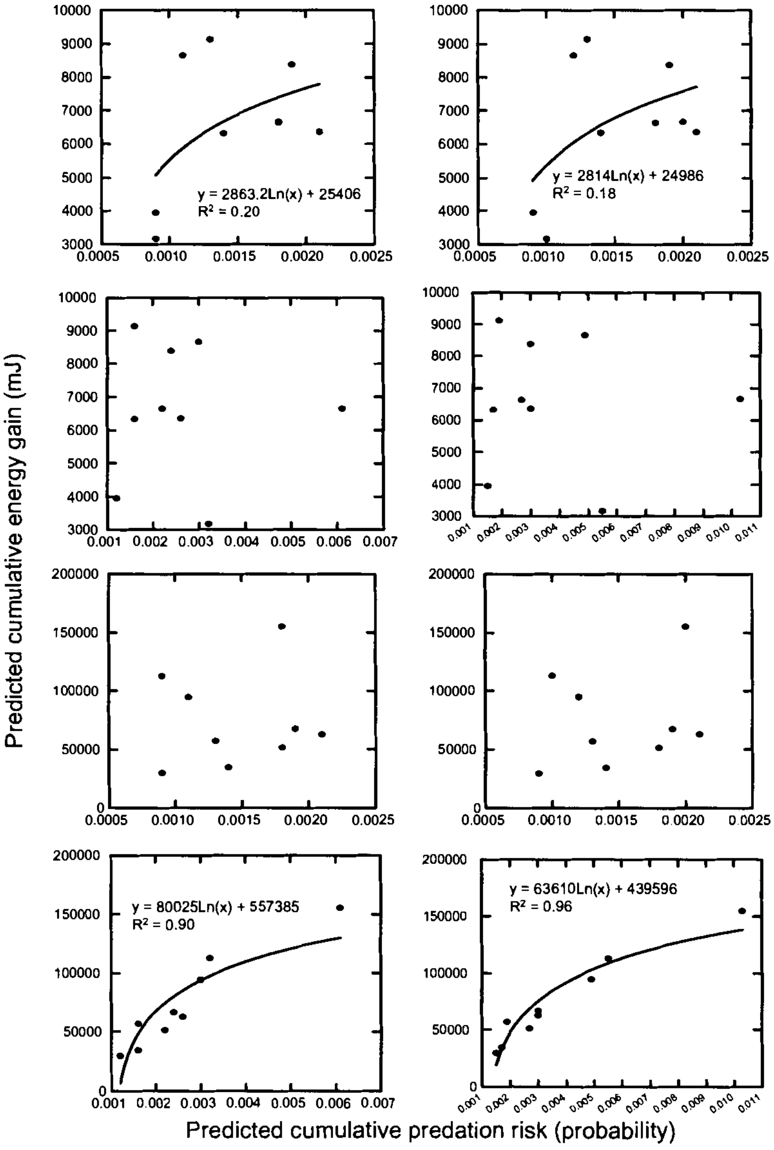
Parameter k

Parameter *k* (see Equation 2) was given a value of 0.99 in the original experiments. Here we re-parameterised it as k = 0.95. As shown in the figure below, the re-parameterisation did not change conclusions derived from the original experiments (Fig. 3.5). (Y-axis values are unrealistic here, yet we are concerned only with the shape and fit of the regression line).



Parameter a_ε

In the original experiments, different levels of ε used different values of a_ε for scaling (see Equation 1). To assess whether a_ε differences might confound ε effects, we here we used $a_\varepsilon = 1$ for both ε levels. As shown in the figure below, the re-parameterisation did not change conclusions derived from the original experiments (Fig. 3.5). (Y-axis values are unrealistic here, yet we are concerned only with the shape and fit of the regression line).



Exploitable sizes of fish

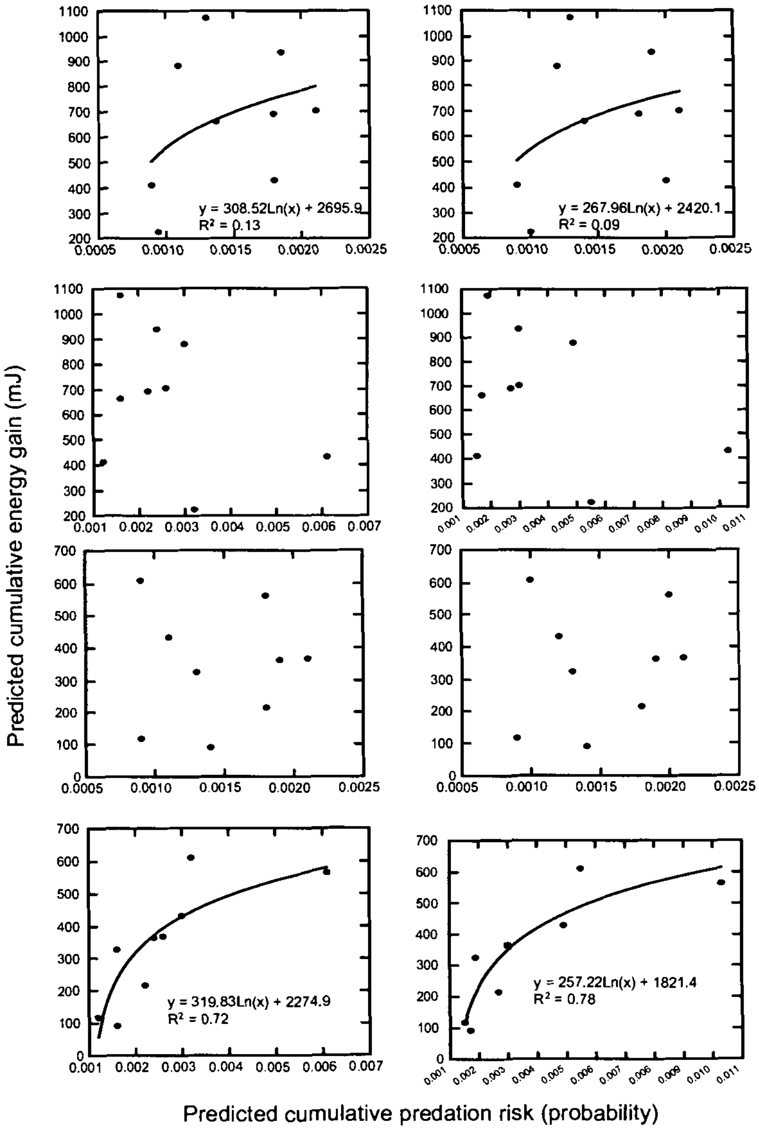
Here we assume a 5-cm decrement in maximum sizes of exploitable fish, which leads to the following re-parameterisation (compare it to Table 3.2).

Seals standard length l (cm)	Depth (m)	*Exploitable proportion of fish	Mean values for characteristics of exploitable fish	
			Mass (g)	Energy content (kJ)[†]
All seals	≤55	1.0	121.57	638.97
≤115	56-95	0.66	192.9	702.97
≤115	>95	0.32	263.02	766.96
≥130	56-95	0.83	240.02	842.13
≥130	>95	0.66	358.46	1045.28

*Assumes maximum exploitable lengths of fish were 35 and 40 cm, respectively, for $l \leq 115$ and ≥130 cm.

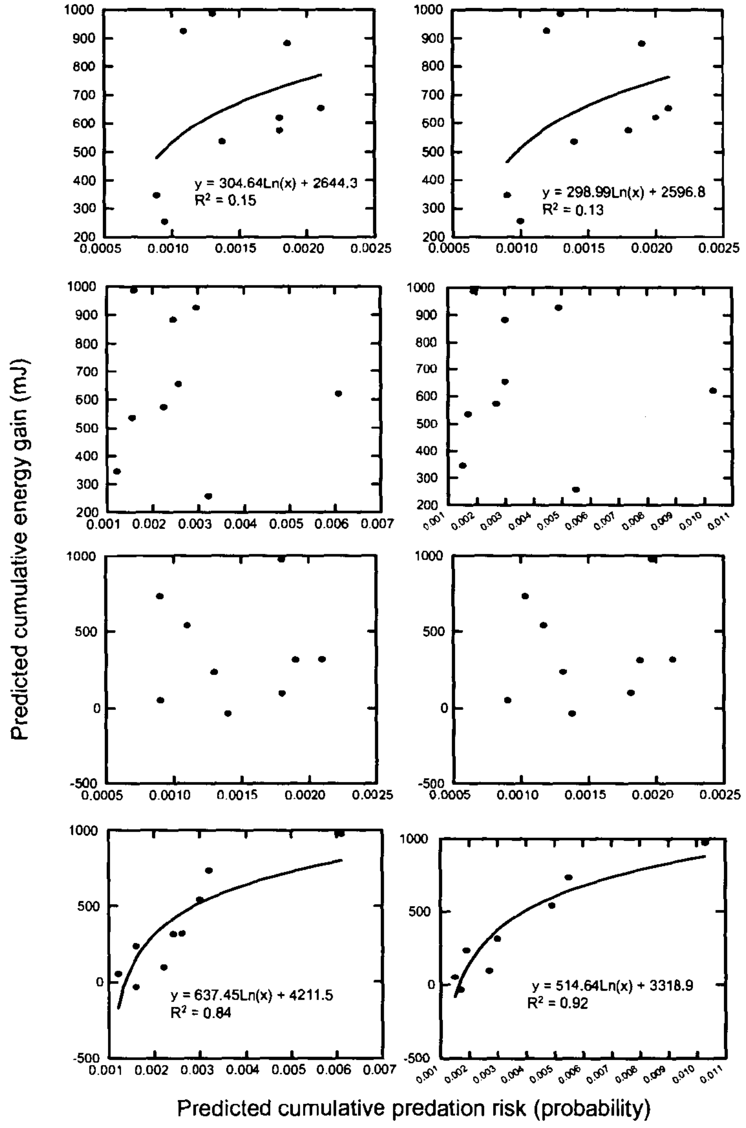
[†] Estimated energy densities in Anthony et al. (2000) multiplied by an assumed assimilation efficiency of 0.9.

As shown in the figure below, the re-parameterisation did not change conclusions derived from the original experiments (Fig. 3.5).



Twice the metabolic costs

We made many assumptions about metabolic costs. Rather than doing numerous sensitivity analyses to address them, we did one extreme re-parameterisation: the doubling of metabolic rates. As shown in the figure below, the re-parameterisation did not change conclusions derived from the original experiments (Fig. 3.5).



Chapter 4. Harbour seals as transmitters of indirect fishery effects: theoretical predictions

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Note: manuscript is formatted for submission to the *Ecology Letters*.

Abstract

We modeled potential indirect effects of herring and pollock fisheries and of the bycatch of sleeper sharks in the Northeast Pacific. Our theoretical study illustrates an asymmetric trophic cascade in which indirect effects of sharks on resources were mediated by harbour seal avoidance of deeper, riskier strata. Risk management by seals reduced mortality on the dangerous resource (deep pollock) while increasing mortality on the safer resource (shallow herring). During simulations without shark risk, seals shifted to deeper strata, increasing pollock consumption and eliminating herring use. The indirect effect of shark intimidation weakened if seals were in poor energetic state and less able to afford avoidance of risky patches. Fishery-induced resource declines forced seals to incur greater risks and higher predation rates, particularly when herring was scarce and seal energy state was poor. Overfishing of sharks and of resources used by pinnipeds are global concerns. Our model can inform management decisions of these issues.

Introduction

Fisheries indirectly precipitate community-level changes in marine systems (Pauly et al. 2002). For instance, in the Gulf of Mexico the rise of industrial fishing drastically reduced the density of large sharks, thereby indirectly increasing the abundance of the latter's prey, small elasmobranchs, in deep strata uninfluenced by the bycatch of shallow shrimp trawls (Shepherd & Myers 2005). Other studies report similar density-mediated indirect interactions (DMII: Abrams 1995) initiated by fisheries (e.g. Jackson et al. 2001; Worm & Myers 2003; Scheffer et al. 2005). Yet DMIIs may be only a partial portrayal of indirect fishery effects (Walters 2000; Alonzo et al. 2003a; Dill et al. 2003).

Consider models of trait-mediated indirect interactions (TMII: Abrams 1995). These models predict when one species inducing a behavioural or morphological response by a second species will indirectly influence the fitness of a third through effects transmitted (or mediated) by the second species (Werner & Peacor 2003). For instance, it is well known that intermediate consumers underutilise dangerous resources yet increase use of the same resource after predator removals (Lima & Dill 1990; Brown & Kotler 2004). Accordingly, top predators indirectly reduce the mortality rate of resource species by scaring intermediate consumers into choosing safer but less efficient foraging modes (Werner & Peacor 2003; Schmitz et al. 2004; Fortin et al. 2005). TMIIs may also propagate upward through the food web. Resource declines will indirectly benefit top predators if the intermediate consumer increases foraging rate at the cost of greater vulnerability (Anholt & Werner 1995). Conversely, resource abundance should enhance the consumer's safe foraging options and indirectly reduce the hunting success of top predators. Thus, resource abundance is predicted to weaken and strengthen, respectively, the influence of DMIIs and TMIIs on trophic cascades (Luttbeg et al. 2003). Clearly, TMII models can be powerful tools for predicting large-scale indirect fishery effects (Walters 2000; Alonzo et al. 2003a; Dill et al. 2003). Surprisingly, this potential is underutilised.

We sought theoretical insight into TMIIs that might be initiated by fisheries and transmitted by an intermediate consumer, the harbour seal *Phoca vitulina richardsi*. Predictions were made with a dynamic state variable model (Clark & Mangel 2000), in which foraging decisions respond to resource availability, predation risk, current energy state and the time remaining before a terminal horizon. Energetic state is inherent to predictions because it might be influenced by fishery-induced resource declines that place individuals between a rock and hard place. The foraging opportunity cost of antipredator behaviour is less affordable to individuals in poor energy state because it might lead to starvation or a net loss of reproductive potential (McNamara & Houston 1987; Clark 1994). Thus, poor energy state promotes greater risk-taking and higher predation rates (e.g. Sinclair & Arcese 1995; Sweitzer 1996). The relative strengths of TMIIs and DMIIs, therefore, should be influenced by synergistic effects of resource level and energy state (Luttbeg et al. 2003).

Our model is inspired by the natural history and conservation issues of Prince William Sound (PWS) and adjacent Gulf of Alaska. It extends an earlier version used to establish that, theoretically, predation rates on harbour seals increase with diminishing resources and energy reserves, despite the assumption of fixed predator densities (Frid et al. 2006). Parameterisation of the current version of the model is updated to reflect our recent findings. During the late winter of 2004, we studied individual variability in foraging tactics of PWS seals, and measured the depth distribution of two primary resources (see Iverson et al. 1997)—walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasi*. These data and information on time-at-depth by predators parameterised theoretical calculations suggesting that Pacific sleeper sharks *Somniosus pacificus* were much more abundant than transient killer whales *Orcinus orca*, and that seals perceived sharks to be their main predator (Chapter 3).

The predictions we present here highlight the ecological consequences of shark intimidation, as mediated by seal behaviour, and how fisheries might alter this TMII. We contrasted simulations in which seals faced risk from sleeper sharks and optimised risk-energy trade-offs accordingly, with simulations in which sharks were absent and seals relaxed their antipredator behaviour. This contrast might be relevant to understanding some current conservation issues. Although there is no target fishery for sleeper sharks, the bycatch of this species by groundfish fisheries in the Gulf of Alaska averaged an estimated 325 t per year between 1997 and 2001 (Courtney et al. 2004). Further, in PWS during 2005 alone, the reported bycatch was 860 individual sleeper sharks caught by the sablefish fishery and 5.2 t of 'sharks' (species unspecified) caught by the pollock fishery (R. Berceli et al., Alaska Dept. of Fish & Game unpublished data). In general, large sharks inhabiting cold waters have late age at maturity and low reproductive rates (e.g. Smith et al. 1998). These life history characteristics caution that the reported bycatch rates—which derive from incomplete logbook data and thus are less than actual rates—might eventually threaten population persistence. Accordingly, the model's shark removal scenarios are heuristic tools for exploring how some ecological dynamics might change if sustained, long-term bycatch drove sharks extinct. Given that bycatch and target fisheries occur concurrently, we also predicted the indirect effects of fishery-induced declines of walleye pollock and Pacific herring, as mediated by seal behaviour in the presence and absence of shark risk.

Methods

The dynamic state variable model presented here is modified from Frid et al. (2006). Readers should refer to that paper for model derivation and to Clark & Mangel (2000) for general aspects of the technique. Internal state variables, $X(t) = x$ (energy reserves) and $Y(t) = y$ (oxygen), were unchanged from Frid et al. (2006) and, as before, the model is specific to adult females. We also note that there is no density-dependence in the model and thus we do not consider games among seals either in energy intake or risk of predation. Below we describe modifications required by our current objectives.

The model covers a 23 d-period during late winter. The time span preceding the terminal horizon, *T*, is divided into 20 s periods, *t*, when decisions are made. Decisions consist of either staying at the current location or initiating a move towards a future location. Moves occur at a rate of 1 m s^{-1}. They are either horizontal, if moving between a haulout and the surface of a foraging habitat located 1.5 km offshore, or vertical, if diving between the surface and either a shallow, mid-depth or deep resource patch, with respective depths of 20, 60 and 140 m.

At the onset of simulations, seals are at the haulout, which provides refuge from predators but no food. Therefore, foraging trips are initiated by travelling horizontally for 75 20 s-time periods to the surface of the foraging habitat (hereafter, 'surface'); the return trip requires an equal amount of time. The surface has no food, but is where oxygen required for diving is uploaded; seals must be there before descending to a resource patch. The descent to the shallow, mid-depth, and deep resource patches requires1, 3 and 7 20 s-time periods, respectively; the ascent to the surface requires an equal amount of time. In the model, seals can visit only one resource patch per dive, and must return to the surface before travelling horizontally back to the haulout. The 5 locations are represented by an environmental state in which the notation $H(t) = h$ indicates that the seal is at location *h* during time *t*. Following Frid et al. (2006), *h*-values correspond to the number of time units required for one-way travel to that location from the haulout or, in the case of resource patches, from the surface. Thus, the haulout and the surface are represented by $H(t) = 0$ and $H(t) = 75$, respectively. The shallow, mid-depth and deep resource patches, are represented by $H(t) = 1$, $H(t) = 3$ and $H(t) = 7$, respectively. These *h*-values were substituted into, Eqs. 1-6 of Frid et al. (2006).

In contrast to our prior model, *T* does not coincide with the reproductive season. (The late-winter timing of *T* was based on the available data for parameterisation; see below.) After *T*, adult females have two months to further build the energy reserves that will partly fuel lactation (see Bowen et al. 2001). Thus, rather than assuming a semi-linear relationship between fitness and

$X(T) = x$ (except when $X(T) = 0$, which implies that fitness is 0), as Equation 10 of Frid et al. (2006) does, we assumed a smoothly decelerating curve and back-iterated from the following terminal fitness function (see Supplementary Material for sensitivity analyses):

$$F(x,y,h,T) = 1-(1-(x/x_{\max}))^{3.25} \qquad (1)$$

Baseline parameterisation

Energetic costs of activity were unchanged from Table 1 of Frid et al. (2006). Expected predation risk and energy gain, however, were re-parameterised based on analyses and assumptions detailed in Chapter 3. Specifically, let $P_{s,d}$ be the probability of encountering a resource at stratum *s* during diel period *d* (day vs. night), as in Fig. 3.1d of Chapter 3. In the present model, $\lambda_{h,d}$, the probability of encountering and capturing a fish at *H*(*t*) = *h* during *d*, is:

$$\lambda_{h,d} = \phi P_{mean(s1\,:\,s2),d} \qquad (2)$$

where $P_{mean(s1\,:\,s2),d}$ is the mean $P_{s,d}$ for the depth range s_1 to s_2, corresponding to 0–55 m if *H*(*t*)=1, 56–95 m if *H*(*t*) = 3, and 96–200 m if *H*(*t*)=7. The constant $\phi = 1.8$ scales energy gain to realistic rates, as determined through preliminary simulations. Table 4.1 lists resulting values.

Similarly, let $T_{i,s,d}$ be the proportions of time spent by predator *i* (killer whale or shark) at *s* during *d*, as estimated in Figs 3.1a,b of Chapter 3. In the present model, $\mu_i(h,d)$, the probability of predation by predator *i* at *H*(*t*) = *h* during *d*, is:

$$\mu_i(h,d) = \rho\omega_i T_{i,s,d} \qquad (3)$$

where ω_i indexes relative danger (*sensu* Chapter 3) from each predator type, such that $\omega_{shark} = 3.75\times10^{-7}$ and $\omega_{orca} = 5.00\times10^{-9}$, as argued theoretically in Chapter 3. Limited data suggest that killer whales are primarily diurnal (R.W. Baird unpublished data), so we reduced the value of ω_{orca} by one third for nocturnal risk. The constant $\rho = 40.6$ has a role equivalent to ϕ in Equation 2. Table 4.1 lists resulting values.

Only one fish can be caught per successful time period at a foraging patch. We assume that 122-g Pacific herring and 424-g walleye pollock are the only resources at $H(t) = 1$ and $H(t) = 7$, respectively. At $H(t) = 3$ we assume that herring and pollock of these sizes are found in equal proportions. Based on March energy densities for herring (5.74 kJ/g) and adult pollock (4.08 kJ/g) (Vollenweider 2004), and an assumed assimilation efficiency of 0.9, gross energy gain per capture is 638.97 kJ at $H(t) = 1$, 937.65 kJ at $H(t) = 3$, and 1236.33 kJ at $H(t) = 7$. (See Table

3.2 of Chapter 3 for assumptions about exploitable fish sizes, but note that energy densities differed in that study.)

Computer experiments

Solution to the dynamic programming equation generates an optimal decision matrix for all combinations of state variables and time periods. Based on this matrix, we used forward iterations (Clark & Mangel 2000) to conduct computer experiments in which herring and pollock were either scarce or abundant. The resource levels used for these treatments were proportional to the maximum and minimum yearly biomass estimates made during 1995-2003, the time series available for both fish species in PWS (Thomas & Thorne 2003; R. E. Thorne unpublished data). We do not claim that exploitation drove biomass fluctuations during that period. Rather, we used the time series data to parameterise a range of variation that, quite plausibly, could be influenced by fisheries.

As noted earlier, baseline parameter values (Table 4.1) derive from data collected in 2004 (Chapter 3). That year, the estimated herring biomass was 24800 t (R. E. Thorne unpublished data). Equivalent data are lacking for pollock, and we assumed a 2004 pollock biomass of 25100 t, which is the mean (SD±2425 t) for 2001–2003 (R. E. Thorne unpublished data). During the available time series, pollock biomass peaked at 38700 t in 1997 and dipped to 22300 t in 2003. These estimates are, respectively, 1.54 and 0.89 times the assumed biomass for 2004; baseline values of $\lambda_{7,d}$ (Table 4.1) were multiplied by these proportional changes to parameterise abundant and scarce levels of pollock. Similarly, estimated herring biomass peaked at 38000 t during 1997 and dipped to 6700 t during 2001. These estimates are, respectively, 1.53 and 0.27 times the 2004 herring biomass, and $\lambda_{1,d}$ baseline values (Table 4.1) were multiplied by these proportional changes to parameterise abundant and scarce levels of herring. For a given treatment, the $\lambda_{3,d}$ baseline value (Table 4.1) was multiplied by the mean of the proportional changes to $\lambda_{1,d}$ and $\lambda_{7,d}$ values. Throughout, we assumed that the depth distribution of resource and predator species and that relative danger from sharks and killer whales remained unchanged from the 2004 estimates (Chapter 3).

Both levels of herring and pollock abundance were combined factorially with good and poor levels of the seal's initial energy state (50% and 90% of maximum, respectively) and with two levels of shark risk (sharks present or absent), while maintaining predation risk from killer whales constant at a low background level (see Table 4.1). Each of the 16 treatment combinations was simulated 1000 times, and we report predicted behaviours as the mean outcome of simulations.

Behavioural predictions include only simulations in which the individual survived to *T*, and thus are analogous to the "risk" manipulations of empirical studies in which modified predators threaten but cannot kill (e.g. Schmitz et al. 2004). Although the model accounts for diel changes in risk-energy trade-offs, for brevity we report overall responses. Following Luttbeg et al. (2003), we quantified the relative size of trait- and density-mediated indirect effects of sleeper sharks on fish as proportional changes in the number of fish eaten by seals due to risk avoidance vs. density reduction, respectively (see Appendix 1 of Frid et al. 2006).

Results

The transmission mechanism

The main transmission mechanism of indirect effects—number of dives by seals to each stratum—depended on interactions between multiple factors. If initial energy state (IES) was good, sharks present, and herring abundant, few dives (<1%) were deep, most were shallow (76–77%), and 22-23% were to mid-depth (values in each range correspond to scarce and abundant pollock scenarios, respectively). Under these conditions pollock abundance had little effect on depth choice, but a change from scarce to abundant pollock caused an 8% decline in the total number of dives (Fig. 4.1a).

If IES was poor, sharks present, herring abundant, and pollock scarce, most dives (69%) were to mid-depth, and the remainder were approximately evenly distributed between deep (19%) and shallow strata (12%) (Fig. 4.1b). Under these conditions, a change from scarce to abundant pollock caused a 9% decline in the total number of dives, an increase in the proportion of shallow and mid-depth dives (21% and 74% of total dives, respectively), and fewer deep dives (5% of total) (Fig. 4.1b).

If herring were scarce, 99-100% of dives were deep, regardless of other factors (Fig. 4.1). Under these conditions, there were fewer dives if pollock were abundant, and the proportional reduction was greatest if sharks were absent and IES high (47% vs. 41% fewer dives for sharks absent vs. present, respectively; corresponding values for poor IES were 39% and 40%).

Removal of sharks led to almost exclusive use of deep strata. The exceptions were when herring were abundant and pollock scarce, in which case dives were approximately evenly distributed between mid-depth and deep strata, regardless of initial energy state (Figs. 4.1c,d). When herring were scarce, the removal of sharks led to a 47–32% increase in the number of deep dives if IES was high but only a 10–13% increase if IES was poor (Fig 4.1; values in each range correspond to scarce and abundant pollock scenarios, respectively).

For all treatment combinations, the total number of dives was greater if initial energy state was poor (Fig. 4.1).

Indirect effect of sharks on resources

The predicted indirect effect of sharks on per capita pollock consumption by seals was substantial. Its strength, however, attenuated with herring scarcity and poor IES (Fig. 4.2). Specifically, if IES was good, removing shark risk increased pollock consumption 5.2- to 4.6-fold if herring were abundant, but only 47–33% if herring were scarce. In contrast, if IES was poor, the shark removal increased pollock consumption by only 28–64% and 10–12% if herring were abundant and scarce, respectively (Fig. 4.2; values in each range correspond to scarce and abundant pollock scenarios, respectively).

The following results apply only to abundant herring scenarios (otherwise herring consumption was nil). Regardless of IES, herring consumption was greater in simulations that included shark risk. If pollock were scarce, removing shark risk decreased herring consumption by 76% if IES was good but only by 43% if IES was poor. If pollock were abundant, the shark removal completely eliminated seal use of herring (Figs 4.3a,b).

Indirect effects of resources on hunting success by sharks

Sleeper sharks are the model's main mortality agent (Table 4.1). For brevity, we do not elaborate on the few killer whale predation events that occurred during simulations. (Briefly, when IES was good, 1 to 3 killer whale mortalities occurred per resource level combination. When IES was poor, 4 killer whale mortalities occurred when both resources were scarce but otherwise there were none.)

The predicted rate at which sharks killed seals and the location of predation events depended on interactions between IES and the abundance of both resources. If IES was good and pollock scarce, herring declines caused a 3.2-fold increase in predation events, and shifted their location from mid-depth and shallow strata to only deep strata. If pollock were abundant, herring declines increased shark predation events by only 18%, and also shifted their location from primarily at mid-depth and shallow strata to only deep strata (Fig. 4.4a).

If IES was poor, the herring decline doubled or caused a 69% increase in shark predation if pollock were scarce or abundant, respectively. In both cases, the herring decline increased the proportion of mortalities that occurred at deep strata (Fig. 4.4b). Overall predation rates were greater for the poor IES (Fig. 4.4).

Relative strength of TMIIs and DMIIs

In all scenarios, indirect interactions initiated by sharks, mediated by seals, and received by herring and pollock had a much stronger TMII than DMII component (Figs. 4.3c, 4.5). Poor IES attenuated the strength of TMIIs on both resources. When pollock was the recipient of the indirect interaction and IES good, DMIIs occurred only when both resource species were scarce (Fig. 4.5a); if IES was poor, DMIIs always occurred except when both resources were abundant (Fig. 4.5b).

Discussion

Our simulations re-affirm some established tenets of ecological theory. Namely, resource declines and poor energy state limit the scope of antipredator behaviour, thereby increasing mortality rates (e.g. McNamara & Houston 1987; Anholt & Werner 1995; Sinclair & Arcese 1995) and reducing the strength of TMIIs relative to DMIIs (Luttbeg et al. 2003).

More importantly, some less recognised indirect interactions emerged from our simulations. The model predicted an asymmetric trophic cascade in which the top-down indirect effect of shark risk on resources is mediated by seal avoidance of riskier strata. This spatial response to predation risk concurrently reduces mortality on the more profitable but riskier resource (pollock) while increasing mortality on the safer resource (herring). Similar interactions were first demonstrated experimentally by Schmitz (2003) in an old-field system and have been recently documented at the scale of entire landscapes (Fortin et al. 2005). Expanding on the insight of Schmitz (2003), our model predicts that the intermediate consumer's energy state affects the level of asymmetry of top-down TMIIs. When herring were abundant and pollock scarce, shark risk caused a proportional increase to herring mortality that was 4.3 times greater if IES was good than if it was poor, and a proportional reduction to pollock mortality that was 3.8 greater if IES was good than if it was poor (Figs. 4.3c, 4.5). (Note, however, that when pollock were abundant shark removals released herring from seal predation completely, regardless of IES: Figs. 4.3a,b). Also, when both resource species were abundant, the TMII of sharks on pollock was twice as large if IES was good than if it was poor (Fig. 4.5). Given that scarcity of one resource increased seal use of the alternative resource, in spite of the risks involved (Figs. 4.2, 4.3ab), these dynamics partly arose from the lateral transmission of indirect effects initiated by alternative resources (see Schmitz et al. 2004).

Our model should be relevant to fishery managers for at least two reasons. First, our simulations suggest how fishery removal of large sharks might alter community dynamics;

intermediate consumers no longer need to avoid foraging areas that were previously risky, which alters the rate at which they consume different fish species. Consistent with results from a wide array of experimental systems (Preisser et al. 2005), our model also predicts that indirect effects arising from shark removals will have a much stronger TMII than DMII component. This is not a trivial matter. Prior studies have recognised only the DMII component of shark removals (Shepherd & Myers 2005), and there is rising concern for the global overfishing of large sharks (e.g. Baum et al. 2003; Ward & Myers 2005). Further, the shark bycatch in the Gulf of Alaska (Courtney et al. 2004) is large enough to merit further examination of its potential ecological consequences.

A second message from our simulations is that fisheries may indirectly increase predation rates on intermediate consumers by contributing to resource scarcity and poor energetic states. This conclusion is important because previous studies on resource competition between fisheries and marine mammals (e.g. Trites et al. 1997; Read & Brownstein 2003) have considered direct energetic consequences while ignoring potential indirect effects on predation. This point was first made by Frid et al. (2006), but the present model specifies that, in PWS, herring overfishing might have a stronger indirect effect than pollock overfishing on the hunting success of sharks on seals.

While the latter result suggests that a herring fishery might indirectly benefit sleeper sharks, future models need to address the net effect of bycatch and target fisheries not only on sharks, but on the ecosystem as a whole. Obviously, no model can include all species, but intelligent selection of the most relevant players (e.g. Soulé et al. 2003) should improve approaches to the problem. Further, top predators like sharks are not behaviourally inert, and future work can incorporate game-theoretical approaches that simultaneously predict state-dependent responses of predator to prey and of prey to predator (e.g. Alonzo et al. 2003b). We also acknowledge that population dynamics are multi-faceted. Still needed are demographic analyses using our model's output for life table parameterisation to assess whether phenomena emerging from our simulations translate into strong numerical responses.

Our model illustrates the application of theory on state-dependent behaviour and TMIIs to predictions about indirect fishery effects. Given the complexity and multi-directionality of potential indirect interactions, these theoretical tools can inform management decisions and guide the empirical research needed to improve parameterisation and test predictions.

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Literature cited

Abrams P.A. (1995). Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. *Am. Nat.*, 146, 112-134.

Alonzo S.H., Switzer P.V. & Mangel M. (2003a). An ecosystem-based approach to management: using individual behaviour to predict the indirect effects of Antarctic krill fisheries on penguin foraging. *J. Appl. Ecol.*, 40, 692-702.

Alonzo S.H., Switzer P.V. & Mangel M. (2003b). Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology*, 84, 1598-1607.

Anholt B.R. & Werner E.E. (1995). Interactions between food availability and predation mortality mediated by adaptive behavior. *Ecology*, 76, 2230-2234.

Baum J.K., Myers R.A., Kehler D.G., Worm B., Harley S.J. & Doherty P.A. (2003). Collapse and conservation of shark populations in the northwest Atlantic. *Science*. 299, 389-392.

Bowen W.D., Iverson S.J., Boness D.J. & Oftedal O.T. (2001). Foraging effort, food intake, and lactation performance depend on maternal mass in a small phocid seal., *Funct. Ecol.*, 15, 325-332.

Brown J.S. & Kotler B.P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.*, 7, 999-1014.

Clark C.W. (1994). Antipredator behavior and the asset-protection principle. *Behav. Ecol.*, 5, 159-170.

Clark C.W. & Mangel M. (2000). Dynamic state variable models in ecology. Oxford University Press, New York.

Courtney D.L., Gaichas S., Boldt J., Goldman K. & Tribuzio C. (2004). Sharks in the Gulf of Alaska, Eastern Bering Sea, and Aleutian Islands. *In*: Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 2005. North Pacific Fishery Management Council, 605 W 4th Ave. Suite 306, Anchorage, AK 99501.

Dill L.M., Heithaus M.R. & Walters C. (2003). Behaviorally-mediated indirect interactions in marine communities and their conservation implications. *Ecology*, 84, 1151-1157.

Fortin D., Beyer H.L., Boyce M.S., Smith D.W., Duchesne T. & Mao J.S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320-1330.

Frid A., Baker G.G. & Dill L.M. (2006). Do resource declines increase predation rates on North Pacific harbor seals? A behavior-based plausibility model. *Mar. Ecol. Prog. Ser.*, 311 (in press). (Also Chapter 2 of this dissertation).

Iverson S.J., Frost K.J. & Lowry L.F. (1997). Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.*, 151, 255-271.

Jackson J.B.C. & 18 others (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629-638.

Lima S.L. & Dill L.M. (1990). Behavioural decisions made under the risk of predation. *Can J. Zool.*, 68, 619-640.

Luttbeg B., Rowe L. & Mangel M. (2003). Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. *Ecology*, 84, 1140-1150.

McNamara J.M. & Houston A.I. (1987). Starvation and predation as factors limiting population size. *Ecology*, 68, 1515-1519.

Pauly D., Christensen V., Guénette S., Pitcher T.J., Sumaila U.R., Walters C.J., Watson R. & Zeller D. (2002). Towards sustainability in world fisheries. *Nature*, 418, 689-695.

Preisser E.L., Bolnick D.I. & Benard M.F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501-509.

Read A. & Brownstein C. (2003). Considering other consumers: fisheries, predators, and Atlantic herring in the Gulf of Maine . Conservation Ecology 7, 2. [online] URL: http://www.consecol.org/vol7/iss1/art2.

Schmitz O. (2003). Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol. Lett.*, 6, 156-163.

Schmitz O.J., Krivan V. & Offer O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.*, 7, 153-163.

Scheffer M., Carpenter S.R. & de Young B. (2005). Cascading effects of overfishing marine systems. *Trends Ecol. Evol.*, 20, 579-581.

Shepherd T. & Myers R.A. (2005). Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecol. Lett.*, 8, 1095-1104.

Sinclair A.R.E. & Arcese P. (1995). Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology*, 76, 882-891.

Smith S.E., Au D.W. & Show C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine Freshwater Res.*, 49, 663-678.

Soulé M., Estes J., Berger J. & Martinez del Rio C. (2003). Ecological effectiveness: conservation goals for interactive species. *Cons Biol.*, 17, 1238-1250.

Sweitzer R.A. (1996). Predation or starvation: consequences of foraging decisions by porcupines (*Erethizon dorsatum*). *J. Mammal.*, 77, 1068-1077.

Thomas G.L. & Thorne R.E. (2003). Acoustical-optical assessment of Pacific herring and their predator assemblage in Prince William Sound, Alaska. *Aquat. Living Resour.*, 6, 247-253.

Trites A.W., Christensen, V. & Pauly D. (1997). Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *J. Northw. Atl. Fish. Sci.*, 22, 173-187.

Vollenweider J.J. 2004. Variability in Steller sea lion (*Eumetopias jubatus*) prey quality in southeastern Alaska. M. S. Thesis. University of Alaska, Fairbanks. Fairbanks, Alaska.

Walters C. (2000). Natural selection for predation avoidance tactics: implications for marine population and community dynamics. *Mar. Ecol. Prog. Ser.,* 208, 309-313.

Ward P. & Myers R.A. (2005). Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology*, 86, 835-847.

Werner E.E. & Peacor S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083-1100.

Worm B. & Myers R.A. (2003). Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, 84, 162-173.

Table 4.1: Baseline probabilities of encountering and capturing a resource, $\lambda_{h,d}$, and of being killed by each predator per 20-s time period when $D(x,y,h,t) = h$ (as defined in Frid et al. 2006).

Location $H(t)$	Probability of obtaining a resource $\lambda_{h,d}$		Killer whale predation probability $\mu_{orca}(h,d)$		Sleeper shark predation probability $\mu_{shark}(h,d)$	
	Day	*Night*	*Day*	*Night*	*Day*	*Night*
0	0	0	0	0	0	0
75	0	0	5.00×10^{-9}	3.30×10^{-9}	0	0
1	2.32×10^{-3}	5.12×10^{-3}	3.86×10^{-8}	2.65×10^{-8}	8.79×10^{-9}	6.26×10^{-8}
3	4.20×10^{-3}	5.60×10^{-3}	2.54×10^{-9}	3.35×10^{-10}	2.14×10^{-7}	2.54×10^{-7}
7	8.15×10^{-3}	8.19×10^{-3}	0	0	7.26×10^{-7}	8.36×10^{-7}

If $D(x,y,h,t) \neq h$, then (a) risk while traveling between surface habitats is 50% of that when remaining at the more dangerous endpoint, and (b) risk while diving to and from a given depth is 25% of that while remaining at that depth.

Figure 4.1: Predicted number of dives by seals to each stratum, as influenced by their initial energy state (IES), herring and pollock abundance, and presence or absence of sleeper sharks.

Values are the means of 1000 forward iterations (minus a few mortalities) covering the 23-d simulation period (see Methods).

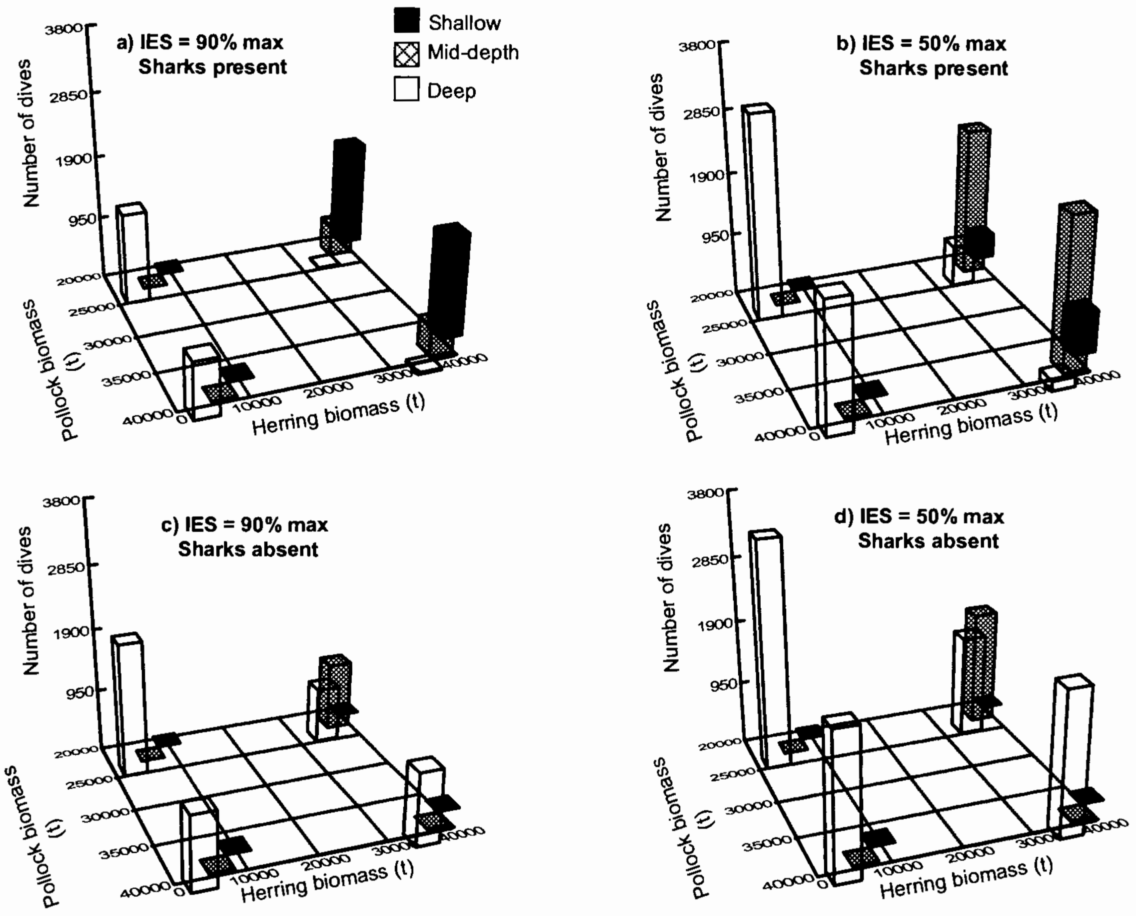


Figure 4.2: Predicted pollock consumption by seals, as influenced by seal initial energy state (IES), herring and pollock abundance, and presence or absence of sleeper sharks.

Values are the means of 1000 forward iterations (minus a few mortalities) covering the 23-d simulation period (see Methods).

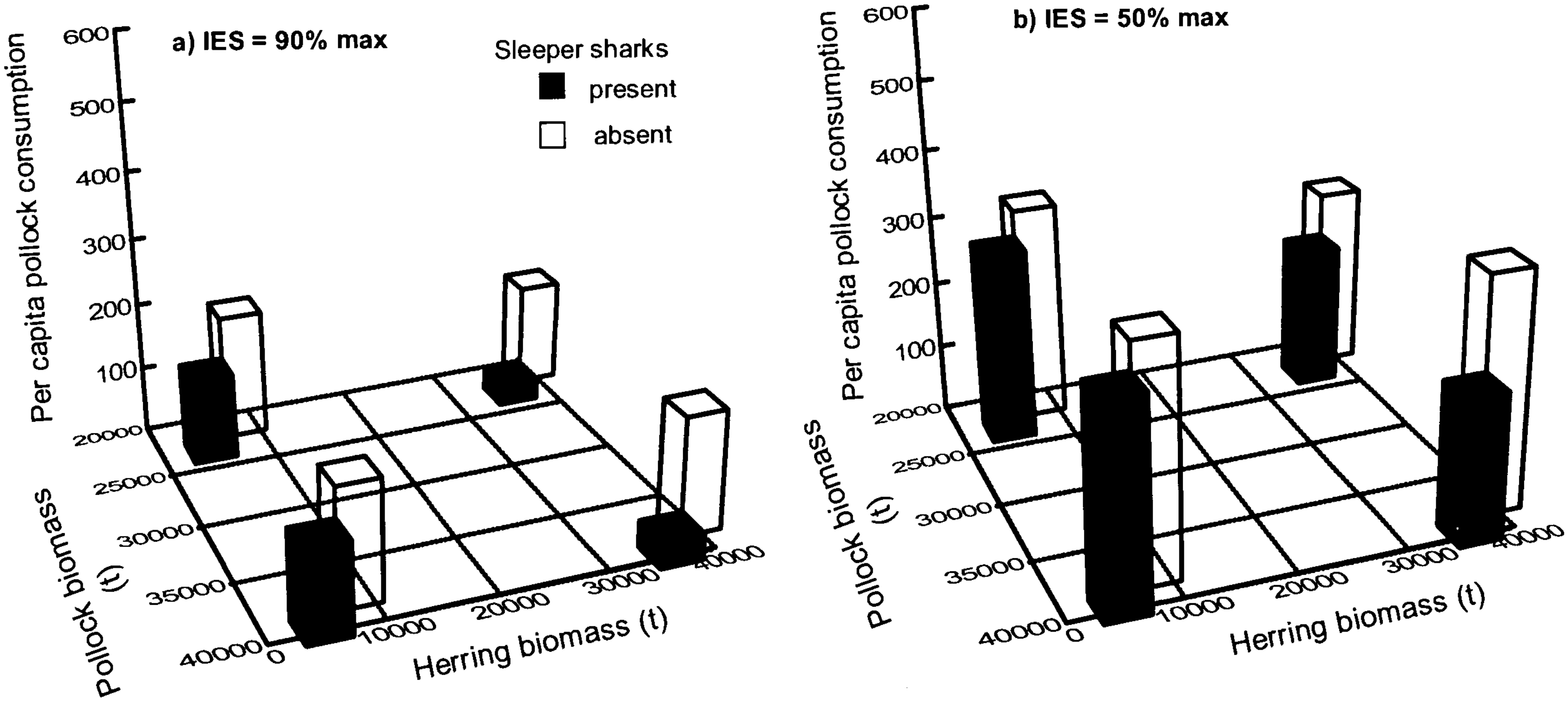


Figure 4.3: Predicted (a, b) herring consumption by seals during abundant herring scenarios and as influenced by other factors, and (c) indirect effect of sharks on herring, as influenced by seal initial energy state (IES) when herring are abundant and pollock scarce.

. The few mortalities caused by killer whales [see Results] are included in the DMII component. Herring consumption values in Figs. 3a,b are the means of 1000 forward iterations (minus a few mortalities) covering the 23-d simulation period (see Methods). In panel c, the few mortalities caused by killer whales (see Results) are included in the DMII component.

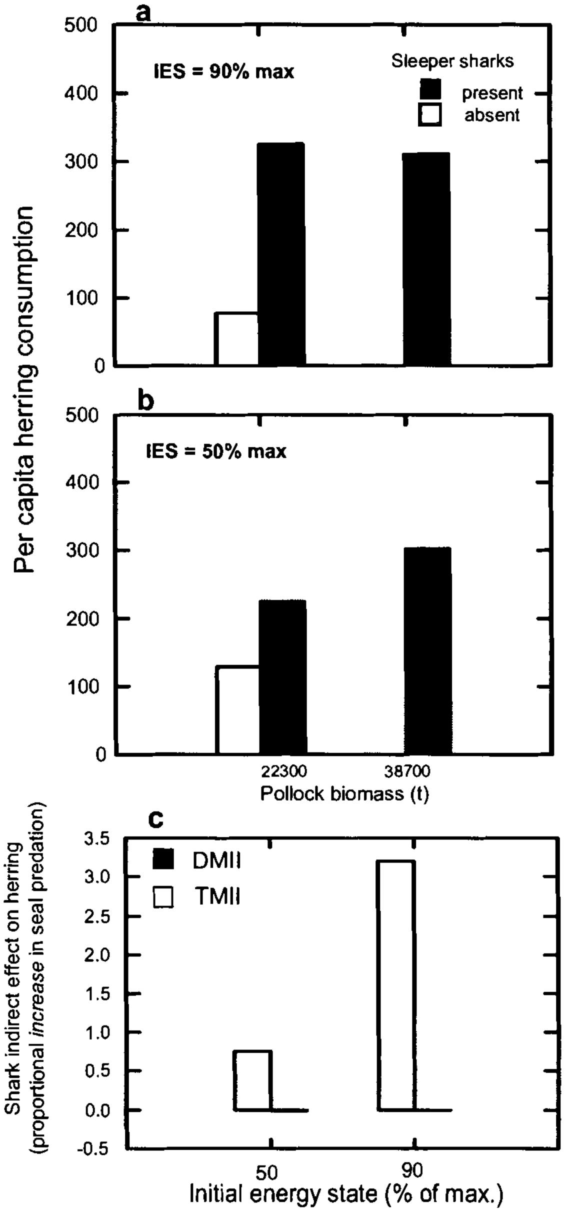


Figure 4.4: Predicted number of events in which sharks preyed on seals at each stratum, as influenced by seal initial energy state (IES) and herring and pollock abundances.

. Values are the number of simulations (out of 1000 per treatment) in which shark predation of seals occurred (see Methods).

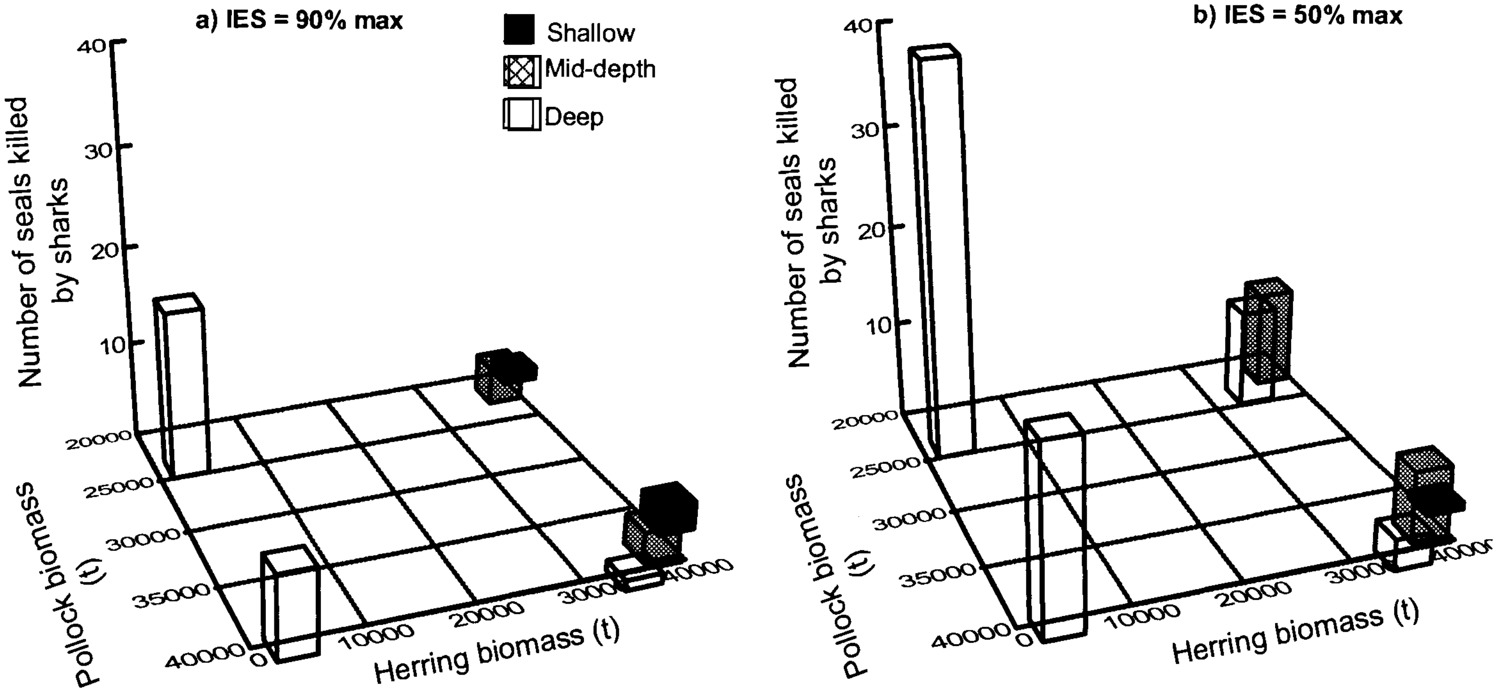
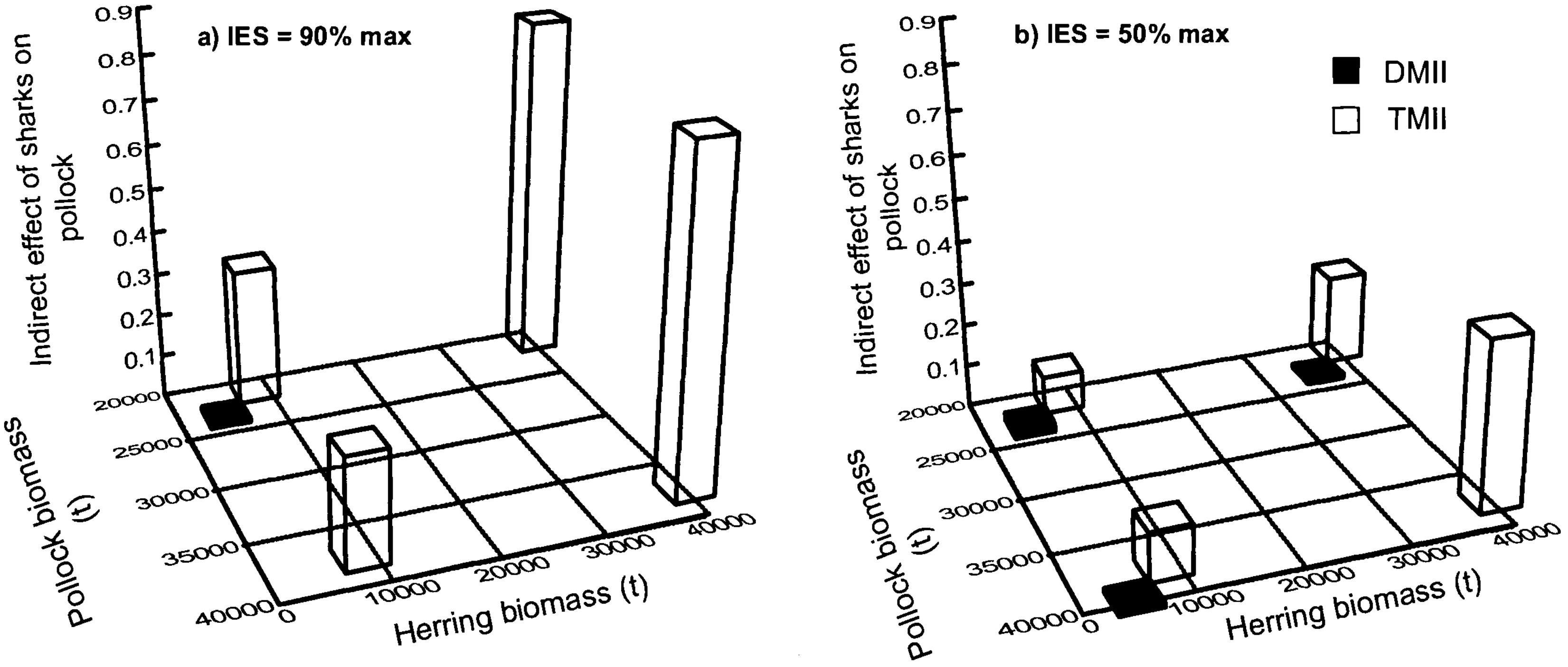


Figure 4.5: Predicted indirect effect of sharks on pollock, as influenced by seal initial energy state (IES), and herring and pollock abundance (see Methods).

The few mortalities caused by killer whales (see Results) are included in the DMII component.



Supplementary material for Chapter 4

This section presents the print version of supplementary material for Chapter 4 that would appear as an electronic appendix in the journal's website (contingent on the manuscript's acceptance for publication).

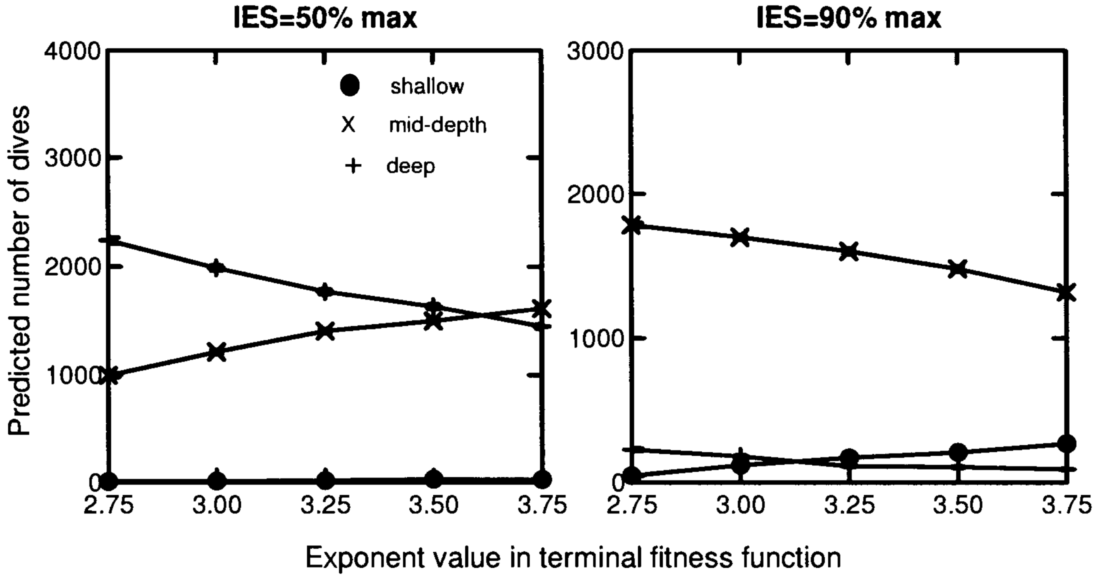
Sensitivity analyses of the terminal fitness function

The terminal fitness function has a power shape with exponent 3.5 (Equation 1). We chose this value because—during preliminary simulations exploring a range of exponents (Fig. 4S.1)—it yielded predictions that were most consistent with behavioural data (Frid et al. in review) for two adult female seals. Due to lack of replication, however, this empirical basis was only a rough guide. Thus, we illustrate how changes to the exponent affect predictions on depth choice. We used this behavioural response as the sensitivity index because it was the main mechanism for transmission of indirect effects.

As Fig. 4S.1 illustrates, predictions changed with the exponent's value, particularly at the extremes of the range of values explored and if initial energy state was poor. So which is the 'best' exponent? Or—for that matter—is an alternative functional shape more appropriate? The first question might be answered by an adequate data set for empirically testing behavioural predictions—something we lack. The second might be answered by year-round monitoring of seal behaviour and body condition, followed by analyses of how these factors influence reproductive success (see Bowen et al. 2001 for an example). Meanwhile—given that predicted changes were moderate when changing the original exponent by ±0.25 (Fig. 4S.1)—the function we used is arguably a reasonable starting point for future research.

Figure S4.1: Predicted depth choice by seals as influenced by initial energy state (IES) and the value of the exponent in Equation 1, the terminal fitness function.

All other parameter values were held constant at baseline values (Table 1). Results are the means (±SE, which are small and barely visible) of 1000 forward simulations per treatment; but simulations in which predation occurred are excluded.



Chapter 5. General conclusions

> ***The choice is not between giving perfect or imperfect advice to managers. It is between giving imperfect advice or none at all.*—R.E. Johannes (1998:245)**

Individual chapters elaborate on the conclusions of each study component and the Epilogue presents my personal view on the philosophical implications of the work. Here I summarise general conclusions as follows:

1) According to simulations, resource scarcity induced by overfishing or other factors may not necessarily starve seals, but instead might increase predation rates suffered by them (Chapters 2 & 4).
2) Theoretically, Pacific sleeper sharks might be the dominant mortality agent for PWS seals during declines of herring or other near-surface fatty fishes (Chapters 3 & 4).
3) According to simulations, seals may be important transmitters of indirect effects of target and bycatch fisheries (Chapter 4).
    a. The bycatch of Pacific sleeper sharks could release seals from predation risk, thereby altering seal use of depth and the rate at which they consume different fish species.
    b. Overfishing of herring may increase seal use of pollock, and vice versa.
4) Long-term empirical studies are needed to test predictions and assumptions and update parameterisation. The modeling approach is flexible, and can incorporate new natural history information as it becomes available.
5) Although the theoretical studies I present here will be most useful when combined with empirical studies, as they stand they suggest that an understanding of trait-mediated indirect interactions (Chapters 2 & 4) is important for optimising fishery and conservation objectives. This applies not only to conservation in PWS, but also to more general concerns regarding the global overfishing of large sharks (e.g. Baum et al. 2003; Ward & Myers 2005) and of resources used by marine mammals and other intermediate consumers (e.g. Read & Brownstein 2003; Frederiksen et al. 2004).
6) In spite of the lack of empirical testing, the models derive from first principles of behavioural ecology and thus can play an important role in the iterative process between empirical analyses, theory, and management decisions (Hilborn & Mangel 1997). Accordingly, this dissertation is a form of Johannes' (1998) 'imperfect advice' to

managers which—by uncovering potential scenarios that would not be elucidated explicitly without theory—is better than no advice at all.

Literature cited

Baum J.K., Myers R.A., Kehler D.G., Worm B., Harley S.J. & Doherty P.A. (2003) Collapse and conservation of shark populations in the northwest Atlantic. Science 299, 389-392

Frederiksen M., Wanless S., Harris M.P., Rothery P. & Wilson L.J. (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes . Journal of Applied Ecology 41, 1129-1139

Johannes R.E. (1998) The case for data-less marine resource management: examples from tropical nearshore finfisheries. Trends in Ecology and Evolution 13, 243-246

Hilborn R. & Mangel M. (1997) The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, NJ.

Read A. & Brownstein C. (2003) Considering other consumers: fisheries, predators, and Atlantic herring in the Gulf of Maine . Conservation Ecology 7, 2. [online] URL: http://www.consecol.org/vol7/iss1/art2

Ward P. & Myers R.A. (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology 86, 835-847

Epilogue

***In our cynical world, where suspicion is a necessity, insisting that something is true is not nearly as powerful as suggesting that something might be true.*-Thomas King (2003:115).**

Since this work transforms me into a 'Doctor of Philosophy', I will take a moment to exercise my newly acquired credentials to philosophise. Perhaps the most notable experience I encountered in pursuit of this research was one of philosophical demarcation between those seeking general principles by working through small scale experimental systems and mathematical theory vs. those battling the myriad practical difficulties of quantifying the natural history of North Pacific pinnipeds. This demarcation is counterproductive and has negative implications for intellectual advancement and conservation.

But before I go any further, let me clarify that not all is black and white. Shades of grey—people that see the benefits of applying theory and results from model systems to large-scale correlative field studies in the ocean—clearly do exist. I happily emphasize that my principal funding agency—the North Pacific Research Board—was open to my framework from the outset. Every time I submitted a progress report I expected to be told to be done with the science fiction and get on with research, but much to my surprise I kept being encouraged. Some anonymous reviewers I encountered—to whom I am greatly indebted—also gave me a hard workout while staying open to my approach—one that was hardly original and which has had a long and venerable history in Ecology, as I will return to in a moment.

Nonetheless, I was astounded by responses to my work—specifically Chapter 2—by some who implicitly presented themselves as 'common sense empiricists'. Here I encountered mindsets that did not allow for the possibility that

Common sense is the set of prejudices acquired before the age of sixteen.—Albert Einstein[1]

and that,

The opposite of a correct statement is a false statement. But the opposite of a profound truth may well be another profound truth.—Niels Bohr[2]

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[1] As quoted in the website of Kent A. Peacock, Associate Professor of Philosophy at the University of Lethbridge http://people.uleth.ca/~kent.peacock/Quotes.html

[2] As quoted in Barrow, J. D. 1999. *Between inner and outer space.* Oxford University Press.

My experience is encapsulated in some quotes from my favourite anonymous reviewers of Chapter 2 (which eventually became Frid et al. 2006):

> *That we need a computer model to suggest theory is ridiculous... This paper is not real research; it is computer games...*—Reviewer 1.
>
> *Basically the model is proposed to show that the hypothesis is plausible; is it necessary to have this model to tell that the proposed hypothesis is plausible? No, what is necessary is real data!*—Reviewer 4.

The first quote speaks for itself. As for the second one, of course we need real data! What kept puzzling me was—if work like mine is such an affront to the 'common sense empiricists'—how come *Is it food?* is the most common question about potential causes of North Pacific pinniped declines? How is it that the only debate has centred on Springer et al.'s (2003) and Williams et al.'s (2004) proposal that it is killer whales, not food, that drives the system? In the end, it may have been Reviewer 7 who tipped the balance in my favour,

> *I find that the authors have taken on board the constructive criticism they have received and that the remaining criticism is indeed philosophical rather than substantial, i.e. the reviewers simply do not like this kind of modelling. This is shallow criticism and modellers rarely make similarly ignorant counter-criticism that experimental research is not worthwhile.*

That the above even had to be said is a sign that the discipline of Ecology has a serious problem—a frequent failure to relate relevant theory to large scale marine systems—which arguably hampers solutions to some conservation problems.

As Chapter 1 elaborates, it is an old idea in Ecology—a widespread yet apparently unknown one to many marine mammal biologists—that we cannot fully understand population dynamics without invoking notions about optimal decision-making and synergistic effects of predators and resources (reviewed in Lima 1998). This is not some obscure concept published in purely mathematical backwater journals, but something that has been in high impact publications (see Chapter 1) presumably read by 'common sense empiricists'.

The model of Chapter 2 that affronted the reviewers was trying to make marine ecosystem managers see—in a mathematically explicit way that removed mechanistic black boxes by considering adaptive variation in behaviour—that it is theoretically plausible for individual seals to maintain a constant rate of food intake through periods of resource scarcity if they invoke compensatory foraging effort, but at the cost of increased predation rates. As detailed in Chapter 2, these behavioural mechanisms, which could not have been elucidated without the modeling approach my colleagues and I used, might explain—at least partly—why the Prince William

Sound harbour seal population has been declining while individuals have maintained good energy stores throughout temporal shifts in resource availability.

Through the school of hard knocks, I eventually learned that the above idea was older than I first thought and merely derivative for those working on general principles. So why was this too radical to be accepted by 'common sense empiricists'? Why do discussions about North Pacific pinniped declines insistently centre on 'bottom up vs. top down forcing' (e.g. National Research Council 2003)? My guess is that the empirical study of large scale systems is logistically so complex that many practitioners are too spent to make theory an inherent part of it. The problem—of course—is two-sided. Those elucidating the general principles do not spend enough time disseminating their ideas to the non-specialists.

Another illuminating experience was the extent to which my intelligent critics attacked parameterisation. I agree that the most reliable available data must be used to parameterise models that we hope to put to practical use. But what happens when no data are available and intuition is all we've got? How should we respond when parameterisation choices regarding complex and experimentally intractable systems reveal "the forest for the trees" but get some details wrong (e.g. the average height of the trees) while providing tractable insight on the main question at hand (e.g. what drives forest structure)?

Interestingly, I experienced these issues even without the benefit of intelligent critics. While Chapter 2 first showed the forest for the trees, Chapter 3— written about two years after the model of Chapter 2 was developed—strongly suggested that the latter got the tree heights wrong. I lost some sleep over this, but not too much because both chapters supported the same general arguments for the determinants of forest structure. Ball (1984:159) summarises the issue:

> *To make progress in understanding all this, we probably need to begin with simplified (oversimplified?) models and ignore the critic's tirade that the real world is more complex. The real world is always more complex, which has the advantage that we shan't run out of work.*

Though said in a very different context, Ball's point is certainly true of the system analysed in these pages; there is no way we can—ethically, logistically and financially—conduct experiments directly on the seal system to examine many model predictions within the time frame in which management decisions are made. (Some predictions you could test if you had a year or two more than I did.)

So where am I getting with all this? To Daniel Pauly's statement: '*The effect of fisheries on marine life is equivalent to that of a large meteor strike on terrestrial life*' (Anonymous 2003: 23), which motivates me to promote an old and unoriginal idea: it *is* okay to combine theory on optimal decision making and the best available field data to address conservation issues in large-scale marine systems. I want the dollars spent and the people that are out there burning fossil fuels to collect more field data to deal—as expediently and rigorously as possible—with the problem of ecological collapse in the oceans (e.g. Pauly et al. 1998; Myers & Worm 2003). Empirical data are undeniably needed to test and refine theory. Such data, however, may require great expense and time to collect in large-scale marine systems. Time may be unaffordable if ecosystem components and the indirect interactions that they are part of are at stake. It is only prudent to use theory on synergistic effects of predators and resources to guide adaptive management decisions (e.g. Alonzo et al. 2003). To paraphrase (subvert?) Johannes (1998), even if models provide imperfect advice, it sure beats having no advice at all. The obvious proviso is that models need to be thought out as well as possible, not over-interpreted, and revised as knowledge advances (Hilborn & Mangel 1997).

The theory available for conceptualising complex interactions that might be relevant to pinniped declines and indirect fishery effects are old, fantastically powerful, and incredibly underutilised by many empiricists striving to understand and conserve marine ecosystems. Almost all of us share the goals of improving knowledge and maintaining healthy oceans. So let's get along and proceed.

Literature cited

Alonzo S.H., Switzer P.V. & Mangel M. (2003) An ecosystem-based approach to management: using individual behaviour to predict the indirect effects of Antarctic krill fisheries on penguin foraging. Journal of Applied Ecology 40, 692-702

Anonymous (2003) Lifelines: Daniel Pauly. Nature 421, 23

Ball J. (1984) Memes as replicators. Ethology and Sociobiology 5, 145-161

Johannes R.E. (1998) The case for data-less marine resource management: examples from tropical nearshore finfisheries. Trends in Ecology and Evolution 13, 243-246

Frid A., Baker G.G. & Dill L.M. (2006) Do resource declines increase predation rates on North Pacific harbor seals? A behavior-based plausibility model. Marine Ecology Progress Series 312, 265-275.

Hilborn R. & Mangel M. (1997) The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, NJ.

King T. (2003) The Truth About Stories. House of Anansi Press, Toronto.

Lima S.L. (1998) Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48, 25-34

Myers R.A. & Worm B. (2003) Rapid worldwide depletion of predatory fish communities. Nature 423, 280-283

National Research Council (2003) Decline of the Steller Sea Lion in Alaskan Waters. National Academy Press, Washington, D.C., USA.

Pauly D., Christensen V., Dalsgaard J., Froese R. & Torres F. Jr. (1998) Fishing down marine food webs. Science 279, 860-863

Springer A.M., Estes J.A., van Vliet G.B., Williams T.M., Doak D.F., Danner E.M., Forney K.A. & Pfister B. (2003) Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Science USA 100, 12223-12228

Williams T.M., Estes J., Doak D.F. & Springer A.M. (2004) Killer appetites: assessing the role of predators in ecological communities. Ecology 85, 3373-3384