



MARINE MAMMAL COMMISSION

Ms. Lynn Barre
Northwest Regional Office
National Marine Fisheries Service
7600 Sand Point Way, NE
Seattle, WA 98115



Dear Ms Barre:

The Marine Mammal Commission has reviewed the National Marine Fisheries Service request for information on southern resident killer whales for use in a 5-year review of the population's status under the Endangered Species Act (75 Fed. Reg. 17377). The announcement requested information on southern resident killer whales that has become available since the stock was listed as endangered in November 2005. The Marine Mammal Commission has not supported any studies on the southern resident killer whale population since that date, but it has supported preparation of two reports on other killer whale populations in the Pacific Northwest that may be useful. Those reports are listed below and copies are enclosed:

Mock, K. J., and J. W. Testa. 2007. An Agent-Based Model of Predator-Prey Relationships between Transient Killer Whales and Other Marine Mammals. Final Report for Marine Mammal Commission Grant #EE0009709.

Wade, P. R. 2005. Population Biology of Killer Whales and their Marine Mammal Prey in the North Pacific. Prepared for the Workshop on the Ecological Role of Killer Whales in the North Pacific Ocean, Marine Mammal Commission, April 19–21, 2005, Seattle, Washington.

If you have questions about information in these reports or any further work the authors may have done on killer whales in the Pacific Northwest, including the southern resident killer whale, please get in touch with them or their organizations directly. If you need information on how to reach them, contact Samantha Simmons, the Marine Mammal Commission's acting Scientific Program Director (ssimmons@mmc.gov; 301-504-0087).

In case they might be helpful, I also enclose copies of the Marine Mammal Commission's comments on the Service's initial proposed listing for the southern resident killer whales (letter dated 22 March 2005); proposed critical habitat designation (letter dated 14 August 2006), the draft recovery plan (letter dated 2 March 2007), and the advance notice of proposed rulemaking to protect southern resident killer whales from effects of vessel traffic, including whale-watching boats (letter dated 15 January 2010). If you have any questions concerning these letters, please let me know.

I hope this information is helpful. We look forward to the results of this review.

Sincerely,

Timothy J. Ragen, Ph.D.
Executive Director

Enclosures

**An Agent-Based Model of Predator-Prey Relationships
Between Transient Killer Whales and
Other Marine Mammals**

by

Kenrick J. Mock and J. Ward Testa

2007

Final Report for Marine Mammal Commission
Grant #EE0009709



Final Report: An Agent-Based Model of Predator-Prey Relationships Between Transient Killer Whales and Other Marine Mammals

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Date: May 31, 2007

Introduction

The role of killer whales (*Orcinus orca*) in the decline of various marine mammal populations in Alaska is controversial and potentially important in their recovery. Springer et al. (2003) hypothesized that declines in harbor seal, Steller sea lion and sea otter populations in Alaska were driven by the over-harvest of great whales in the 1950's – 1970's, leading to a cascade of prey-switching by killer whales from these large prey species to smaller, less desirable prey species. That hypothesis is opposed by many cetacean researchers, who cite inconsistencies in the timing of declines, insufficient killer whale predation on large whales, and the absence of declines in other areas with the same patterns of commercial whaling (DeMaster et al. 2006, Mizroch and Rice 2006, Trites et al. 2007 In Press, Wade et al. 2007 In Press). Whatever the role of commercial whaling, it is known that killer whales prey on threatened marine mammal populations in the North Pacific (e.g., sea otters, *Enhydra lutris*, and Steller sea lions, *Eumetopias jubatus*), and that the magnitude of that predation is at least a plausible factor either in their decline or in their failure to recover (Estes et al. 1998, Heise et al. 2003, Springer et al. 2003).

Estimation of killer whale numbers and the rates of predation on various marine mammal species now have high research priority, but how we interpret these new data is dependent on having an adequate theoretical framework. Thus far, only simplistic, static models of killer whale consumption have been constructed to test the plausibility of killer whale impact on other species (e.g., number of whales \times killing rate of Steller sea lions = estimated impact; Barrett-Lennard pers. comm.). Classical approaches to modeling predator-prey relationships are rooted in the Lotka-Volterra equations. These entail estimation of a "functional response" that defines the number of prey that can be captured and consumed as a function of the densities in which they are encountered, and a "numeric response" of the predator that describes the efficiency with which prey are converted into predators. Data to support a form for either of these functions in transient killer whales and their prey are essentially non-existent. Studies of diet in transient killer whales are accumulating, but are rarely combined with information on prey-specific abundance or availability. Moreover, there is little theoretical development for dynamic predator-prey systems involving a single predator interacting with the number and diversity of prey species hunted by transient killer whales, and less of a framework for understanding how hunting in groups might affect even simple models.

While data to support development of a classical predator-prey model for killer whales are sparse, research on the biology and behavior of killer whales as individuals and groups has greatly accelerated in recent years. This suggests that one approach to theoretical development of predator-prey models might be the implementation of Individual-Based Models (IBMs) that use these recent studies to evaluate properties of

predator-prey relationships that emerge from our knowledge, and uncertainties, about the biology of individuals and social groups of transient killer whales. At this point, we do not know the relationship between killing rate of killer whales and prey densities (functional response), nor the relationship between prey abundance or consumption and population growth in killer whales (numeric response). However, we have some ideas about the energetic requirements of these large predators, the size and structure of hunting groups, and the number and kinds of prey pursued and killed in certain places and times of the year. Following the guidelines proposed by Grimm and Railsback (2005) (Grimm and Railsback 2005) for IBM modeling in ecology, we propose that our knowledge at these levels can be used in an IBM to reproduce the characteristic emergent patterns in group size, prey consumption and demographics of killer whales and their prey, and to then explore how assumptions of such models influence more complex emergent properties such as functional and numeric responses, or how depletion of selected prey resources (e.g., removal of large whales by humans) might change predator-prey dynamics under different assumptions. Perhaps more importantly, such an exercise may also identify critical conceptual elements and critical real-world data essential to understand the most obvious characteristics of the killer whale predator-prey system in the NE Pacific Ocean...e.g., the persistence and basic population dynamics of transient killer whales and their marine mammal prey.

Our objectives here are to reproduce characteristic patterns of demography, social structure and prey consumption observed in transient killer whales by implementing models of life history, energetics, and social associations at the level of individual killer whales, and predator-prey interactions at the level of hunting groups of killer whales. Recent studies of prey consumption and the structure of hunting groups (Baird and Dill 1995, Baird and Dill 1996, Baird and Whitehead 2000) of transient killer whales were used to (1) formulate and parameterize the components of an agent-based model, and (2) make comparisons to the emergent properties of these models as a form of model validation. Detailed information on demography of transient killer whales is unavailable, so we relied on comparisons to the demography of resident killer whales (Olesiuk et al. 1990) to arrive at similar vital rates and age-sex composition, and to patterns characteristic of density-dependent changes in other large mammals (Gaillard et al. 1998, Eberhardt 2002) when confronted with food shortages that have not been reported from studies of transient killer whales thus far. Knowledge of killer whale energetics is sparse (Kriete 1995, Williams et al. 2004), but we patterned our approach after that of Winship et al. (Winship et al. 2002) for Steller sea lions with adjustments for the allometric relationship suggested by Williams et al. (2004). We view this model as a first step toward models that incorporate better formulations of any of these components, and models with explicit movements and spatial structure. As such, it is a work in progress; various upgrades and innovations in implementation are likely to be found when consulting documentation and downloads at our website: <http://www.math.uca.alaska.edu/~orca/>. The model components will be described below, with additional details given on our website and in the Appendix. This report and links to our downloads are available at www.mmc.gov.

Model Components

Individual Transient Killer Whales

Individual killer whale agents in this model possess characteristics allowing for complete age and sex structure of the population to be “sampled” at a user-chosen day or days of the year (usually summer, to correspond with most field research on transient killer whales), as well as mass, reproductive status, and known maternal parent to establish kinship along matriline. Each whale therefore has:

- Unique ID
- Birthdate (and therefore age)
- Sex
- Mass
- Reproductive status (pregnant, lactating)
- Identity of mother (and therefore relationships to siblings and other relatives)
- Group membership with other killer whales while hunting
- Record of past associations with other whales

Baseline Demography

The model assumes underlying rates of birth and death that derive from causes unrelated to rates of prey consumption, as distinct from those that are mediated by the ability to maintain an expected body mass for that age and gender. These can be given as baseline probabilities of becoming pregnant or dying (Fig. 1) that yield maximum rates of growth with unlimited food. Olesiuk et al. (1991) suggest that the maximum rate of growth in resident killer whales is around $\lambda = 1.04$, and default values for this model (Table 1) are drawn from their life table to produce such growth when prey are abundant.

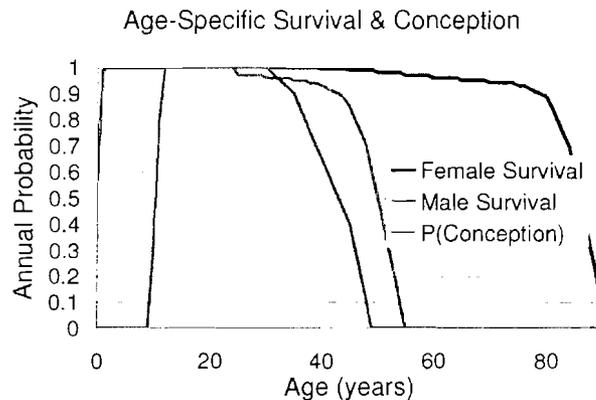


Figure 1. Baseline annual probabilities of survival and conception for a population of transient killer whales unlimited by prey availability.

Body Mass Dynamics

Individual Target Mass (TM)

Mass dynamics are based on a von Bertalanffy (von Bertalanffy 1938) growth curve (Fig. 2) defining a gender and age-specific target mass (Table 1). Asymptotic weights and growth rates were approximated from captive killer whales (Clarke et al. 2000).

Table 1. Parameters and files used in agent-based simulation model and controlled by the user.

Killer Whale Model Parameters			
Model Compartment	Model Component	Parameter or File Name	Default Value
Execution			
	Day of year that model variables are sampled for output	SampleDate	243
	Starting files and conditions for model execution	BatchFileName	batch.txt
	Run Length	BatchRunLength	1
	Demographic Rate File	Fileparameters	popparms.csv
	Starting Population File	FilePopulations	population50.csv
	To control diagnostic messages	ShowDiagnostics	FALSE
	To suppress screen output	BatchMode	TRUE
	Prey populations and vulnerabilities	FilePrey	prey.csv
Demographic	Age-specific annual probabilities of conception	popparms.csv	
	Age-specific annual probabilities of survival	popparms.csv	
	Beginning age & sex structure, relatedness	population50.csv	
	Conception date	MeanDayPregnant	165
	Conception date standard deviation	StDevDayPregnant	35
	Gestation length	DaysPregnancy	510
Mass Dynamics			
	Von Bertalanffy asymptotic female mass	FemaleMaxMass	2400
	Von Bertalanffy growth exponent for females	FemaleVonBert	0.0003
	Von Bertalanffy asymptotic male mass	MaleMaxMass	4000
	Von Bertalanffy growth exponent for males	MaleVonBert	0.0025
	Proportion of target mass needed to maintain pregnancy	AbortionThreshold	0.75
	Mass of calf at birth	BirthMass	182
	Maternal mass gained, then lost at birth as proportion of calf mass	PregnancyTissueMass	0.2
	Proportion of target mass at which all lactation stops	LactationCease	0.75
	Proportion of target mass needed to maintain full milk production	LactationDecrease	0.85
	Extra mass gained during pregnancy to support future lactation	PregnancyWeightGain	0
	Proportion of target mass at which metabolism is reduced	StarveBeginPercent	0.9

	Proportion of target mass needed to avoid death by starvation	StarveEndPercent	0.7
	Fetal Growth	$\text{BirthMass} / (1 + e^{(a \times (t+b))})$	a = -16, b = -0.68
Energetics			
	Efficiency of energy conversion into fetal growth	EnergyToFetusEfficiency	0.2
	Efficiency of energy conversion into tissue growth	EnergyToMassEfficiency	0.6
	Efficiency of energy conversion into milk	EnergyToMilkEfficiency	0.75
	Field Metabolic Rate Constant (kcal)	FMRConstant	405.39
	Field Metabolic Rate Exponent (kcal)	FMRExponent	0.756
	Maximum daily prey consumption as proportion of target mass	GutMassPercent	0.055
	Efficiency of tissue catabolism for maintenance energy	MassToEnergyEfficiency	0.8
	Energy content of milk (kcal/g)	MilkKcalPerGram	3.69
	Digestive efficiency of converting milk into energy	MilkToEnergyEfficiency	0.95
	Digestive efficiency of converting prey tissue into energy	PreyToEnergyEfficiency	0.85
	Caloric value of killer whale mass (kcal/kg)	WhaleKcalPerKg	3408
Group Dynamics			
	Daily probability of meeting another group of killer whales for hunting	ProbGroupsMeet	0.7
	Daily probability that group is unrelated	ProbJoinRandomGroup	0.1
Predator-Prey			
	Prey population parameters (see text)	Prey.csv	User specified
	Predator-prey interaction parameters (see text)	Prey.csv	User specified
	Age killer whales reach full hunting effectiveness	HuntAgeMax	12
	Age juveniles begin to contribute to prey capture	HuntAgeMin	3
	Maintain constant annual prey population size for debugging	UseConstantPreyPopulation	false
	Starting population of juvenile prey	n_0	prey-dependent
	Starting population of non-juvenile "adult" prey	n_adult	prey-dependent
	Day of prey's annual birth pulse	BirthDate	prey-dependent
	Mass of juveniles at birth	n0_startmass	prey-dependent
	Mass of juveniles after 1 year	n0_endmass	prey-dependent
	Mean mass of adult prey	ad_mass	prey-dependent

	Caloric value of juvenile prey	n0_kcals_gram	prey-dependent
	Caloric value of adult prey	ad_kcals_gram	prey-dependent
	Maximum birth rate of adults (>1 year)	BirthMax	prey-dependent
	density dependent birth parameter a in $\exp(-a * N^b)$	Birth_a	prey-dependent
	density dependent birth parameter b in $\exp(-a * N^b)$	Birth_b	prey-dependent
	Maximum juvenile survival	n0Surv_Max	prey-dependent
	density dependent juvenile survival parameter a in $\exp(-a * N^b)$	n0Surv_a	prey-dependent
	density dependent juvenile survival parameter b in $\exp(-a * N^b)$	n0Surv_b	prey-dependent
	maximum adult survival	AdSurv_Max	prey-dependent
	density dependent adult survival parameter a in $\exp(-a * N^b)$	AdSurv_a	prey-dependent
	density dependent adult survival parameter b in $\exp(-a * N^b)$	AdSurv_b	prey-dependent
	probability of encounter between killer whale group and juvenile prey	0_encounter_rate	prey-dependent
	maximum vulnerability of juvenile prey to large killer whale groups	0_VulnMax	prey-dependent
	logistic parameter a for group-dependent vulnerability of juveniles	0_VulnA	prey-dependent
	logistic parameter b for group-dependent vulnerability of juveniles	0_VulnB	prey-dependent
	probability of encounter between killer whale group and adult prey	ad_encounter_rate	prey-dependent
	maximum vulnerability of adults to large killer whale groups	ad_VulnMax	prey-dependent
	logistic parameter a for group-dependent vulnerability of adults	ad_VulnA	prey-dependent
	logistic parameter b for group-dependent vulnerability of adults	ad_VulnB	prey-dependent
	day of year prey become available to killer whales	Available_Start	prey-dependent
	day of year prey become unavailable to killer whales	Available_End	prey-dependent

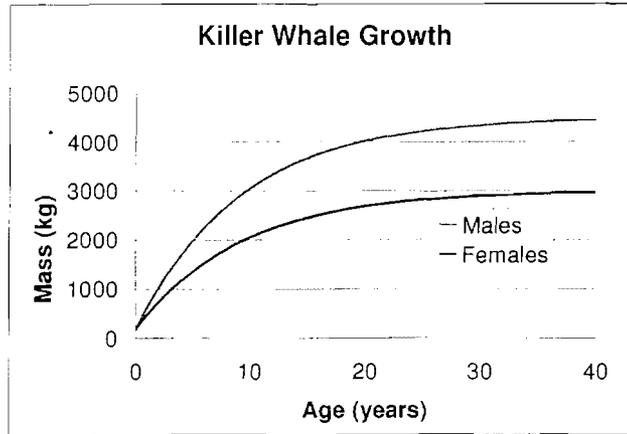


Figure 2. Von Bertalanffy growth model of age-specific target mass for transient killer whales.

Gestation

Growth of the fetus and associated maternal tissues is considered additional to the normal age-specific mass of a female calculated in Fig. 3. A general fetal growth model was used (Winship et al. 2002):

$$\text{Fetal Mass} = (\text{BirthMass}) / (1 + e^{(a \times (t+b))}),$$

where t is proportion of total gestation length (510 days, BirthMass=182, a = -15 and b = -0.68.

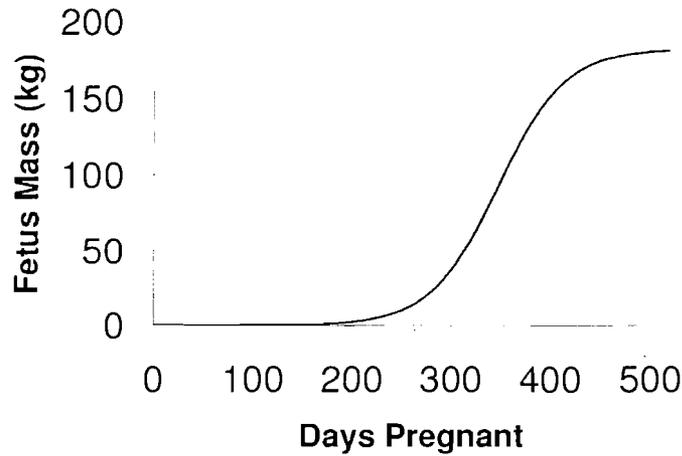


Figure 3. Fetal growth in model killer whales.

It is assumed that the pregnant female supports an additional mass (BirthMassLoss=0.2) proportional to fetus mass for placenta and blood that must be grown during pregnancy, but is lost from her actual mass and Target Mass (TM) at birth.

An additional parameter (*PregnancyTissueMass*) is allowed for mass gain that may occur in preparation for lactation following birth, but it is unknown if killer whales actually store energy for this purpose and the default setting is 0.

Regulation of Body Mass

Body mass is regulated by reducing the amount of food consumed when an individual killer whale approaches or exceeds its age and sex-specific target mass. Our model assumes that a killer whale's maximum daily consumption (*GutMassPercent*) is a fixed proportion of its Target Mass as computed by the von Bertalanffy growth curve. If an animal is underweight, we expect it would attempt to eat an amount near this maximum, and if very fat would eat only as much as it takes to meet its daily metabolic requirements, including those for gestation and lactation demands. We estimated the proportion of a whale's maximum daily consumption that would be required to meet daily metabolic requirements and used the remainder to estimate the remaining gutfill that could be used to fuel body growth. We used a logistic function to describe the proportion of remaining *GutMassPercent* that an animal would attempt to consume (i.e., beyond its metabolic needs) in relation to its actual mass/target body mass (Fig. 4). The mass of food required to meet this satiation level is based on the energy content of a preferred prey (harbor seals), rather than the energetic content of the diet on that particular day.

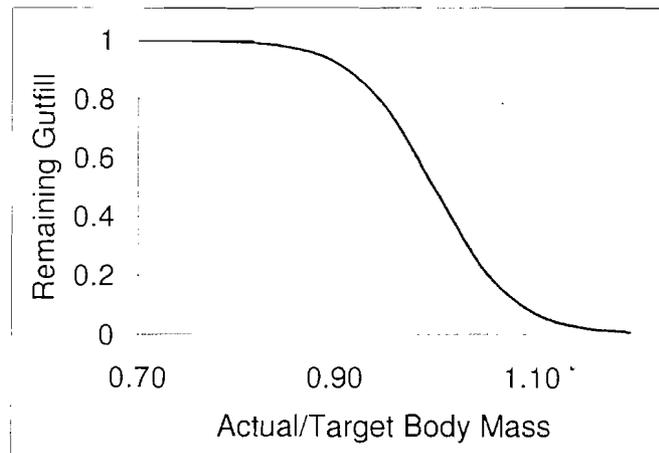


Figure 4. Proportion of remaining stomach volume (beyond that needed for maintenance metabolism) that will satiate an individual killer whale in relation to body condition (actual mass/target mass).

Killer whale calves transition gradually from milk to prey that are killed by its mother or other members of its pod or hunting group, probably within their first year (Heyning 1988). We assumed a logistic model ($a=6.1$, $b=-0.02$) that reduces the proportion of milk in a calf's diet gradually (Fig. 5). The energetic needs of the calf and food volume required for satiation were calculated by the same metabolic formula described for adults, with higher metabolism generated by the exponent of the field metabolic rate (FMR) and by requirements for body growth. The proportion of that target that was milk was used to calculate the energetic demand on the female as part of

her daily energy requirement, and if she could provide it the calf's diet included that energy. The remainder of the desired amount of food for the calf came from prey captured by the calf's hunting group, if available.

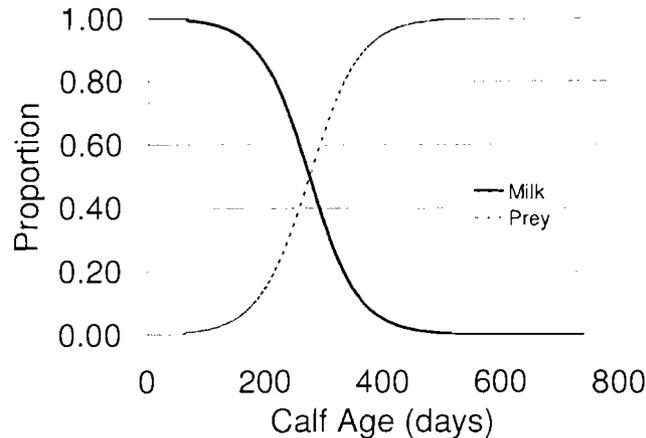


Figure 5. Logistic model of calf diet describing age-related transition from milk to prey.

Thresholds

The growth and consumption models described above produce individuals with variation in realized mass around that predicted from the age and sex specific growth curve, much as we see in natural populations. The model uses realized individual body mass to impose demographic consequences (e.g., births, deaths, aborted pregnancies or termination of lactation) when the killer whale fails to maintain its mass above user-specified thresholds of its target mass (Moen et al. 1997, Moen et al. 1998). The ability to maintain body mass is determined by the energetic requirements of the killer whales and their prey consumption. The parameters controlling thresholds (Table 1) are expressed as proportions of the age specific target mass of a whale, and can be modified at the start of a simulation. Our default assumptions are that whales begin to starve at 0.85 of their target mass and their field metabolic rate declines to half normal in a linear fashion until starvation occurs at 0.7 of their target mass. Similarly, milk production by lactating females is reduced linearly from its normal value to 0 as the female's mass falls from 0.85 to 0.75 of its target mass (Table 1). Tissues associated with gestation (fetus and maternal tissue) are considered part of the female's TM additional to that calculated from her age-specific growth curve (Fig. 2) when setting mass-dependent satiation (but not GutMassPercent) levels.

Energetics

The requirements and efficiencies of converting prey or body mass into energy, and using that energy to support field metabolic rate (FMR) or somatic production (Fig. 5) are similar to those used by Winship et al. (2002) for Steller sea lions (*Eumetopias jubatus*). We make the simplifying assumption of a constant ratio of lean to fat tissue in the body of killer whales with an average energetic value of killer whale tissue of 3.4 kcals/g. Given that the metabolic rate of lean probably exceeds that of fat

tissue, this may underestimate the metabolism of starving whales and overestimate that of well conditioned whales, but this was considered an acceptable cost for simplifying the model, and its effect could be compensated for by adjustments in threshold values. Moreover, actual metabolic rates of starving and well-conditioned whales are unknown.

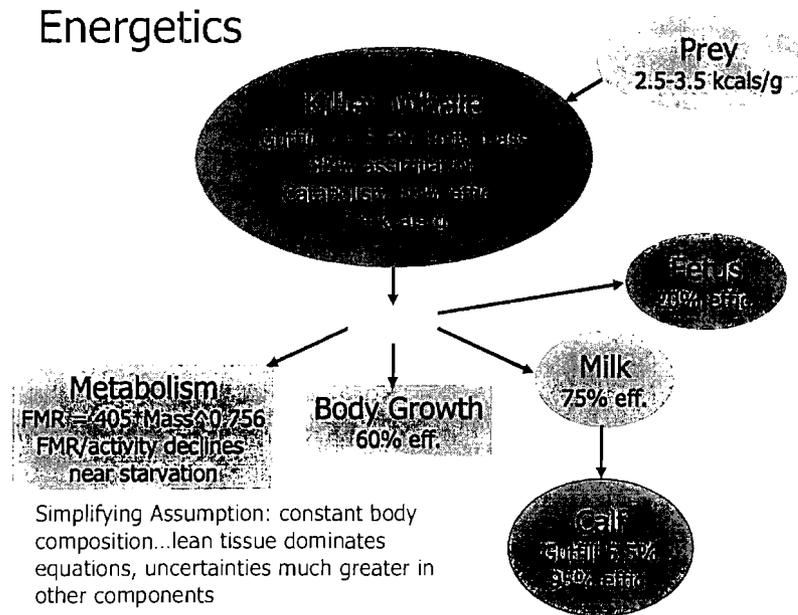


Figure 6. Energetic model by which prey are converted into energy for metabolism, body growth and reproduction of individual killer whales.

The energetics of transient killer whales are based on the estimates of field metabolic rate (FMR) for delphinids (Williams et al. 2005):

$$FMR = 405.39 \times M^{0.756} \text{ kcal/day,}$$

where M = mass in kg. Metabolic and catabolic conversion efficiencies are similar to those suggested by Winship et al. (2002: Fig. 6 & Table 1), though few are based on killer whale studies and many are poorly known or unknown in any marine mammal. The requirements for fetal growth and lactation, including the efficiencies in Fig. 6, are added to the female's FMR when determining the daily energetic maintenance requirements. The higher mass-specific energy generally needed by juveniles (Winship et al. 2002) is accounted for by explicitly modeling somatic growth and by the allometric parameterization of FMR (Williams et al. 2005).

Group Dynamics

We modeled the self-formation of groups based upon rules for aggregation and dispersal to optimize a fitness function that explores the tradeoff between individual and group optimality (Aviles et al. 2002, Parrish et al. 2002). Because there is no spatial component that could be used to generate "encounters" between groups, these are

generated probabilistically, with weighting toward groups that have a history of associations, such as near relatives. Our model allows approximate optimization of group size by maximizing the expected amount of prey each individual can expect to eat in a group while incorporating the effect of familial bonds that constrain the possible choices of hunting partners.

The Maternal Unit

Our model for social aggregation into hunting groups is based primarily on the mother-calf bond, which probably persists for female calves until they begin to reproduce and nearly indefinitely for male offspring unless an older brother is already present (Baird and Whitehead 2000). Dispersal of females occurs with the birth of their first calf (see demographics for age of first reproduction). For males in groups with an older male sibling already resident, dispersal occurs at sexual maturity, which is currently set at 12.

Histories of Association

Each model killer whale maintains a “memory” of its past associations with all other killer whales. It is this history that determines the probability of associating with a whale that is not its mother in the future, rather than relatedness *per se*. The effect is that siblings will tend to associate with their mother and with other siblings even after dispersal, but that those associations will be weaker with larger discrepancies in age.

The association memory is implemented by incrementing counters for all whales in a group during the daily time step. For example, consider two groups of whales shown below. Group 1 consists of two whales with ID’s #1 and #2. Group 2 consists of one whale with ID #3. In group 1, whale #1 and whale #2 have been in the same group for 150 time steps. Whale #1 and whale #3 were previously in the same group for 20 time steps, although both whales are currently in different groups.

Group 1		Group 2	
Whale ID	Counters	Whale ID	Counters
1	3→20, 2→150	3	1→ 20
2	1→150		

If whale #1 has a newborn calf then in the next time step a counter for the calf will be added for all other whales in the group. Additionally, the counters are incremented for all whales in the group. This is shown below where the newborn is whale #4.

Group 1	
Whale ID	Counters
1	3→20, 2→151, 4→1
2	1→151, 4→1
4	1→1, 2→1

If the calf is in the same exact group the next time step then those counters will be incremented to 2. If at some point in the future a new whale joins the calf’s group then a

similar suite of new counters will be created for that whale that are initialized to 1. When a whale dies the counters are removed. In this manner, each whale maintains a count of how frequently it has associated with other whales, which forms the basis from which whales can organize into hunting groups. A majority of these associations will be due to familial relationships.

Hunting Groups

The grouping behavior of the whales affects vulnerability of prey and ability to hunt certain types of prey. Field research indicates that 3 whales may be the optimal group size for medium-sized mammals like harbor seals or harbor porpoises, while larger groups may be more effective for hunting gray whale calves (Baird and Dill 1996). Association of maternal groups with more extended family members is sometimes observed when transients are hunting, and is likely related to the effectiveness of larger groups for certain types of prey, such as whales or large pinnipeds. We assume that there is an optimum group size for hunting each type of prey available to killer whales (described in section on Predator-prey Interactions), and that the optimum group size at any time depends on the numbers of each prey type available.

We have implemented a model for groupings larger than the basic family unit by allowing smaller groups to combine together. As modeled here, the probability of a group of whales interacting with a different group each day is controlled by two stochastic variables chosen by the user: *ProbGroupsMeet* for the probability that a group of whales will meet another group of whales during the time step, and *ProbJoinRandomGroup* for the probability that the group encountered is an arbitrary group of whales that may or may not have been associated together in the past. A uniform random number generator is used to generate these encounters. The number is generated per group, so it is possible for some groups to join and others to maintain their existing group structure during one time step. Note that *ProbGroupsMeet* is applied before *ProbJoinRandomGroup*. Only after it is determined that groups will meet is the decision made whether the group will be arbitrary or based on association histories.

If two groups are meeting based on association histories then this group is chosen randomly with a weight proportional to the number of past associations of all group members. An example is shown in Figure 7. Here we are trying to determine if group 3 should meet with group 1 or group 2. Whales from group 3 have interacted a total of 60 times with whales from group 1 (whale #4 twenty times with whale #1, whale #4 ten times with whale #2, and whale #5 thirty times with whale #2). Similarly, the whales from group 3 have associated a total of 50 times with whales from group 2. As a result, group 3 will meet group 1 with probability (60/110) and it will meet group 2 with probability (50/110).

Group 1		Group 2	
Whale ID	Counters	Whale ID	Counters
1	3 →30, 2 →150, 4 →20	3	1 → 30, 4 →20, 5 →50
2	1→150, 4→10, 5→30		

Group 3	
Whale ID	Counters
4	1→ 20, 2→10, 3→20, 5→100
5	2→ 30, 3→50,4→100

Weight(Group 3, Group 1) = (20 + 10 + 30) = 60
 Weight(Group 3, Group 2) = (20 + 30) = 50
 P(Group 3, Group 1) = 60 / (60 + 50) = 55%
 P(Group 3, Group 2) = 50 / (60 + 50) = 45%

Figure 7. Determining probabilities for group encounters.

More formally, we compute the probability $P(g_x, g_y)$ of group g_x encountering group g_y where whale w_i refers to a whale within a group we use:

$$Weight(g_x, g_y) = \sum_{w_x \in g_x} \sum_{w_y \in g_y} NumAssociations(w_x, w_y)$$

$$P(g_x, g_y) = \frac{Weight(g_x, g_y)}{\sum_{g_i \in AllGroups - g_x} Weight(g_x, g_i)}$$

Two exceptions to these calculations are groups with mature males that have left their mother's group due to an older sibling or females that have left their mother's group due to the birth of a calf. The dispersal rules prevent these whales from joining their mother's group and in these cases the mother's group is removed from the calculations.

When two groups meet they do not automatically join together. Only after two groups of whales have been selected that satisfy the encounter conditions do we evaluate whether or not the two groups will join together. Larger groups can more effectively hunt larger prey, but captured prey must now be shared among all group members. To optimize these competing factors the model uses the larger of the two groups to determine the outcome by computing the expected amount of food per individual based on the vulnerability of the prey as a function of group size (see *Group-size Dependent Prey Vulnerability* below). The list of prey used in this calculation is the actual prey that the group has encountered in the simulation the previous day, as opposed to the true number of prey that exists globally in the simulation. If this "energy" value is larger in

the combined group than the original group then the two groups join together. Otherwise, no join occurs even if the smaller group might experience a larger energy gain by joining the larger group. This amounts to an assumption of optimal foraging for the larger group, with constraints imposed by the size of the groups interacting (e.g., 2 groups of 3 can only form a group of 6, or remain separate on the day of their encounter).

In addition to accretion a group will also consider whether or not it is advantageous to split into sub-groups on a daily basis. In this operation the largest sub-group (what was once an original group that joined to form a larger group) computes whether the energy value will be optimized by remaining in the larger group or by splitting into its own group and selects the optimal choice. Conditions that may lead to this scenario include the death of whale(s), a change in the prey encountered, or a change in the group's composition based on the rules described in the section on the Maternal Unit.

Predator-prey interactions

Density-dependent Prey Populations

Models of the prey populations were constructed to be as simple as possible while incorporating features considered essential, both from the standpoint of allowing different vulnerability of juveniles and adults, and of incorporating realistic potential for density-dependent population productivity. We considered the following elements to be essential to our prey populations:

- Density-dependent growth rates of marine mammals is non-linear, with maximum productivity declining rapidly near equilibrium (Fowler 1981, Eberhardt and Siniff 1977, Eberhardt 2002).
- The magnitude of density-dependent changes is likely to be greatest in juvenile survival followed by adult reproduction, and be least in adult survival (Gaillard et al. 1998, Eberhardt 2002).
- Many prey species, including whales and large pinnipeds, are more vulnerable to predation by killer whales in their first year of life than as older animals (Heise et al. 2003, Wade et al. 2007 In Press)).

All prey populations were modeled as 2 age-classes: "age 0 years" and "adults", with 3 density-dependent (DD) vital rates: a survival rate for each age class and per capita birth rate for the adult class. A Ricker function with 2 parameters (a & b) was used for all 3 rates as a function of total prey population size, N:

$$\text{Rate} = \text{Max Rate} \times \exp(-a * N^b).$$

All parameters in the model are defined at the annual rate, so that difference equation models on a 1 year time step could be used to generate plausible values and validate outputs; the 365th root of the calculated survival was used to model daily survival proportions while the birth rate was applied on the species-specific birthing day annually. Maximum survival and birth rates were chosen to produce maximum population growth rates (λ) typical of particular species and life histories (e.g., ~1.12 for pinnipeds and small cetaceans, 1.08 observed of humpback whales) with adjustments to compensate for the fact that full age-sex structures were not being used (e.g., less than observed adult birth rates to account for pre-reproductive ages being included in the "adult" model class). Similarly, density dependent parameters were chosen to produce the general pattern of

maximum productivity at 70-75% of equilibrium, and the greatest magnitude of changes in juvenile survival, birth rates and adult survival, in that order (Fig. 8). All the parameters, and prey populations used in the model are user-controlled, and developed in an interactive spreadsheet (PreyWorksheets.xls available in download package online). Default values for a complex prey-field were derived to be consistent with published accounts of 11 prey populations important to the stock of transient killer whales known to inhabit the coastline from California to SE Alaska (Appendix). However, most simulations to date were conducted using a single, or few prey species with parameters generating much larger populations of prey in order to compensate for the absence of those alternative prey populations. These simpler models were used to assess whether the model was producing realistic population-level behavior of killer whales under conditions of abundant or limiting prey, and to compare the dynamics to classical models of a single predator and single prey species. Changes in prey vital rates and density dependence to simulate "regime shifts", or extraneous "removals" of known numbers to simulate human harvest can be input as options during execution.

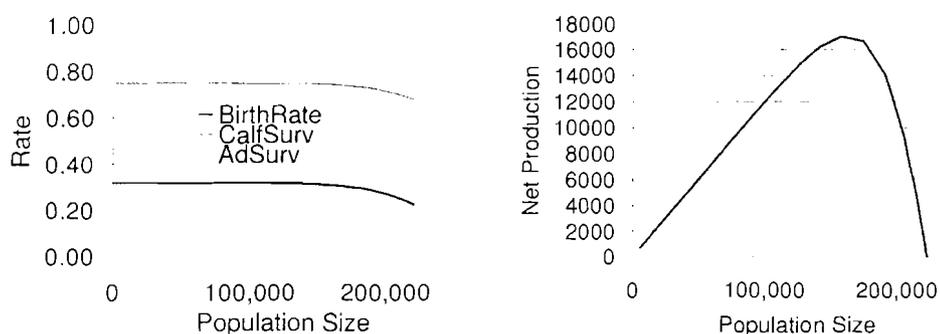


Figure 8. General density-dependent properties of vital rates (left) and net productivity (right) of model prey populations.

Group-size Dependent Prey Vulnerability

While relatively little is known about vulnerability of prey with age, greater vulnerability of juveniles is a common feature of predator-prey interactions, particularly as the size of the prey species relative to that of the predator becomes larger. In the case of transient killer whales, vulnerability of large whales is largely limited to calves (Wade et al. 2007 In Press), and there also appears to be greater vulnerability of Steller sea lion pups in comparison to older animals (Heise et al 2003). This was considered an essential element to the prey model, while finer distinctions of sex and age were ignored. We also assumed that larger groups of killer whales would be more effective at killing prey, especially large prey, but the effect of sharing the prey in larger groups would produce an optimum group size for each prey type that produced the greatest amount of prey biomass per individual in the group (Baird and Whitehead 2000).

We implemented a model of killing rate similar to a classical formulation of attack rate \times number of prey, with attack rate partitioned into an encounter rate (e) defined as the probability that a group of killer whales would encounter a particular individual prey, and vulnerability (v) equal to the probability of being killed by the group once encountered (i.e., expected kills per day equals $e \times v \times$ number of prey available).

To make this dependent on group size (x), we used a simple logistic function (e.g., Fig. 9) with a user-defined maximum vulnerability and logistic parameters a and b :

$$v = v_{\max} * \exp(a + b * x) / (1 + \exp(a + b * x))$$

The logistic function was chosen for its generality and congruence with potential analyses of field data. Calf and juvenile killer whales are not as effective hunters as adults, so group size for this purpose was considered to be “adult equivalents”, where juveniles began a linear increase in hunting effectiveness at age 3 (HuntAgeMin equivalent to 0 adults) and were considered fully effective hunters at age 12 (HuntAgeMax equivalent to a single adult). Thus, a group of killer whales comprised of animals aged 1.5, 7.5, 24.5, 36.5 and 60.5 years would have an effective group size of 3.5 for hunting purposes. We also linearly reduced the effectiveness of whales that become malnourished from full effectiveness to 0 effectiveness as metabolic rate declines (BeginStarve = 0.85 to EndStarve = 0.7, see section on Energetics). Thus, a group of two adult killer whales where one is at 0.95 of target mass and the other is at 0.75 of target mass would have an effective group size of 1.33. In this way each age class of each prey species could be assigned plausible maximum vulnerabilities when encountered by a large group of killer whales, and differences in vulnerability with hunting-group size could be modeled with a simple form that produces optimal predictions of individual gain per kill. Fig. 9 shows this relationship for a small prey species such as harbor seals, while Fig. 10 shows a similar relationship for a large species class, such as gray whale calves. When adjusted for the size and energy value of particular prey and summed over all prey types available, the expected optimum group size for any suite of prey abundances can be calculated (and employed in choosing group sizes, as described earlier). This assumes no foraging specialization by killer whale groups, which we consider a reasonable default assumption that might be studied later.

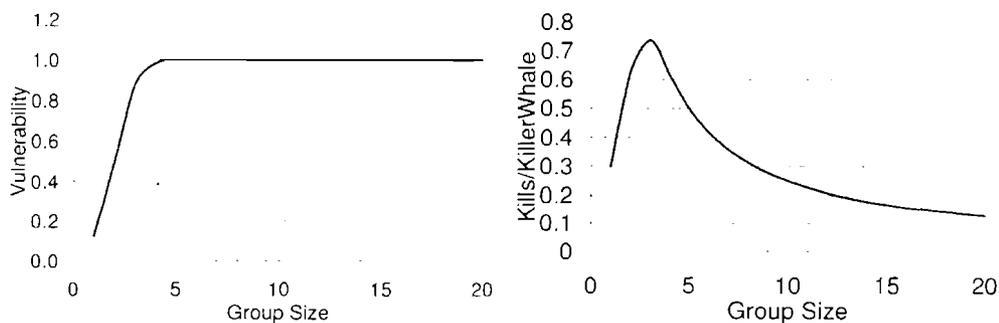


Figure 9. The left graph shows the modeled relationship between the vulnerability (probability of being killed given an encounter with a group of transient killer whales) of a vulnerable prey type (e.g., harbor seals) and the effective size (adult equivalents) of the hunting group, while the right graph gives the resulting expectations of kills available as food per killer whale from each encounter.

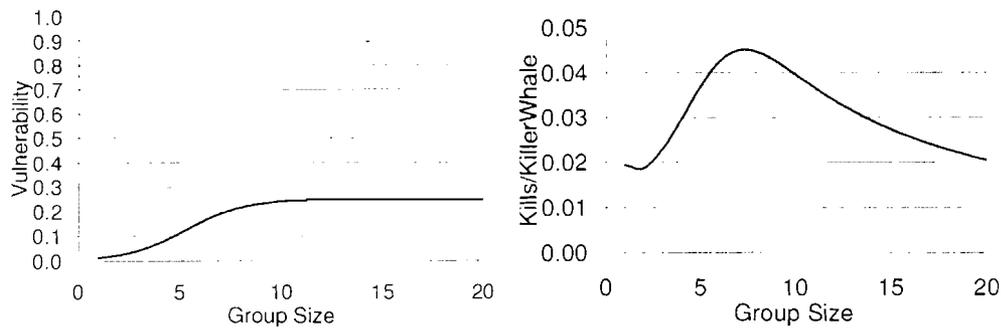


Figure 10. The left graph shows the modeled relationship between the vulnerability (probability of being killed given an encounter with a group of transient killer whales) of a difficult-to-kill prey species (e.g., gray whale) and the effective size (adult equivalents) of the hunting group, while the right graph shows the resulting expectations of kills available as food per killer whale from each encounter.

Prey Capture

In executing a daily time step of foraging for a killer whale group, the model steps through all prey types to determine the number of prey encountered of each type, drawing random variables from a Poisson distribution with expectations equal to $e_i \times \text{number } (n_i)$ of prey type i . Once all prey encounters are identified, their order is randomized and each is subjected to a random trial to see if the encountered prey is killed by comparing its vulnerability (e.g., Figs. 9 & 10) to a uniform random variable. The group kills prey in the list until the list is exhausted or enough prey are consumed to sate all the individuals in the group (Fig. 3). The kills are shared proportional to the mass required for each killer whale in the group to satisfy its maintenance metabolic requirements and reach satiation.

Model Execution and Output

The model is executed in daily time steps as illustrated in Fig. 11. At the beginning of each simulated day whales hunt and feed. Once all feeding has occurred, metabolism and growth algorithms are applied, and demographic actions are taken. Finally, any changes in group membership for the following day are determined. Various flags are set to mark annually occurring events such as birthing and sampling for model output (Table 1). Running annual totals are kept of births, deaths, and prey consumption by killer whale age and sex class. Graphical output is provided during interactive computer runs, but practical running times are obtained only in batch mode, where pre-programmed commands control program variables and output files that are analyzed after execution is complete.

The model is written in Repast, a Java-based software package for agent-based modeling (North et al. 2006). Output data are compiled on user specified sampling dates and written to spreadsheet files for post-processing in spreadsheet or statistical software (e.g., Microsoft Excel). Instructions for downloading the software and running the model are at <http://www.math.uaa.alaska.edu/~orca/>.

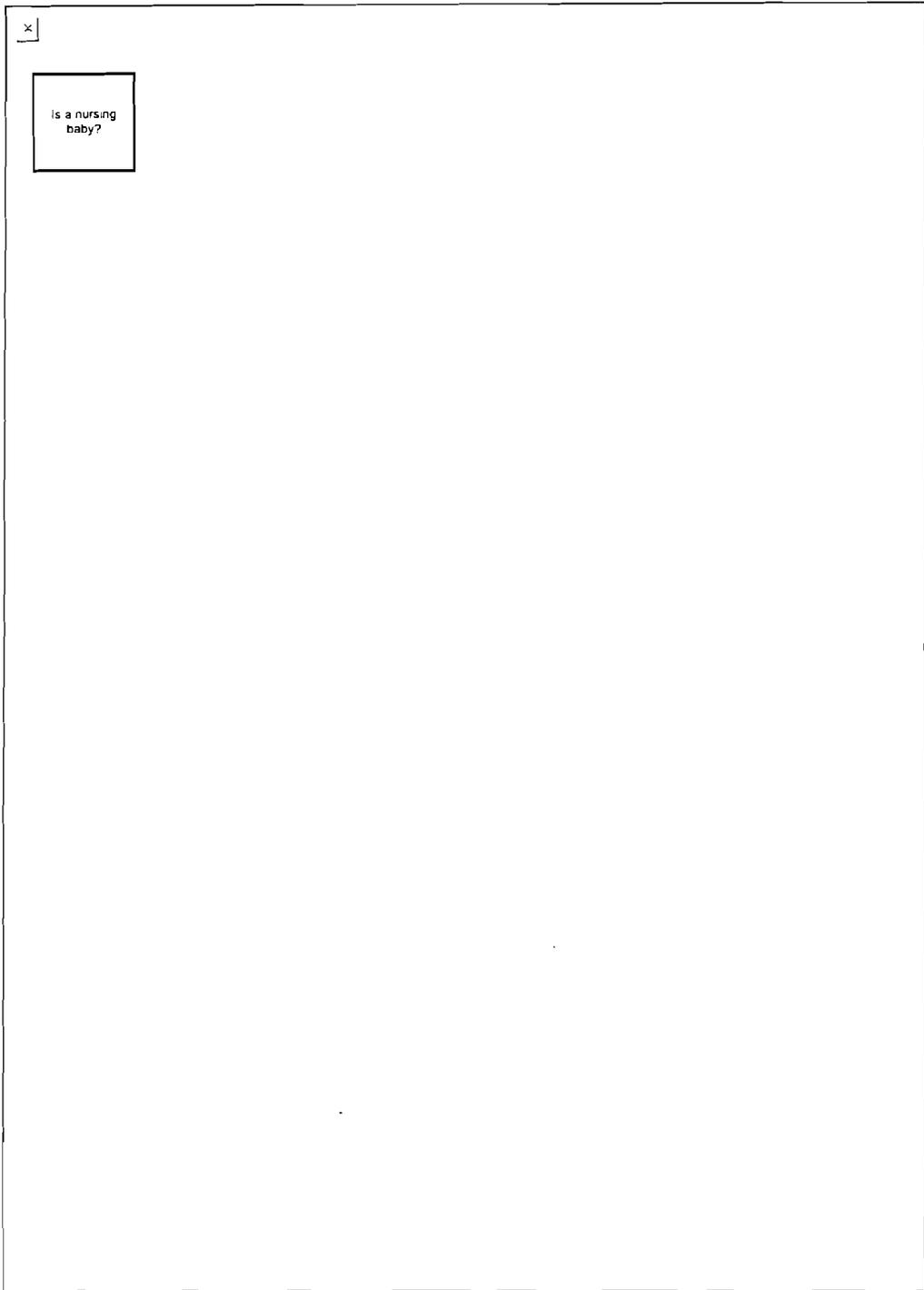


Figure 11. Model execution of daily routines is illustrated with a flow diagram. Object shapes denote actions taken at either group, individual or model level.

Sensitivity to Input Parameters

The conditions for these simulations were set to the simplest scenario of a single prey population (harbor seals) sufficiently large to support an average population of 200-300 killer whales (to minimize the effects of demographic stochasticity). Williams et al. (2004) estimated that the average food requirements for a population of transient killer whales would be equivalent to roughly a harbor seal/day/killer whale. If we assume that the maximum net productivity of harbor seals occurs at 70% of equilibrium (K), and that the growth rate is roughly 80% of maximum ($\lambda \sim 1.10$), a population of 200 transient killer whales would require at least 73,000 harbor seals/year. For this to be sustainable with the assumed vital rates, a harbor seal population of at least 730,000 and a density-dependent equilibrium in excess of 1,000,000 would be required. Our single-prey test simulations therefore used a population of harbor seals that would equilibrate at $\sim 1,400,000$ in the absence of predation, with vital rates, density dependence, and predator encounter and vulnerability given in `prey1.csv` (in download package online). The model was allowed to run until both predators and prey experienced periods of growth, decline and relative stability. Sensitivity of relevant model output variables to variation across plausible ranges of parameters was evaluated graphically while holding other parameters constant during multiple runs of 1000 years.

In general, the parameter space that allowed both species to persist was narrow. Many of the parameters chosen for inclusion in the model have values or likely ranges that can be supported with field data and do not generally lead to extinction of the predators. However, some parameters are poorly known, and the plausible ranges may greatly exceed the narrow parameter space that allows both species to persist. In classical predator-prey models the attack rate, modeled here as the product of encounter rate and vulnerability, greatly affects the persistence of a single predator-single prey system (Metzgar and Boyd 1988); low attack rates lead to steady decline and extinction of predators while high rates lead to oscillations and the extinction of one or both species. Attack rates of transient killer whales in SE Alaska (Dahlheim and White, Pers. comm.) suggest that encounter rates (probability that a particular group of killer whales would encounter a single individual prey) might be on the order of 10^{-4} to 10^{-6} . For models with a single super-abundant prey, encounter rates producing relatively stable killer whale populations comprised a narrow range (Fig. 12) within the range plausible. For a set of fixed parameters, encounter rates of $<3.00\text{E-}06$ led to rapid extinction of the killer whales, while increasing the encounter rate above this threshold lead to increasing numbers of killer whales, but eventually also to oscillatory behavior above $4.00\text{E-}06$ (Fig. 12). The actual values needed to produce this progression varied with the choice of other values for parameters (e.g., greater energetic efficiency could lower the values of encounter rates needed for stability, or lower energetic efficiency could lead to extinctions), but a narrow range of encounter rates needed for relatively stable numbers of killer whales was characteristic of all simulations. The low number of reproductive killer whales and simplistic assumptions about random encounters undoubtedly contribute to model instability as encounter rates increase. Nevertheless, as a first approximation of how killer whales might interact with prey, we proceeded by

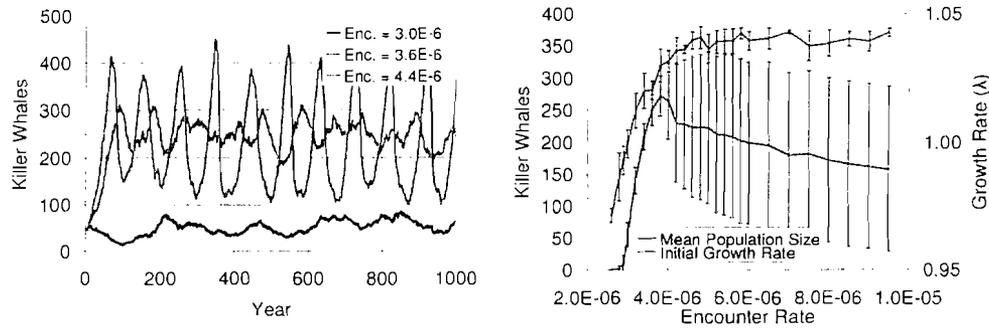


Figure 12. Three trajectories are shown (left) for different assumed encounter rates between hunting groups of killer whales and individual prey. The initial (maximum) growth rate of the killer whale population in the first 50 years of simulations, and the mean abundance of killer whales (SD in error bars) after 200 years of 5, 1000-year simulations in relation to encounter rates (right) illustrates the effects of increasing predatory efficiency on basic killer whale population dynamics.

determining a range of encounter rates that allowed persistence and relative stability of killer whales as a necessary precondition for assessing other model parameters.

Many of the remaining parameters in the model are expected to have redundant effects on model performance. For example, energetic efficiencies are part of a chain of conversions, any one of which could be used to lower or raise the overall efficiency with which prey are converted into predator biomass. Similarly, several thresholds set for killer whale mass relative to target mass influence birth and age-specific survival rates, and are therefore likely to affect population recruitment, survival and growth. Our implementation includes some redundancy in function in relation to the objective of simulating predator-prey dynamics. We therefore tested sensitivity of certain model output variables in relation to plausible variation in model parameters, but ignored parameters whose action duplicated the effect of others (e.g., energetic efficiency of milk production, milk energy content, and calf digestive efficiency all have similar effects on energy transfer from mother to calf) or obviously had small influence. (e.g., birth mass alters both fetal and calf growth trajectories, but with little expected influence on mortality, so it was ignored). We focused on (1) thresholds of body mass (as a proportion of desired target mass) for abortion, cessation of lactation, and starvation, (2) gut size as a constraint to daily consumption and (3) energetic efficiencies of producing milk and digesting prey. Each of the parameters was evaluated graphically for its effect on mean number and standard deviation of killer whales after 200 years of growth from identical starting conditions in simulations of 1000 years for each value of the parameter. Where a likely demographic mechanism for the effect of a changing parameter value was apparent (e.g., decreasing efficiency of milk production is expected to decrease neonate survival) the mean value of the appropriate vital rate was also graphed against the value of the parameter. The results are summarized in Figure 13 for 6 parameters.

The threshold body mass (as a proportion of an individual's age-specific target mass) that caused a pregnancy to be aborted was a sensitive parameter, causing little effect when set near the starvation threshold (0.7-0.72), but it led to a lowered calving

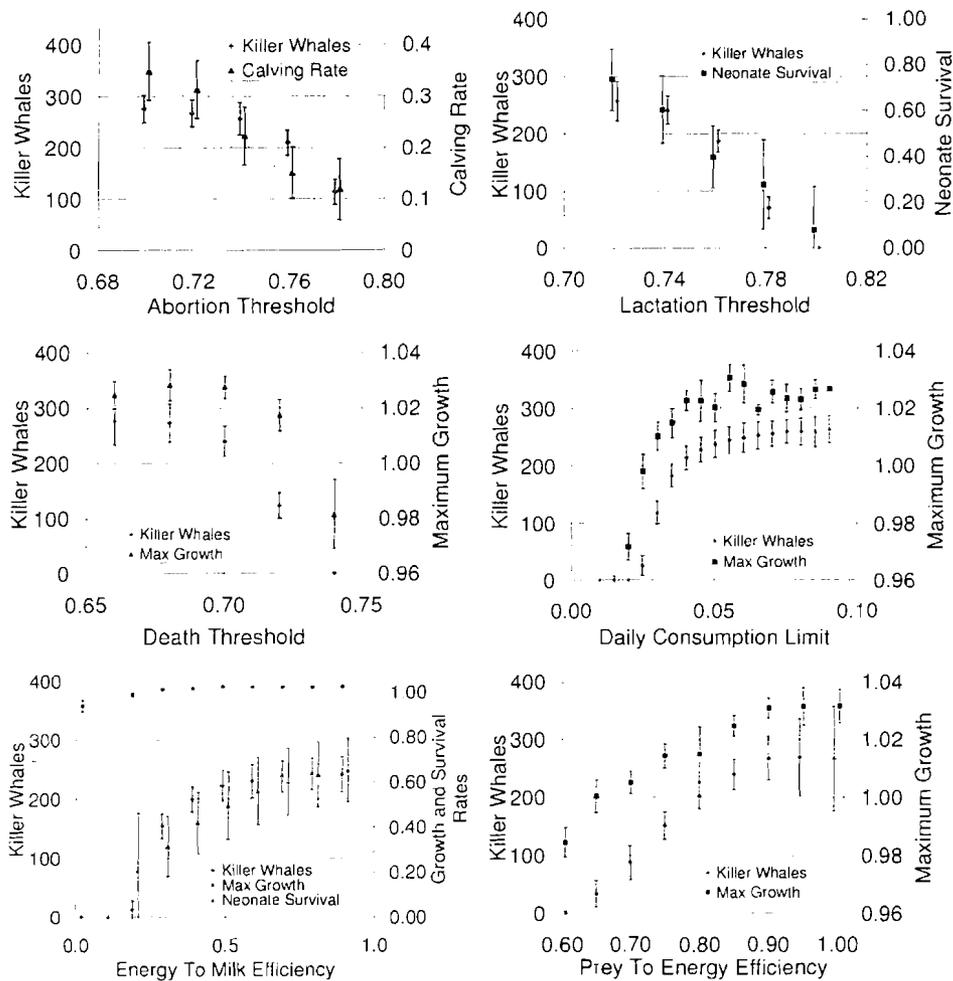


Figure 13. Sensitivity of killer whale numbers in the final 800 years of 1000-year simulations, maximum population growth in the initial 50 years, and other key output variables are shown as key input parameters were varied (5 replicates each, error bars = SD). Thresholds at which killer whales aborted pregnancies (top left), stopped lactation (top right), and died (center left) are expressed as the proportion of age-specific target mass. Daily consumption limit (center right) is also a proportion of age-specific killer whale target mass. Efficiency of milk production and the efficiency with which prey were converted to energy are shown at bottom left and right, respectively.

rate at 0.74, and rapid extinction of the killer whales by 0.80 of target mass. The threshold for cessation of lactation, and therefore death of neonates was also influential, with a nearly linear effect on neonate survival from just above that causing death of the mother (0.70) to complete mortality of neonates and extinction of killer whales at a threshold of 0.80. The default threshold was selected to be 0.75, which produced neonate mortality from birth to the first summer similar to that reported by Olesiuk et al. (1991) while making it responsive to variable adult consumption rate in the models. The

starvation threshold less than the default of 0.7 had little effect on equilibrium killer whale numbers, but higher thresholds led to lower growth rate, lower numbers and extinction by a threshold of 0.74.

Energetic efficiencies modeled were essentially part of a conversion chain producing predator biomass from prey biomass. The metabolic efficiency of converting prey to energy (Fig. 13, bottom right) encapsulates the effect of any link in that energetic chain and demonstrates a strong effect on total number of whales that could be sustained and on the stability of whale numbers as efficiency was increased. It is very similar in functional form to that of encounter rates (Fig. 12). The particular functional shape illustrated in the figure can be shifted in either horizontal direction by changing some other parameter affecting the metabolic or hunting efficiency of the killer whales, but the progression from smaller to larger populations and toward more unstable population trajectories with increasing efficiency was consistent. The results shown should not be interpreted as supporting the assumption of a particular metabolic efficiency.

Group Size

We first evaluated whether model killer whale groups approximated the expected optimum group size when we altered the shape of functions relating prey vulnerability to group size. We chose parameters to create modal values of 2, 3, 4 and 5 for the test case of superabundant harbor seals (Fig. 14). The optimizing models were based on “adult equivalents” (downgrading juveniles for their expected lesser effectiveness) while the model output included all individuals, so we expected the observed group size might exceed the modal optimum, but group sizes are constrained by the available groups of related whales with which each group might join. The logistic functions relating killer whale group size to maximum vulnerability of prey produced shapes of the killing rate per killer whale that were unimodal at the optimum group size (Fig. 14, upper graphs). Adjusting the shapes of the vulnerability and killing rate curves altered the overall killing rates and resulting equilibrium population size of killer whales, so the simulations were standardized (by altering the encounter rates) to produce killer whale populations that varied around 200 whales in the last 800 years of 1000-year runs (Fig. 14, bottom left). The mean group size was close to the modal optimum size expected in the 4 test cases, and the histogram of daily observed group sizes for an optimum group size of 3 (Fig. 14, bottom right) was plausible when compared to those reported by Baird and Dill (1996). Mean Group size was larger by 0.2-0.9 whales during the initial population growth phase of the simulations, but this effect incorporates complex relationships of mother-offspring association rules and the skewness of the per capita consumption to group size curves, so was not quantified in a precise way.

Parameter ProbGroupsMeet sets the probability of encountering a group of killer whales and evaluating the foraging advantage of combining with that group. The group encountered is weighted by known previous associations (the more past associations, the higher the chance of considering that group as hunting partners the following day). The parameter ProbJoinRandomGroup sets the probability that the group encountered and considered for partnership is a random group irrespective of past associations. This was considered a plausible, but unlikely possibility based on literature accounts (Baird and Dill 1996, Baird and Whitehead 2000). A randomly selected group would be more likely to reflect the distribution of group sizes in the entire killer whale population, while the choices among those groups previously known would be more limited, reflecting the

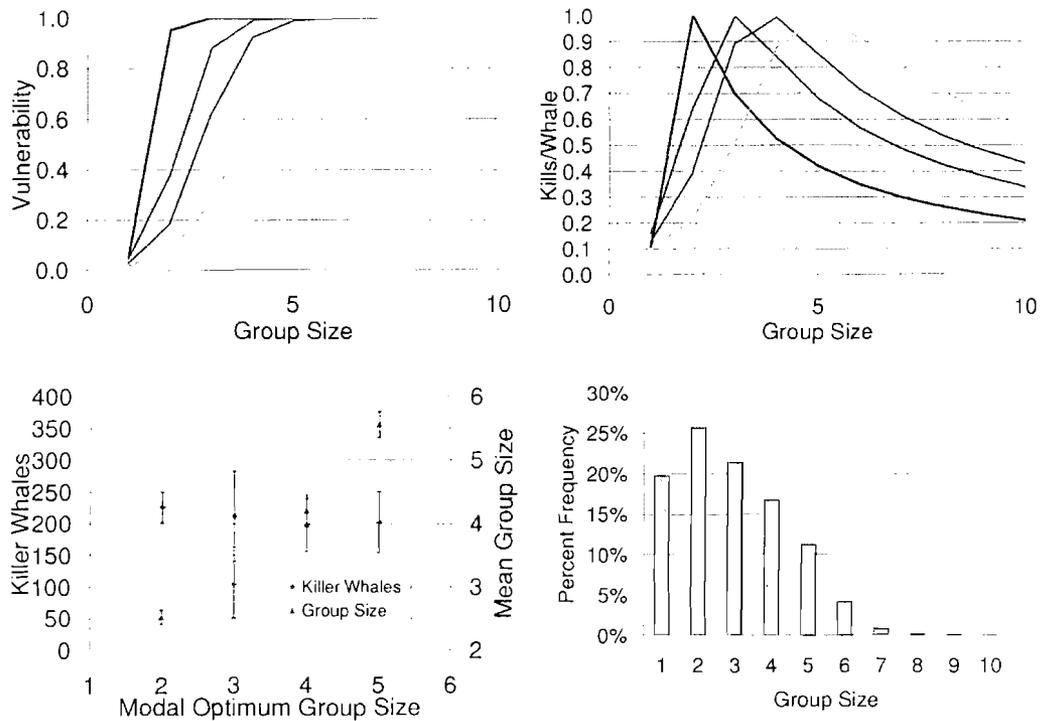


Figure 14. The logistic functions relating killer whale group size to a maximum vulnerability (probability of killing given an encounter) of prey (top left) produce expected payoffs in consumable prey per group member (top right, scaled to the maximum value with colors to match curves at top left). Simulations of 1000 years with encounter rates scaled to produce roughly the same numbers of killer whales in the last 800 years of each run demonstrated that mean group size approximates the modal optimum group size (bottom left). A Histogram of group sizes for a modal optimum of 3 killer whales demonstrates the variability in daily group size (bottom right).

number of living relatives, their reproductive success and their own particular hunting associations. We tested the sensitivity of group size to variation in ProbGroupsMeet while ProbJoinRandomGroup was held to 0, and varied ProbJoinRandomGroup while ProbGroupsMeet was held at 1 (ProbJoinRandomGroup only operates after a simulated encounter occurs, which depends on ProbGroupsMeet>0). The effect of increasing the probability of encounters between groups with past histories was slightly positive but asymptotic (Fig. 15). The effect of increasing the probability that the groups meeting and joining would be unrelated was also positive and asymptotic, with a marked decline in the proportion of whales hunting alone (Fig. 15). The increasing standard deviation as simulations progressed across increasing ProbGroupsMeet, then ProbJoinRandomGroup (Fig. 15) was an artifact of the higher variation in population size...i.e., increasing mean group size to the optimum group size had the effect of increasing killing efficiency and raising population size and variability. Group size was greatest during periods of increase

and smallest during population declines, leading to greater variability in mean group size as an artifact of more variable population size. Adjusting encounter rates between

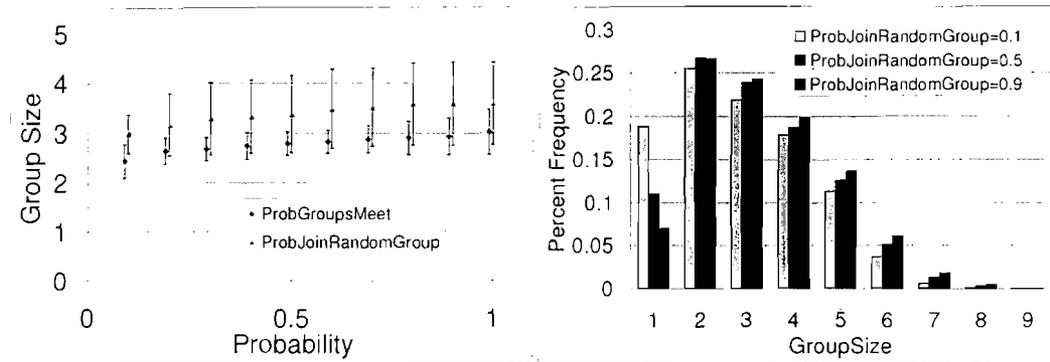


Figure 15. For an optimum hunting group size of 3, parameters controlling the daily probability of meeting and considering joining another group of killer whales (ProbGroupsMeet), and the probability that it would be a random group or a group of relatives (ProbJoinRandomGroup) had positive effects on the mean group size of hunting killer whales (left). The increase in mean group size with increasing ProbJoinRandomGroup was accompanied by a marked decline in the proportion of whales hunting alone (right).

predators and prey to control this effect showed the effect of ProbGroupsMeet and ProbJoinRandomGroup on mean group size was robust. The mean group size counting all adults and juveniles was greater than the optimum based on “adult equivalents” when these controlling parameters allowed the greatest model flexibility in joining groups, which was consistent with our expectations.

Model Validation

Model validity was assessed by concurrence of emergent population-level properties of the model killer whales with comparable properties reported in the literature. Specifically, maximum growth rates, age-sex composition, age-specific survival, pregnancy and calving rates (Olesiuk et al. 1992), prey consumption rates and the size of hunting groups (Baird and Dill 1995) were compared to values reported in the literature. We also attempted to evaluate the plausibility of model behavior in conditions of prey abundance and scarcity by comparison with other species of large mammals that have been reported in those conditions (e.g., the demography of irruptive ungulate populations or cyclic lynx (*Lynx canadensis*) suggest plausible demographic changes in response to food abundance/scarcity).

Population Dynamics of Model Killer Whales

A representative simulation of killer whales preying on a superabundant population of harbor seals was analyzed to evaluate whether killer whale population dynamics conformed to those found in resident killer whales (Olesiuk et al. 1991) and large mammals in general (Eberhardt 2002). There are no demographic data from field populations of killer whales that can encompass the period and the range of growth rates simulated. Olesiuk et al. (1990) estimated a life table of resident killer whales with a

stable population growth rate of $\lambda=1.029$. A stable projection from that table produced similar age-class composition and survival rates to those of the initial growth phase in our agent-based simulations (Table 2).

Table 2. Comparison of age structure and survival from agent-based simulations (SD in parentheses) during 50 years of growth to those of a stable population estimated from a life table of resident killer whales (Olesiuk et al. 1990) growing at a comparable rate.

	Stable Projection	Agent-Based Simulation
Growth Rate (λ)	1.029	1.032
Females >10 Years	0.40	0.41 (0.03)
Males >10 Years	0.24	0.19 (0.02)
Juveniles 1-10 Years	0.30	0.34 (0.03)
Calves	0.04	0.05(0.02)
Adult Female Survival	0.989	0.987 (0.020)
Adult Male Survival	0.969	0.966 (0.051)
Juvenile Survival	0.952	0.967 (0.037)
Calf Survival	0.96	0.895 (0.152)
Calving Rate (10-40)	0.14	0.18 (0.07)

The trajectory of killer whale and harbor seal abundance in a typical simulation where both populations fluctuate are shown in Figure 16. From an initial population of 50 the killer whale population grew at a rate of just over $\lambda=1.03$ in the first 50 years, reaching a peak of 280 after 66 years and fluctuating between 135 and 270 for the remainder of the 1000-year simulation. Periods of decline were generally marked by reduced calving rates and juvenile survival in comparison to periods of increase, leading to poor recruitment (Fig. 16). Population trends in model killer whales were therefore driven primarily by changes in calving rates and juvenile recruitment, with large fluctuations in age structure that persisted for decades. This is consistent with the high stability of adult survival and the species' extreme longevity, but unique to large predators. It is of interest that in this extremely long-lived species with a long post-reproductive phase for females, modeled fluctuations in numbers were accompanied by large shifts in population age-sex structure that affected reproductive potential. During periods of decline, post-reproductive females came to outnumber reproductive ones, and juveniles were reduced to less than half their proportion during periods of population growth (Fig. 16). These features could be expected to lead to substantial lags in predator numeric response to prey abundance, and unstable predator-prey interactions on long time scales. This was observed in the illustrated 1000-year time series (Fig. 16), where the mean lag between clear troughs in prey and predator numbers was 31 years ($n=5$, range 16-38).

Consumption-Dependent Vital Rates

If we assume that most density-dependent changes in vital rates (Eberhardt and Siniff 1977, Gaillard et al. 1998, Eberhardt 2002) are driven by consumption, what are often thought of as density-dependent responses in vital rates are more usefully analyzed as consumption-dependent responses in vital rates that control predator abundance. We expected these to adhere to density-dependent patterns in that juvenile survival and

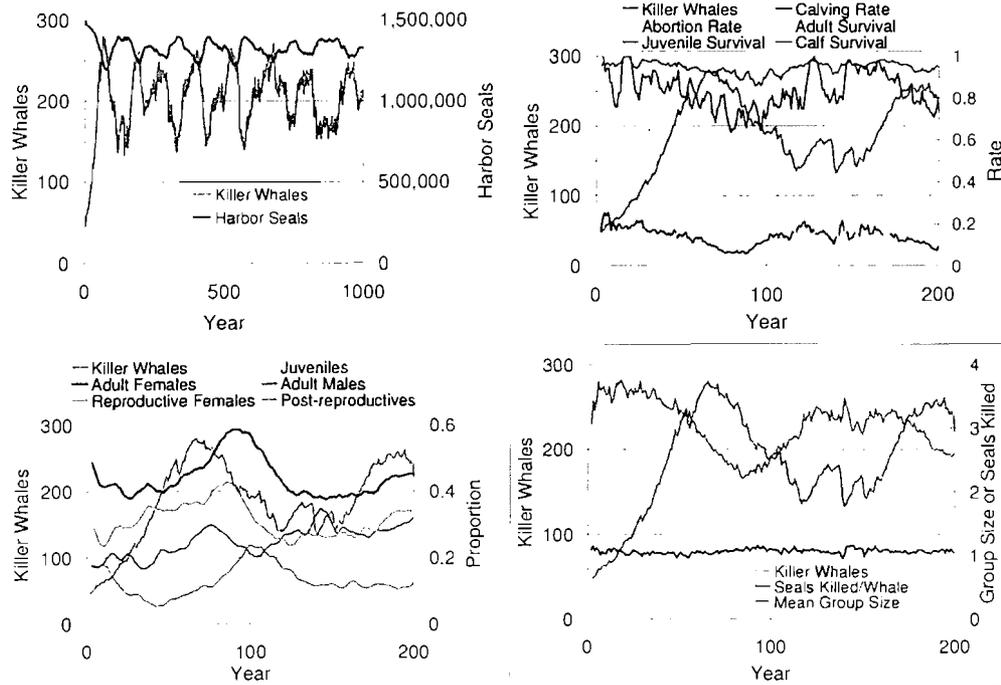


Figure 16. A typical simulation of transient killer whales and a superabundant, single prey population of harbor seals shows fluctuating population size of predators and prey (top left) over 1000 years. Changing vital rates (top right; rates are 5-year running averages), age structure (bottom left), mean hunting group size and annual consumption rates (bottom right) are illustrated for the first 200 years. For analyses, juveniles are those 1-10 years old, and reproductive females include ages 10-40 years. Calving and calf survival rates are calculated as if data were collected in summer (*sensu* Olesiuk et al. 1990).

reproductive rates should be the most responsive to changes in the per capita prey consumption rates of killer whales. This expectation was confirmed by a high degree of consumption-dependence in calving rate (as driven by the rate of abortions, Fig. 16) and juvenile (especially calf and yearling) survival ($P < 0.05$, Fig. 17). These relationships drove the strong shifts in juvenile recruitment and changing age structure apparent in the trajectories of Fig. 16.

Surprisingly, finite growth rate (λ) was negatively correlated to total per capita consumption rate (Fig. 17). This counter-intuitive result was driven primarily by changes in population age structure as the population fluctuated in size (Fig. 17). Highest consumption rates occurred when juvenile recruitment was low, leading to a high proportion of adults whose larger body size required greater energy. This resulted in high rates of per capita consumption while reproductive potential and population growth rate were relatively low, and senescent mortality was increasing. This is an intriguing aspect of the predator-prey relationship for transient killer whales that suggests caution when

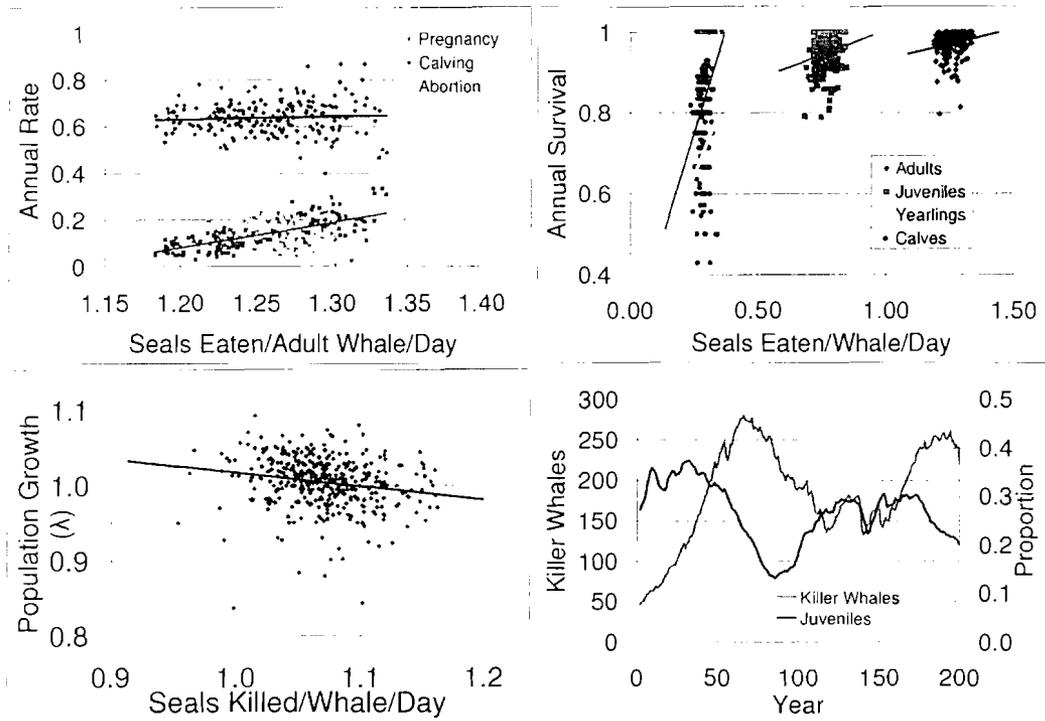


Figure 17. Scatterplots from the first 200 years of a simulation of killer whales preying on a single, superabundant prey population of harbor seals. Calving rates were positively and abortion rates negatively correlated with the number of seals eaten/adult (>10 years) killer whale/day (top left; reproductive females were defined as those from 10-40 years of age). Annual survival rates were positively correlated with class-specific consumption (top right), but finite population growth (λ) was negatively correlated with total per capita killing rate (bottom left) due to shifting age structure during population fluctuations (bottom right, see text).

examining killer whale functional or numeric responses to prey abundance. Functional and numeric responses of killer whales were, at best, weakly correlated to both seal abundance and ratio of seals/killer whales when considered without time lags. When time lags were considered using cross correlations, the strongest responses were to seal abundance directly rather than to seals available per killer whale {i.e., model killer whales were more nearly “prey-dependent” than “ratio dependent” (Arditi and Ginzburg 1989)}. Seal abundance was positively correlated ($r = 0.395$) to killing rate per killer whale 24 years earlier, and negatively correlated ($r = 0.390$) to killing rate 19 years later (Fig. 18). Similarly, killer whale numeric response (λ) was most highly correlated ($r = -0.39$) with seal abundance 13 years earlier (Fig. 18). Such simulations suggest that the standing age and social structure, with the broad range of age-specific body sizes and reproductive potentials possible with killer whales, are more important to interpreting killer whale impact on their prey, and predator-prey dynamics in general than killer whale numbers *per se*.

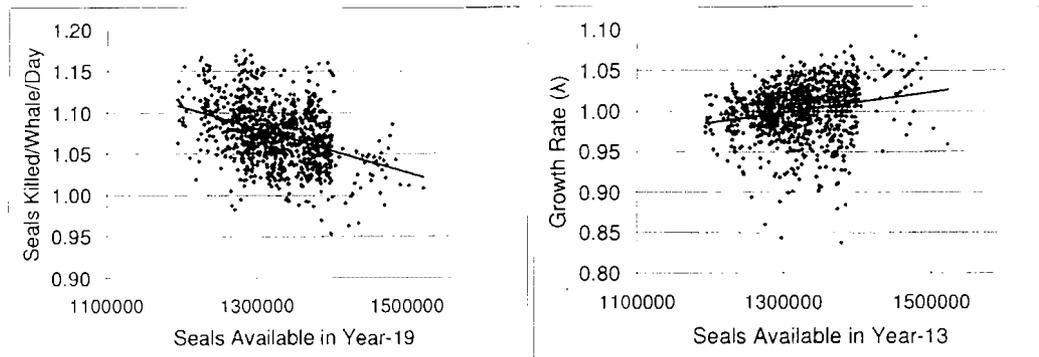


Figure 18. Functional (left) and numeric (right) responses of killer whales to prey abundance were more dependent on absolute abundance than the seals/killer whales ratio, with anti-regulatory properties indicated by long time lags.

Multiple Prey and Other Features

We used the single-prey model as a baseline to explore interactions between killer whales and multiple prey by calculating the amount of biomass provided by the addition of a new prey species to the model (number of prey \times expected encounter rate \times average vulnerability), and reducing the number of harbor seals to remove a comparable biomass of those prey from the whales' diet. In this way the addition of new prey species would lead to a similar standing stock of killer whales. Two species of particular interest are Steller sea lions, because of their threatened and endangered status in parts of their range, and gray whales because of their apparent importance as prey during a narrow window of time in the spring when calves are known to be preyed upon. We added Steller sea lions and gray whales at stock sizes similar to those existing on the North American coast from California to SE Alaska (Appendix), and reduced the super-abundant population of harbor seals to compensate for the two additional prey. Steller sea lions were assumed to be somewhat less vulnerable than harbor seals, and to require slightly larger group sizes for optimal foraging. Gray whales were the least vulnerable and required optimal group sizes of 5 or 10 adult killer whales to reach optimum hunting efficiency on calves and adults, respectively. Seasonal availability and increased hunting specialization on gray whale calves was simulated by limiting the window of time during each year to days 50-150, and increasing the encounter rate for them in comparison to harbor seals and Steller sea lions.

The 3-species simulation is illustrated with a period of killer whale population growth and equilibration with the prey community followed with a "regime shift" affecting the primary prey population of harbor seals, a return to the original regime, and later by the harvest removal of seasonally available gray whales. We reduced the carrying capacity of harbor seals in year 200 by ~60% for a period of 30 years, then returned the system to its starting parameters until year 400, when 12,000 gray whales were removed by harvest over 10 years. The simulation (Fig. 19) shows the increase in killer whales and the reduction of prey populations as killer whale numbers increased. The impact of the growing killer whale population on gray whales was small, while the fluctuations in both pinniped populations are roughly synchronous. As modeled, harbor seals represent a large prey base (that might simulate a conglomeration of multiple

species) that dominates the effect on killer whale population dynamics. Their sudden precipitous decline in year 200 caused a decline in killer whale numbers that reached its nadir 59 years after the first regime shift and 29 years after the carrying capacity for harbor seals had returned to its original condition (Fig. 19). This was caused primarily by the collapse in killer whale recruitment for most of that 30 year period of poor harbor seal conditions. A small increase (~15%) in predation on the other 2 species occurred in the decade following the harbor seal reduction, but both species increased their numbers as the killer whale population declined. The effect on killer whale numbers and recruitment of removing gray whales in years 400-409 was not noticeable. Mean group size of killer whales increased from 2.73 to 3.66 when gray whales became available seasonally.

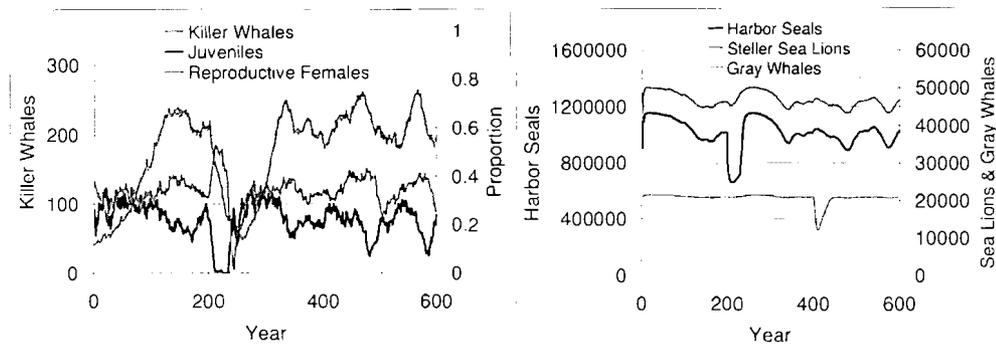


Figure 19. Simulation of a 3-species prey community (see text) over 600 years in which a 30-year “regime shift” reducing the carrying capacity of harbor seals by ~60% begins in year 200, and a harvest of 12,000 gray whales occurs in years 400-409.

Discussion

Our overall objective of producing an individual-, or agent-based model with emergent properties similar to those that have been estimated from live killer whales was met, and some non-intuitive properties of those models were discovered. Rates of prey consumption were (not surprisingly, given their shared derivation) similar to those published (Barrett-Lennard et al. 1995, Baird and Dill 1996, Williams et al. 2004), though somewhat higher due to inclusion of growth and reproductive costs. Demographically, baseline rates were easily adjusted to mimic those expected under exponential growth, while energetic mechanisms provided plausible responses in vital rates when prey became scarce. Confirmation that such changes occur in wild populations is not now feasible, but the use of an individual-based model might identify other indirect properties that could strengthen an argument that food shortages affect demography of transient killer whales. For example, the existence of thresholds in body mass that lead to decreasing lactation, abortion or starvation might be confirmed and estimated as potential physiological mechanisms that would logically affect demography; field studies would be unlikely to obtain sufficient sample sizes to definitively link consumption to these mechanisms.

Many other results, particularly those pertaining to long-term predator-prey dynamics, are speculative, but rich in detail about possible mechanisms and consequences. There are essentially no theoretical models relevant to a single predator

and the number of prey routinely taken by killer whales, or of a predator with such longevity and likely demographic inertia...factors that lead to substantial lags in the prey scenarios modeled here. The importance of standing age structure to the interpretation of demographic trends in killer whales was amply demonstrated in model simulations. In some cases the prey population began its recovery over 30 years before the killer whale population, and numbers of killer whales sometimes remained stable for decades into a prey decline before dropping. The ability to determine age- and sex-specific demographic rates and age structure in killer whale field studies is essential to understanding population productivity and other potential responses to changing prey availability. This is due to the narrow age window for reproduction and the existence of a large post-reproductive class in killer whale populations. The predator-prey dynamics that follow from this do not lend themselves to classical forms of difference equation models, though the output from individual-based simulations may aid in developing simpler mathematical models with long time lags.

Current controversies about the role of transient killer whales in the decline of species such as Steller sea lions have taken little account of the reciprocal numeric effect such declines might have on killer whales. The simulations performed here indicate that such effects could be profound, and suggest some attendant changes that might be relevant to future studies. One is that there are significant lags in total numbers of killer whales following prey reduction: reduction of prey numbers might increase the impact of killer whale predation and accelerate a prey decline until the effects of reduced recruitment and shifting age structure act to decrease killer whale numbers. The practical significance of this is that reductions in prey could have significant effects on the age-sex structure of transient killer whales that are persistent and measurable with current methods at the population or social group level, even while total numbers of killer whales appear stable. In simulations per capita consumption rate varied with age structure and reproductive success, which also could affect assessments of the impact of transient killer whales on prey populations. Estimates of individual metabolic requirements may need to be weighted by the actual age-sex structure, not simple estimates of average killer whales (Williams et al. 2004) or a calculated stable structure (Barrett-Lennard et al. 1995). The potential to explore these relationships with the present model has not been exhaustively pursued here.

Future Direction

Our intention was to implement an individual-based model built on biological components that have empirical support, and to explore the emergent properties of models based on these biologically realistic elements. Uncertainties about the likely value of many parameters are important to those properties, but assumptions about the model structure also need to be addressed in the future. We feel that the most obvious and important of these is the simplifying assumption that hunting groups of killer whales and their prey encounter each other at random, without spatial structure and with very little temporal structure. The various species on which transient killer whales prey have widely different dispersion across the range of a given killer whale stock, as well as pronounced differences in habitat use. Strictly speaking, it is impossible for a killer whale group to daily traverse a small part of its range and have the same probability of encountering, say, a Steller sea lion and Pacific white-sided dolphin every day of the year. Basing the predator-prey interaction on established theoretical assumptions allowed both for useful

comparisons to conclusions from theoretical ecology, and for segue into spatial models in the next generation of a killer whale IBM. The natural spatial implementation would be a spatial grid (hypothetical or one based on GIS maps) which incorporates information on the dispersion of prey stocks. The probabilistic mechanisms of encounter between groups of transient killer whales and between those groups and prey are much more plausible at smaller spatial scales, and a variety of decision mechanisms could be implemented and tested against the movement patterns inferred from resighting data or satellite telemetry. Spatial segregation of prey is a plausible mechanism providing potential for refuges and aggregation for prey species, factors that tend to prevent prey extinction and increase model stability in simpler predator-prey models (Hassell 1981, Akcakaya 1992, McCauley et al. 1993).

Conclusion

There is no intention to imply specific predictive ability to the model described here. Its value is primarily heuristic and the lessons are general. Mechanisms of interaction between transient killer whales and their prey can be simulated and altered, and the logical consequences of such changes in our conceptualization can be observed. The model often suggests responses to real changes that we might not at first predict, suggesting measurements we could make in the field to detect demographic or ecosystem changes. Changes in age structure and extreme lags in predator-prey dynamics are two such responses to declining prey abundance suggested by the model. To the extent that energetic requirements of transient killer whales are adequately captured in the model, we might expect that changing consumption patterns might cause changing demographic patterns, and simulations can suggest what data to collect in order to detect these responses. Our experience in developing and experimenting with these models has been a positive one of being forced to examine the details of physiological and ecological processes from their first assumptions to logical consequences that follow. Even where realism is stretched to breaking, we believe that our understanding of how real systems work can only be improved by the exercise of modeling. Our primary hope is that students of killer whale ecology will find a useful tool herein, and be stimulated to use and improve on this beginning.

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Appendix: Prey species and associated parameters

Sea Otters – Wade et al. (2007 In Press) estimated population size of sea otters from SE Alaska to California at just under 18,000. With relative stability in California, and rate of expansion apparently slowed in Alaska and BC, we assumed the population was above MNPL, with growth slowing from r_{\max} . Life history parameters provided by Gerber et al. were used to set vital rates that produced $r_{\max}=0.18$. Due to a greater diversity of observed vital rates and population growth rates in relation to density, a slightly more conservative approach to equilibrium than that used for remaining species was assumed, with MNP ~ 0.65 .

While evidence supports substantial impact on sea otters by transient killer whales in western Alaska, there is little evidence for significant predation by transient killer whales in SE Alaska or further south, so default vulnerability maxima were set very low for both pups and non-pups, with little increase in success with increasing group size (<http://www.math.uaa.alaska.edu/~orca/>).

Harbor Seals – The stocks on the west coast of North America were combined by Wade et al. (2007 In Press) to estimate 102,657 available to transient killer whales. Observed rates of population growth by small populations of harbor seals are variable, so we assumed the observed estimate was $>80\%$ of equilibrium. We assumed $r_{\max} = 0.12$ and the parameters to produce that rate given in <Http://www.math.uaa.alaska.edu/~orca/>. Density dependent parameters were selected to produce MNPL between 75-80% of equilibrium, with greatest changes in calf survival, reproduction and adult survival, respectively.

Harbor seals are widely reported as prey to transient killer whales, and dominate the diet in British Columbia (Baird and Dill 1995). In that study, pups were more abundant in the diet than adults, and the relationship of hunting success to group size suggested an optimum group size of 3 across all prey types (small cetaceans and sea lions were also taken). We modeled vulnerability to reproduce these conclusions, with maximum vulnerability reached at smaller group size for harbor seal pups.

California Sea Lions – The 2001 estimate based on corrected pup counts was $\sim 240,000$ animals, with recent growth of 0.06 annually, though El Nino conditions and recent disease outbreaks suggest the population is close to equilibrium. Default parameter values produce an equilibrium close to the 2001 estimate and $r_{\max}=0.12$.

Default vulnerability parameters are the same as for harbor seals, but encounter rates are lower due to the more restricted range and concentration around a small number of rookeries. Pups are born in May and June, but the model uses July 1 as birthdate (day of year) to reflect the approximate time that pups regularly enter the water, becoming potentially vulnerable to predation by killer whales.

Steller Sea Lions – The eastern stock extends from SE AK to California, likely numbering around 43,000 animals when rookery and haul-out counts are corrected for animals at sea (Wade et al. 2007 In Press). Pups born in SE Alaska have increased at a rate of $r=0.059$ from 1979-2000 but this rate had declined in the later part of that period, and our default population for the eastern stock is modeled for $r_{\max} = 0.10$. Vital rates

were derived from an equilibrium life table provided by (Holmes and York 2003). While rookeries in Oregon and California are relatively stable, pups born annually at 3 rookeries in SE Alaska have been increasing at roughly $r=0.059$, though that rate has declined in recent years. Rookeries in British Columbia are also expanding after prolonged culling and extirpation of rookeries in the mid-20th century.

Default vulnerability parameters assume that the difference between pups and non-pups in maximum vulnerability is greater than that of harbor seals, due to the large degree of sexual dimorphism and average size of adults, many of which are adult males that pose a significant risk of injury to killer whales trying to eat them. Pups are born in May and June, but the model uses July 1 as birthdate (day of year) to reflect the approximate time that pups regularly enter the water, becoming potentially vulnerable to predation by killer whales.

Northern Elephant Seals – The U.S. population was derived from a remnant population of a 10's or hundreds of seals surviving commercial hunting in the 19th century. The first pup was born on Ano Nuevo island in 1961, but the present population occupies 3 islands some mainland beaches, growing exponentially at $r_{max} = 0.078$. The equilibrium level of this stock is unknown, but the continued growth and expansion to new breeding beaches suggests it could be some way off. We assume that the population is starting to slow its growth and will level off around 145,000.

Birthing date and mass of pups is adjusted to early April to account for delayed entry into the ocean and availability to killer whales. First year growth in mass is assumed to be minimal, as pups enter the water with huge fat reserves and end the year as much leaner, longer seals of similar mass. Assumed mass of non-pups is much less than adults to account for the likely greater vulnerability of juveniles and females to killer whale predation. Vulnerability as a function of killer whale group size was similar to that of Steller sea lions, but encounter rates were reduced to reflect more restricted range and seasonal availability.

Harbor Porpoise – (Barlow and Boveng 1991) suggested a maximum theoretical growth rate of 0.094 for harbor porpoises, but actual estimates of porpoise and dolphin growth rates have been well below this. The default parameters used here reflect maximum age of less than 15 years and annual reproduction, producing a growth rate $r_{max}=0.05$

Harbor porpoise are of similar size to harbor seals, but faster and swimmers requiring energetic pursuit by killer whales. Optimal group sizes for capture of calves and non-calves were assumed similar to harbor seals, but maximum vulnerability was assumed to be lower.

Dall's Porpoise – Excellent information on body growth and reproductive parameters were obtained from (Ferrero and Walker 1999). A theoretical maximum growth rate of 0.12 was assumed. Capturing Dall' Porpoises requires energetic pursuit by killer whales, but yields less success than for smaller harbor porpoises. Also, successful group size was more variable across these two species than across pinniped species observed by Dahlheim and White (Pers. comm.). Default parameters assumed that optimum group size was slightly higher, and maximum vulnerability slightly lower than for harbor porpoise. Optimum group size was still below that observed when transients killed gray

whales (below). This means that vulnerability was assumed to increase more slowly with group size than for harbor seals and harbor porpoises.

Pacific White-sided Dolphin – Wade et al. (2007 In Press) estimated a population size of 59,274 available on the west coast, and we assumed that this was >80% of equilibrium. Estimates of reproductive rates (Ferrero and Walker 1996) and the maximum known ages of around 40 years suggest vital rates more similar to Spotted Dolphins than to the similar-sized Dall's porpoises. We assumed $r_{\max} = 0.05$ with lower reproductive and mortality rates than used in Dall's porpoises (<http://www.math.uaa.alaska.edu/~orca/>). Density dependent parameters were selected to produce MSP between 75-80% of equilibrium, with greatest changes in calf survival, reproduction and adult survival, respectively (<http://www.math.uaa.alaska.edu/~orca/>). Vulnerability was assumed similar to that of Dall's porpoises.

Minke Whales – The Pacific stock of minke whales is the most poorly known of the large whales considered in this model, but they are also the smallest and most vulnerable to attack by killer whales (Ford et al. 2005), with a higher proportion of adult kills among those observed than in gray whales. It was therefore essential to include them as potential prey. Population size along the west coast is estimated at ~1015 (Wade et al. 2007 In Press). Minke whales were not a target of commercial whaling in the 20th century so this might be considered an equilibrium level. It is, however, a much smaller density than other populations in the Atlantic and Antarctic, and predation by killer whales may be a significant limiting factor. Therefore, the present level is unlikely to be a purely density-dependent equilibrium in the absence of predation, but there is no way to derive an estimate for a purely density-dependent minke whale population. We therefore chose to assume the present level to be below, but near the MSP level (80% of equilibrium) to make it as robust to predation pressure as possible. Density dependent parameters were selected to produce MSP between 75-80% of equilibrium, with greatest changes in calf survival, reproduction and adult survival, respectively. We used the highest values for adult survival and fecundity provided by (Horwood 1990), based primarily on commercial catches in Antarctica and the North Atlantic. Assuming minimum juvenile mortality was ~ twice that of adults, $r_{\max} = 0.088$. Density dependent parameters were selected to produce MSP between 75-80% of equilibrium, with greatest changes in calf survival, reproduction and adult survival, respectively (<http://www.math.uaa.alaska.edu/~orca/>).

There are no estimates of minke whale vulnerability except anecdotes that indicate adults are more vulnerable than gray whale adults. They are capable of escaping killer whale attacks during long chases, but not if trapped by geography (Ford et al. 2005). They are also smaller, so we assumed that maximum vulnerability would be higher and be attained by smaller groups of killer whales than is assumed for gray whales (below). Minke whale body weights available for consumption by killer whales were derived from parameters for length and age, and weight at length equations (Horwood 1990). Non-calf mass was the mean of mass at mid-year age weighted by the expected age structure. Fat content of minke whales is the lowest of any large whale and set at 2.35 kcals/gm wet weight (Horwood 1990).

Gray Whales – The western pacific gray whale stock is estimated to have grown at 0.024-0.044 from 1967-1998, reaching a maximum population estimate of ~26,000 in 1998. Gray whale numbers subsequently declined after environmental changes in their feeding areas, and with known predation on calves. We used 25000 to be the default equilibrium in our model. Birth intervals are longer than those of humpback whales that have been observed to increase $r = 0.08$. Maximum survival estimates are high (Wade 2002). We used default vital rates that produced $r_{max} = 0.05$ rather than the observed rate of growth in the late 20th century because of the likelihood that observed rates were obtained while killer whale predation was occurring. Density dependent parameters were selected to produce MSP between 75-80% of equilibrium, with greatest changes in calf survival, reproduction and adult survival, respectively.

Predation by transient killer whales on gray whales is known to occur primarily on calves, and group size of attacking killer whale is over twice that during attacks on pinnipeds (Dalhlein and White, Pers. comm.). We therefore modeled vulnerability to increase with group size more slowly than for pinniped prey, producing a maximum rate of return for individual killer whales at group sizes ~ 8 for calves, and 13 for non-calves, with maximum vulnerability of calves being 4 times that of adults (0.1).

Humpback Whales – Two stocks overlap the population of west coast transients. Wade et al. used estimates of the eastern North Pacific stock together with that portion of the Central North Pacific stock that occupies SE Alaska in summer to conclude that ~2352 humpbacks were available to west coast transients. For the entire North Pacific stock, (Ricc 1978) estimated that ~ 15,000 humpbacks were present prior to commercial whaling, which is roughly twice the present NOAA stock assessment. Therefore, the default equilibrium level used in the model population was ~5,000.

Maximum rate of growth of the population has been reported as $r=0.08$. (Barlow and Clapham 1997) provided parameter estimates suitable to derive maximum birth and survival for the Atlantic population that was growing at 0.065, which were adjusted slightly to obtain default values that produced the 8% growth rate observed in the Pacific (http://www.nmfs.noaa.gov/prot_res/PR2/Stock_Assessment_Program/individual_sars.html). Density dependent parameters were selected to produce MSP between 75-80% of equilibrium, with greatest changes in calf survival, reproduction and adult survival, respectively (<http://www.math.uaa.alaska.edu/~orca/>).

Evidence of predation is seen almost entirely on calves, usually before the spring migration in the E North Pacific stock, with roughly 11% seen with rake marks and 7% acquiring scars after first being seen (Steiger and Calambokidis 2005). Other reports of large whales being attacked involved large numbers of killer whales. Prey vulnerability was therefore considered to be a more gradually increasing function of killer whale group size than other prey, with calf vulnerability greatly exceeding that of non-calves. Non-calf vulnerability is likely to be primarily among juveniles in this and other large whales. Little is known about predation rates on any of the larger whales, but population characteristics and vulnerability to predation may be similar amongst them. Also, a single large whale is likely to satiate any group of killer whales when killed. Therefore, the modeled humpback population might be used as a surrogate for the remaining large whales by simply increasing the modeled stock size and equilibrium levels.

**Population Biology of Killer Whales and their
Marine Mammal Prey in the North Pacific**

by

Paul R. Wade

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POPULATION BIOLOGY OF KILLER WHALES AND THEIR MARINE MAMMAL PREY IN THE NORTH PACIFIC

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SECTION 1: ABUNDANCE OF KILLER WHALES (*ORCINUS ORCA*) IN THE ALEUTIAN ISLANDS AND GULF OF ALASKA

The material in this section is based on Zerbini et al. (unpublished *a*), which is available as a background paper.

Ship surveys were conducted in coastal waters off western Alaska and the eastern and central Aleutian Islands in the summer of 2001-2003 to examine distribution and movement patterns of killer whales, to determine the ecotypes using this area and to estimate killer whale abundance. Killer whale ecotypes were determined by a combination of morphological, group size, behavioral, genetic and acoustics data. Conventional (CDS) and multiple covariate distance sampling (MCDS) methods were used to estimate the size of the population of the different ecotypes inhabiting the region. Abundance estimates were calculated for two sets of data about group sizes, initial (IGS) and post-encounter (PEGS). 'Resident'-type (fish-eating) killer whales were more abundant near Kodiak Island and around Umnak and Unalaska Islands. This ecotype was not observed between 156 and 164°W, south of the Alaska Peninsula. Total resident population size was estimated at 991 (95% CI = 379-2585) (IGS) and 1587 (95% CI = 608-4140) (PEGS). 'Transient'-type (mammal-eating) killer whale sightings were found at higher densities between the Shumagin Islands and the eastern Aleutian Islands. Abundance was estimated at 200 (95% CI = 81-488) (IGS) and 251 (95% CI = 97-644) whales (PEGS). Only two sightings were recorded of 'offshore'-type killer whales during the surveys, one north of Unalaska Island and the other west of Kodiak Island. The PEGS estimate of transient killer whales is likely more accurate than the IGS, while for residents, the IGS is the most conservative because the PEGS estimate may be overestimated. Numbers presented in this study correspond to the first estimates of abundance of killer whales in the Aleutian Islands and Alaska peninsula area.

The best estimate of abundance for transients for these surveys is thought to be the PEGS estimate of 251 (95% CI = 97-644), because the post-encounter estimate of group size is more accurate and there is little chance of additional sub-groups joining the additional group without being detected. This might still be an under-estimate, as it is possible that $g(0)$ (the probability of detection on the trackline) is less than 1.0 for transient killer whales, because they usually occur in relatively small groups.

The IGS estimate is thought to be the best estimate to use for resident-type killer whales, as there are circumstances where it is not always possible to exclude the possibility that sub-groups not initially within sight are included in the post-encounter group size. This IGS estimate is likely an under-estimate, as initial group sizes appear to under-estimate the actual group size. Combining the PEGS transient estimate with the IGS resident estimates leads to an overall estimate of 1,242, though if one assumes that resident group sizes are initially under-estimated to the same degree as transients groups (a fairly safe assumption), the overall estimates would be 1,495. This indicates that transients represent approximately 17-20% of the total number of killer whales in this region. Regardless of what exact number is used, the overall killer whale densities estimated here (including all ecotypes) are among the highest in the world and similar to estimates made for other high latitude productive waters, such as Norway and Antarctica (Forney and Wade, in press).

Durban et al. (unpublished) are estimating the abundance of transient killer whales for this region using mark-recapture methods applied to photo-identification data. This study combines data from the line-transect surveys described above, but also includes substantial additional photo-identification data collected by Matkin and Barrett-Lennard, particularly in the eastern Aleutians. Preliminary analyses indicate the mark-recapture transient abundance estimates will be higher and more precise than the line-transect estimate reported above. It should be kept in mind that these estimates have somewhat different interpretations. The line-transect estimate is an estimate of the number of whales that are in the study area in July and August, averaged over the 3 survey years. The mark-recapture estimate is an estimate of the total number of whales that were in the study area in July and August in any of the 3 years, so this estimate can potentially be higher if the home range of individual whales is greater than the study area. Perhaps the best way to understand the difference between the estimates is by a simple example. If one individual is in the study area in one year and not in a second year, and, conversely, a different individual is not in the study area the first year, and is in the study area the second year, the line-transect methods would estimate this as one whale over the two years, and the mark-recapture methods would estimate this as two whales over the two years.

Gulf of Alaska

Few transient killer whales were seen east of the Shumagin Islands (Fig. 1). The transient abundance estimates for the 8 survey blocks west of the Shumagins was only 27 (95% CI ~4-179). Matkin et al. (1999) reported a catalogue of 54 individual transients collected over a number of years from Kenai Peninsula, Prince William Sound, and the Kodiak areas. This number has risen somewhat since that catalogue was published, adding new whales and subtracting individuals thought to have died (Matkin, pers. comm.).

It should be noted that there are two distinct populations of transients killer whales in the Gulf of Alaska. AT1 killer whales, which have declined since the 1980s, are a small group of whales that currently number only about 8 individuals. They have been observed to primarily prey on harbor

seals and Dall's porpoise (Saulitis et al. 2000). Stable isotope values of these whales are consistent with that observed diet (Herman et al. accepted).

The so-called Gulf of Alaska transients represent the majority of transients in this region. They have been seen to prey on a variety of prey, including Steller sea lions (Saulitis et al. 2000). A group of 5 killer whales have been observed frequently in the Kodiak Island region, including Kodiak Harbor, preying on Steller sea lions.

Aleutian Islands

It is as yet unknown whether transient killer whales in the eastern Aleutian Islands are a part of the same population as the Gulf of Alaska transients. Genetically the most common mtDNA haplotypes seen in the EA are the same haplotypes seen in GOA transients. Further genetic studies are necessary to fully investigate population structure.

The line-transect estimate for the survey blocks that include the Shumagin Islands and all areas to the west is 226 (95% CI ~ 97-524). It can be seen that the highest densities of transient killer whales occur in the eastern Aleutian Islands, roughly between False Pass and Umnak Island (Fig 1). As mentioned above, both NMML and NGOS have conducted photo-identification studies in this area. The combined photo-identification catalogues from NMML and NGOS (unpublished data) resulted in 221 individual transient killer whales in all areas from False Pass to the west for the years 2001-03.

Bering Sea

Waite et al. (2002) estimated 391 (CV=0.43) killer whales of all types in the southeastern Bering Sea using line-transect methods; that estimate applies to an area to the north of the area surveyed in 2001-2003, with no overlap. If the same proportion of transients occurs in the Bering Sea as in the Aleutian Islands and Gulf of Alaska (17-20%), this suggests there would be approximately 66-72 estimated transients in the southeastern Bering Sea.

SECTION 2: ABUNDANCE, BIOMASS, AND TRENDS OF TRANSIENT KILLER WHALE PREY

The material in this section is from Wade et al. (submitted).

Data on observed marine mammal prey of killer whales, and biomass and trends of marine mammal populations are summarized for 3 major regions in the North Pacific (Fig 2). The three regions are the Bering Sea and Aleutian Islands, the Gulf of Alaska, and the western coast of North America (from southeastern Alaska to California). Marine mammal trend data from the Commander Islands are also summarized.

Observations of marine mammal prey of killer whales

Western Coast of North America

In this region, 62% of all predation event observations ($n = 342$) were of pinnipeds (Fig 3A), including 112 harbor seals, 48 California sea lions (*Zalophus californianus*), 26 Steller sea lions, and 20 northern elephant seals (*Mirounga angustirostris*) (Table 1). The next largest category was that of small odontocetes, with 24% of the observations, including 40 harbor porpoise (*Phocoena phocoena*), 33 Dall's porpoise (*Phocoenoides dalli*), and a total of 10 Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and common dolphins (*Delphinus capensis*). Large baleen whales represented 12% of the observations, with all of these observations of predation on gray whales (40 events). Minke whales represent 2% of the total (6 events). Little predation (<1%) has been reported on sperm whales (1 event) and sea otters (1 event).

Gulf of Alaska

In this region, the greatest number of predation event observations (total $n = 74$) involved pinnipeds (Fig. 3B), with 42% of the observations, including 25 harbor seals and 16 Steller sea lion predation events. The next largest category was small odontocetes (31%), consisting of observations of 16 Dall's porpoise, 4 harbor porpoise, and 3 beluga (*Delphinapterus leucas*) whale predation events (Table 1). Minke whales were the next highest category, with 8% (6 events), and sea otter predation events were 3% (2 events). Only 1 predation event on a large baleen whale (a fin whale) has been reported for this region, and none on sperm whales (it should be noted that most reports are from shelf waters which do not include the habitat of sperm whales, but substantial numbers of fin and humpback whales are on the shelf).

Bering Sea and Aleutian Islands

There have been relatively few reports of killer whale predation in this region (total $n = 17$). This is likely primarily due to the lack of killer whale studies in this region until recently. In the BSAI region, 41% of the observations of predation involve pinnipeds (Fig. 3C), including 2 northern fur seals, 2 walrus (*Odobenus rosmarus*), 2 harbor seals, and 1 Steller sea lion (Table 1). The next largest category was that of small odontocetes, with 24% of the observations (4 beluga whale events). Large baleen whales represented 18% of the observations, representing reports of 3 predation events on gray whales. Minke whale predation events have been reported twice (12%), and a confirmed kill of a sea otter has been reported once (the three other attacks reported in Hatfield *et al.* 1998 were not reported as confirmed kills). No predation events on sperm whales have been reported. It should be noted that several observations of killer whales killing and eating fur seals in the Bering Sea have been reported in the literature before 1950 (Tomilin 1957, Hanna 1923, Zenkovich 1938), and were not included in these totals.

Current Biomass of Marine Mammals

Details of how these calculations were made are in Wade *et al.* (submitted).

Western Coast of North America

In the WCNA region, 74% of the marine mammal biomass is represented by large baleen whales and sperm whales (Fig. 4A), with fin and blue whales representing the greatest portion (Table 6).

Pinnipeds represent 16% of the biomass, sperm whales represent 5%, and minke whales and small odontocetes together represent 5%.

Gulf of Alaska

Overall, the total marine mammal biomass in the GOA region was approximately one third of the biomass in the other two regions (Table 7). Large baleen whales represent 94% of marine mammal biomass (Fig. 4B), with the greatest proportion of that accounted for by fin and humpback whales. Pinnipeds represent 4% of the biomass, and minke whales and small odontocetes together represent 6%.

Bering Sea and Aleutian Islands

Total biomass of marine mammal species available as prey to killer whales in the Bering Sea and Aleutian Islands was the highest of the three regions (Table 8). Large baleen whales represent 83.4% of the estimated marine mammal biomass (Fig. 4C), with the majority of that biomass in fin, gray, and humpback whales. Pinniped biomass was 10.2%, with the majority of that biomass northern fur seals. Minke whales and small odontocetes represent 5.1% of the biomass, with sea otters representing 0.3% of the biomass.

Trends in Biomass

Western Coast of North America

At least three species of large whales have increased within this region in recent decades: humpback, gray and blue whales have likely been increasing since commercial catches ceased, although conclusions are limited by an inadequately extensive time series. Biomass of blue whales is the highest of any species; estimates of abundance of blue whales have been relatively stable since 1992, but this species is strongly believed to have increased from previous decades. Mark-recapture abundance estimates indicate that humpback whales have increased since 1992 (Fig. 5). Gray whales, which seasonally pass through this region, have increased since at least 1967 (but are not plotted here – see BSAI region). Fin whales and sperm whales have also likely increased since the cessation of commercial catches, but trend data are not available. Current abundance of sei whales is not large, but catches of this species were never large, so it is not clear whether sei whales were ever abundant in this portion of the eastern North Pacific. Minke whales were never heavily exploited in the eastern North Pacific, and may not have experienced significant changes in abundance.

Pinniped species and sea otters have all increased overall since the 1960s (Fig 5). Some of these species were hunted for fur (sea otters and fur seals), or were subject to bounty hunting in parts of their range (e.g. harbor seals and sea lions) because they were perceived as competitors for fish with humans. With the cessation of bounties in the 1960s, pinniped populations have increased. Elephant seals represent by far the largest biomass of the pinnipeds, which is estimated at more than three times the size of the next species. Elephant seal biomass has increased by ~25 times since the 1960s, and they have increased the range of their haul-outs in California. Harbor seal biomass has increased by a factor of ten since 1970, and has been relatively stable since the mid-1990s. This overall trend is reflected in most areas within the

region, with harbor seals having increased and then leveled off in British Columbia (Olesiuk et al. 1990), Washington (Jeffries *et al.* 2003), and Oregon (Brown 1997, ODFW unpublished data); they may also be leveling off in California. Available count data indicate that harbor seals have increased or remained stable in two regions of southeastern Alaska since the mid-1980s (Small *et al.* 2003), yet declined substantially in Glacier Bay during the 1990s. In the WCNA region, the next greatest current biomass is that of California sea lions, which have increased by a factor of eight since the late 1950s. Steller sea lion biomass has approximately doubled since the mid-1970s; most of this biomass is in southeastern Alaska, followed by British Columbia, with relatively little biomass in California and Oregon. Sea otters have also shown an overall increasing trend during this time period, but currently represent less than 2% of the biomass of elephant seals, and less than 10% of the biomass of Steller sea lions.

Several species of dolphin that are preyed on by killer whales are found in this region, including long-beaked common dolphins (*Delphinus capensis*) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Dall's porpoise (*Phocoenoides dalli*) and harbor porpoise (*Phocoena phocoena*) also exist in relatively high abundance. Little trend data are available for these species, but there is no specific information to suggest that they have changed in abundance through time in this area. Some bycatch has occurred in the drift gillnet fishery for swordfish, but take reduction measures are thought to have reduced the bycatch sufficiently to have prevented large declines in the populations concerned. Harbor porpoise are thought to have declined during the 1980s because of fisheries bycatch in gillnets, but have been relatively stable since 1990 (Forney 1995, 1999).

Gulf of Alaska

In the GOA, humpback whales represent the greatest biomass and have increased since at least the late 1980s (Fig. 6). Humpbacks have likely been increasing since the 1970s following the cessation of whaling in the 1960s. Estimates of fin whale abundance have increased since the late 1980s, but the increase is not significant. Humpback and fin whale biomass was similar to that of Steller sea lions in the mid 1980s, but is much greater now.

Steller sea lions represent the largest pinniped biomass, but have declined since monitoring started in the mid-1970s (Fig. 6). Harbor seals have been monitored in the eastern Kodiak Archipelago and in Prince William Sound, with declines in Kodiak from the late 1970s through the early 1980s, followed by increasing numbers since the early 1990s (Pitcher 1990, Small *et al.* 2003) when the Steller sea lion decline continued. Seal numbers in Prince William Sound have declined since the mid-1980s.

Quantitative trend data have not been reported for sea otters in this region, but unpublished descriptions of trends are available. Sea otters are reported to have declined throughout a large portion of the range of the southwestern stock in the GOA, particularly along the southern side of the Alaska Peninsula and in the Kodiak Archipelago (USFWS Stock Assessment Report). However, sea otters have slightly increased in the Shelikof Strait area, although this does not offset the declines seen in other portions of the stock's range. The south-central stock of the sea

otter includes Prince William Sound, Cook Inlet and Kenai Fjords. Although sea otters were killed during the Exxon Valdez oil spill in 1989, the current trend of this stock is thought to be stable or slightly increasing.

Bering Sea and Aleutian Islands

Current biomass in this region is dominated by gray, fin, and humpback whales. The gray whale population has substantially increased since the late 1960s, and has been roughly stable in size since the mid-1980s (Fig 7). Note that the gray whale biomass is plotted as 50% of the total population biomass – this was an arbitrary determination to reflect that the great majority of the gray whale population is further north in the Bering Sea for about half of the summer, and is thus unavailable to killer whales in the eastern Bering Sea and Aleutian Islands. Fin whale biomass is approximately equal to this gray whale biomass, and was estimated to be about three times greater than humpback whale biomass. Humpbacks have been documented to have increased in the eastern Aleutians Islands; fin whales appear to have increased but the increase is not significant. Both species are thought to have increased since the 1970s following the cessation of commercial whaling.

The species with the next greatest biomass is the northern fur seal, reflecting the very large breeding population on the Pribilof Islands. Overall, fur seals declined from 1950 until recent years. There is a rich history of information and data associated with the population of northern fur seals that breeds on the Pribilof Islands extending back hundreds of years (Gentry 1998). There were at least 3 periods of population decline between the mid-1800s and 1984, the last of which (mid-1950s to 1984) is the one discussed by Springer *et al* (2003). Based on pup production estimates, the Pribilof Island fur seal population declined from 1956 to 1970, increased slightly from 1970 to 1976, then declined again through 1984 for a total decline of approximately 57%. Between 1984 and the late 1990s, the fur seal population on the Pribilof Islands was relatively stable, but has declined at approximately 6% per year since 1998 (Towell *et al.*, in review).

A conservative estimate of minke whale abundance (uncorrected for whales missed on the trackline) leads to an estimate of biomass similar to that of the current biomass of fur seals. No trend information is available for minke whales; the lack of substantial commercial takes suggests that minke whale abundance may have been relatively stable over the last several decades.

In the mid 1970s, the biomass of Steller sea lions was similar to the biomass of fur seals, but Steller sea lions declined substantially during the 1980s and by the 1990s were only about one fourth the biomass of fur seals. Observations reported in the literature suggest that Steller sea lions started declining prior to the 1980s, perhaps as early as the late 1960s. Northern fur seals and Steller sea lions appear to have declined simultaneously during the early 1980s, but the fur seal population leveled off while the Steller sea lion population continued to decline. Both populations declined during the 1990s, but during this time period fur seals declined at a greater rate than Steller sea lions.

Walrus (*Odebenus rosmarus*) were estimated to have increased substantially during the 1960s, and were roughly stable in the 1970s and early 1980s. Walrus biomass in the southeastern Bering Sea (note that this is only ~20% of the total population biomass) was approximately the same as the biomass of Steller sea lions in the 1990s. The largest concentrations of harbor seals are in southern Bristol Bay, and numbers in the late 1980s and early 1990s appear similar to the late 1960s and early 1970s, with an apparent increase in the mid-1970s. A preliminary comparison of counts in the Aleutian Islands, west of Samalga Pass, indicate numbers decreased substantially from the late 1970s through 1999 (USFWS, NMFS, and ADF&G unpublished data). Seal biomass was never great in the Aleutian Islands and therefore regional biomass is dominated by the harbor seals in Bristol Bay. Sea otter biomass in the 1960s was similar to harbor seal biomass, but declined substantially in the 1990s (Estes *et al.* 1998).

Sperm whales occur in deeper water areas of the BSAI, including the continental slopes, but no surveys have been conducted to reliably estimate their abundance.

Commander Islands

The largest pinniped biomass in the Commander Islands has been that of northern fur seals. Overall, fur seals have increased throughout the entire time period they have been monitored (1958 until 1994) (Fig. 8). In the 1970s, fur seal biomass was approximately five times greater than Steller sea lion biomass, and twenty-five times greater than harbor seal biomass. Steller sea lions declined from the late 1970s through the 1980s, and approximately leveled off in the 1990s at a similar biomass to that of harbor seals. Harbor seals were roughly stable throughout the period they were monitored. Sea otters increased in the 1980s, declined in the 1990s, increased again in the early 2000s, and overall were roughly stable. In the 1990s, sea otter biomass was roughly half the biomass of both harbor seals and Steller sea lions.

Potential causes of the declines of pinnipeds in Alaska

The western stock of Steller sea lions declined substantially in the central and western Gulf of Alaska and Bering Sea/Aleutian Islands regions (NMFS 1992). The decline was first observed in the eastern Aleutian Islands and may have begun as early as the late 1960s or early 1970s (Braham *et al.* 1980). The decline spread west through the Aleutian Islands and east throughout the central and western Gulf of Alaska, reaching its maximum rate of decline between 1985 and 1989 at approximately -15% per year (Loughlin *et al.* 1992; York 1994). Through the 1990s, the decline slowed across the range of the western stock to approximately 5% per year (Sease and Gudmundson 2002), and may have nearly abated since 2000 (Fritz and Stinchcomb, in press).

During the 30 years of population decline, both top-down and bottom-up forces likely affected the sea lion population. Over 20,000 Steller sea lions were killed between the 1960s and 1980s as a result of being accidentally caught during groundfish fishing operations (Loughlin and Nelson 1986, Perez and Loughlin 1991), but in the 1990s, incidental catches totaled less than 300 (Perez 2003). In addition, approximately 45,000 pups were killed in the eastern Aleutian Islands

and Gulf of Alaska between 1963 and 1972 (Pascual and Adkison 1994). Numbers of sea lions shot illegally may also have been high in the 1980s (Trites and Larkin 1992). However, direct mortality sources alone were not responsible for the decline experienced by the sea lion population in the 1970s and 1980s (Pascual and Adkison 1994), suggesting that density-dependent factors were also implicated.

The primary bottom-up, density-dependent factor responsible for the sea lion decline is a reduction in prey biomass and quality caused by either environmental variability (Trites and Donnelly 2003) or commercial fisheries (Braham *et al.* 1980; NMFS 2000). Density-dependent responses in the western Steller sea lion population were lower growth and pregnancy rates in the 1980s than the 1970s (Calkins and Goodwin 1988; Pitcher *et al.* 1998). Thus, during and following a period when direct sources of sea lion mortality were at high levels, the carrying capacity was likely declining as well. This apparently continued through the 1990s as evidenced by the persistent decline in sea lion counts (Sease and Gudmondson 2002) as well as a possible decline in fecundity (Holmes and York 2003), even as the rates of human-related direct mortality were greatly reduced. These shifts in life history parameters during the declines argue against killer whale predation as a main cause of the decline, as, for example, there is no direct reason why increased killer whale predation would lead to a decline in fecundity.

The declines of northern fur seals have been investigated by several authors. York and Hartley (1981) estimated that known direct kills of females alone explained approximately 70% of the decline in the Pribilof fur seal population from 1956 to 1980. From 1956 to 1968, approximately 315,000 female fur seals were killed on land at the Pribilof Islands in an attempt to increase the productivity of the stock (York and Hartley 1981; Gentry 1998). In addition, approximately 40,000 fur seals were killed as part of U.S., Canadian and Japanese scientific pelagic collections in the North Pacific Ocean from 1958-1974, with roughly three-fourths of these females (R. Ream, pers. comm.). Interestingly, instead of increasing the productivity of the stock, pregnancy rates declined and the mean age at first reproduction increased (Trites and York 1993). The remaining 30% of the decline is unexplained, but York and Hartley (1981), Fowler (1987) and Gentry (1998) attributed it largely to one or all of a variety of factors: 1) methodological problems associated with pup production estimation; 2) changes in oceanic conditions; 3) entanglement in marine debris such as packing bands or discarded trawl netting; or 4) competition with groundfish fisheries whose catches in the eastern Bering Sea increased considerably in the early 1970s and have remained at approximately 2 million mt per year (NPFMC 2004). Furthermore, an unknown number of female fur seals and pups were killed by Russia during both on-land and pelagic collections. With the major portion of the population decline from 1956 to 1980 due to direct kills of females by humans, and the population relatively stable thereafter until 1998, it is unlikely that killer whale predation contributed significantly to the population dynamics of Pribilof fur seals during this period.

Not all northern fur seal breeding colonies in the North Pacific had similar population dynamics through the late 20th century. Pup production on Robben Island, Russia, was somewhat similar to that of the Pribilof Islands, peaking in 1967, declining steadily through 1989 (Gentry 1998),

but increasing between 1995 and 1999 (V. Burkanov, pers. comm.). Interesting with respect to the Springer *et al.* (2003) hypothesis were the increases in pup production at the Commander and Kuril Island fur seal rookeries from the mid-1960s through the mid-1980s while the Robben and Pribilof populations were declining by over 50% (Gentry 1998). Furthermore, rookeries became reestablished on San Miguel Island, CA (in the mid-1970s) and on Bogoslof Island, AK (in the late 1980s) (Gentry 1998; Ream *et al.* 1999).

The amount of research on harbor seals has been substantially less than that for Steller sea lions or for fur seals. Unfortunately, the information that would be required to fully assess the possible causes of harbor seal declines in the 1970s and 1980s was not obtained during the period of decline. In particular, unlike sea lions, there are no data to investigate whether reduced growth or pregnancy rates occurred for harbor seals, and thus evidence for reduced survival or reproduction due to reductions in prey biomass or quality does not exist. There is some indirect evidence, based on the timing of pupping and haul-out behavior, that harbor seals may have been nutritionally limited in the late 1970s in the Kodiak area (Jemison and Kelly 2001); however, this evidence is not definitive. Thus, although predation could have been a factor in the decline of harbor seals, numerous other factors could also have been the cause, including contaminants, disease, parasites, subsistence hunts, disturbance, illegal shooting, incidental take, and reduction in prey biomass and quality.

SECTION 3: TRANSIENT KILLER WHALE DENSITY VERSUS DENSITY OF PREY

Material in this section is from Wade *et al.* (unpublished).

The line-transect surveys conducted from 2001-2003 have been used to estimate the abundance of killer whales in the nearshore waters of the Aleutian Islands and western Gulf of Alaska (Zerbini *et al.* unpublished *a*). Of course, data on other species of cetaceans was collected as well. Abundance and density estimates of fin, humpback, and minke whales were calculated in Zerbini *et al.* (unpublished *b*). Density estimates of Dall's porpoise and northern fur seals (from 2003 data only) have also been calculated (Zerbini unpublished data). Abundance and trend data are also available for Steller sea lions (F. Lowell, pers. comm.).

The density of transient killer whales was plotted against the density of these other marine mammal species, by area. The spatial areas approximately match those defined for monitoring Steller sea lions, and are 1) eastern Gulf of Alaska, 2) central Gulf of Alaska, 3) western Gulf of Alaska, 4) eastern Aleutian Islands, and 5) central Aleutian Islands). No data on cetacean density is available from the western Aleutian Islands.

Correlation plots are shown in Figure 8. With only 5 data points, it is not surprising that most of the correlations are not statistically significant at the 0.05 level. A negative correlation is shown for Dall's porpoise ($p=0.15$). Little correlation is seen for minke, fin, humpback, fur seals, and Steller sea lion abundance (p -values all >0.40). The one strongly significant correlation was a

positive correlation between transient killer whale density and Steller sea lion trends from 1990 to 2004. ($p=0.02$).

In this context, correlations between killer whale density and the density of their potential prey can be viewed in two ways. On one hand, a positive correlation could be interpreted as killer whales have aggregated where that prey is at the highest density. On the other hand, a negative correlation could be interpreted that killer whale predation has led to a decrease in the density of that prey. Correlation data alone cannot distinguish these two possibilities.

There are many other factors that determine the distribution and density of marine mammal species, and bottom-up forcing may have more to do with the distribution of these species than killer whales (e.g., Dall's porpoise may be at higher densities in areas that contain a high density of their prey). However, the significant positive correlation between killer whale density and trends in Steller sea lions suggests, at least, that transient killer whales have not had a major role in restricting the trends of Steller sea lions. The area of highest transient killer whale density (and abundance) is the area where Steller sea lions have actually increased over the last 14 years. It should be noted that to make this conclusion, one has to assume that the distribution and density of killer whales from 1990 to 2004 was similar to their distribution and density as measured in 2001-03. Barrett-Lennard et al. (1995) hypothesized that killer whale predation could be sufficient to retard the recovery of Steller sea lions once they had become depleted (fallen into a so-called "predator pit"). This positive correlation suggests that, at least in the eastern Aleutians and western Gulf of Alaska, Steller sea lions were not in a "predator pit" due to predation by killer whales.

SECTION 4: TRANSIENT KILLER WHALE ENERGETIC REQUIREMENTS

Material in this section is a preliminary analysis from Wade *et al.* (unpublished).

From Table 1, it is clear that killer whales can prey on a variety of marine mammal prey, though the exact proportions of prey may be unknown. A hypothetical diet for transient killer whales in the Aleutian Islands, Bering Sea, and Gulf of Alaska was constructed, using the list of species shown in Table 1 for those regions. The one exception was that fin whales were left off, even though there is one reliable report of killer whales killing a fin whale in the Gulf of Alaska. Energetic information was used to extrapolate to numbers killed of each marine mammal prey species.

A population size of 250 transient killer whales was assumed. Killer whale daily energetic requirements were assumed to be between 176,000 and 200,000 kcal per whale/day (Williams et al. 2004, Barrett-Lennard et al. 1995). Specifications of prey energy and other parameters are shown in Table 2, based mainly on numbers presented in Williams et al. (2004). A hypothetical diet is shown in Table 3, by month, roughly based on the hypothesis of seasonal prey switching (Durban et al. unpublished) and proposed movements (i.e., Durban and Pitman unpublished). In

this scenario, the killer whales feed on primarily gray whales and fur seals in May and June, and October (when gray whales are available in the eastern Aleutians during migration), and feed on all other marine mammals (except large whales) that are available in March, April, July, August, and September. During the four months from November through February, it is assumed the killer whales are eating something else, either because they have moved south to feed on pelagic populations of Dall's porpoise, Pacific white-sided dolphins, and minke whales (populations whose abundance is not reflected in abundance estimates compiled in Figure 3 and Table 4), or, alternatively, on other species that become available in the SE Bering Sea in winter, such as ice seals, larger populations of beluga, and bowhead whales. The allocation of prey (as proportion individuals preyed upon) was compiled across the 8 months to create a total fraction of transient killer whale prey represented by that species. The daily energetic requirement of killer whales was multiplied by 243 days, and given the specifications in Table 2. The number of individuals of each species that would be required to meet the total energetic requirements was calculated.

Values of parameters were randomly sampled from the given ranges to make the calculations. This was repeated 1000 times, and the mean number killed of each species was summarized. Total number of individuals preyed upon is shown in Table 4, along with the estimated abundance of each species in the Aleutian Islands, SE Bering Sea, and Gulf of Alaska (from Wade et al. submitted). The fraction of each population killed per year is also shown. For the most part, these represent fractions of each population that are roughly sustainable (i.e., less than $\frac{1}{2}$ of an assumed maximum rate of increase for each species). It should be noted that the abundance estimate used for minke whales is likely to be negatively biased by at least 50% (because the probability of detection on the trackline is much less than 1.0), so that fraction is likely much smaller than what is presented. Abundance of the other cetacean species is also likely under-estimated, as not all areas have been covered by surveys.

It should be re-emphasized that the calculations are based solely on the hypothetical diet shown in Table 3, and the assumed energetic values in Table 2. However, it suggests that a population of 250 killer whales could be sustainably supported by the species of marine mammal prey that killer whales have been observed to prey on in the Aleutian Islands, Bering Sea, and Gulf of Alaska.

ACKNOWLEDGMENTS

Much of the material presented here has been pulled in from manuscripts at various stages of completion that include a multitude of co-authors, and I appreciate greatly their efforts that have led to this accumulation of information. I particularly thank Josh London for help with energetic calculations.

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Table 1. Summary of observations of marine mammal prey killed or eaten by killer whales in the three regions considered in the eastern North Pacific since 1950. Most records are visual observations of live killer whales, but recent data from stomach contents of killer whales are also included. Attacks which were not confirmed as kills were not included. From Wade *et al.* (submitted).

Species	WCNA	GOA	BSAI
Sea otter	1	2	1
Walrus	0	0	2
Harbor seal	112	25	2
N elephant seal	20	0	0
California sea lion	48	0	0
Steller sea lion	26	16	1
unid.sea lion	5	1	0
Northern fur seal	0	0	2
Harbor porpoise	40	4	0
Dall's porpoise	33	16	0
L-b common dolphin	3	0	0
P white-sided dolphin	7	0	0
Beluga	0	3	4
Minke whale	6	6	2
Gray whale	40	0	3
Fin whale	0	1	0
Sperm whale	1	0	0
Total	342	74	17

Table 2. Specifications for energetic calculations. Fraction consumed relates to the part consumed.

Species	Mean Kcal/Kg (low-high)	Fraction assimilated	Fraction consumed	Part consumed
Gray whale	2500 (2000-3000)	0.87	0.50	muscle and blubber
Minke whale	2500 (2000-3000)	0.87	0.50	muscle and blubber
Beluga whale	2500 (2000-3000)	0.87	0.50	muscle and blubber
Harbor porpoise	2500 (2000-3000)	0.87	1.00	muscle and blubber
Dall's porpoise	2500 (2000-3000)	0.87	1.00	muscle and blubber
Pacific walrus	3250 (2000-4500)	0.87	0.75	muscle and blubber
Steller sea lion	3250 (2000-4500)	0.87	1.00	muscle and blubber
Northern fur seal	3250 (2000-4500)	0.87	1.00	muscle and blubber
Harbor seal	3500 (3000-4000)	0.83	1.00	whole animal
Spotted seal	3500 (3000-4000)	0.83	1.00	whole animal
Sea otter	1800 (1500-2100)	0.83	1.00	whole animal

Table 3. Hypothetical diet allocation of transient killer whales by month in the Aleutian Islands, SE Bering Sea, and Gulf of Alaska. The numbers represent the fraction, as individuals killed, that each species represents in the diet of the killer whales. "Fraction of total" represents total fraction of diet, as individuals, for each species for the entire year.

	Gray whale	Minke whale	Beluga whale	Dall's porpoise	Harbor porpoise	Pacific walrus	Steller sea lions	Northern fur seals	Harbor seals	Spotted seal	Sea otter	Other
January												100
February												100
March		15	1	3	2	6	9	50	8	3	3	
April		15	1	3	2	6	9	50	8	3	3	
May	80							20				
June	80							20				
July		15	1	3	2	6	9	50	8	3	3	
August		15	1	3	2	6	9	50	8	3	3	
September		15	1	3	2	6	9	50	8	3	3	
October	80							20				
November												100
December												100
Fraction	0.200	0.063	0.004	0.013	0.008	0.025	0.038	0.258	0.033	0.013	0.013	0.333

Table 4. Hypothetical diet that could support 250 mammal-eating killer whales in the Aleutian Islands, Bering Sea, and Gulf of Alaska for eight months of the year. Fraction population is the fraction represented by the number of individuals killed of the estimated abundance of each species. The estimated number killed is based on the hypothetical diet allocation by month shown in Table 3.

Species	Abundance	# killed	Fraction population
Gray whale	22,052	458	0.021
Minke whale	3,327	186	0.056
Beluga whale	2,274	82	0.036
Harbor porpoise	77,862	2128	0.027
Dall's porpoise	53,505	1659	0.031
Pacific walrus	10,000	261	0.026
Steller sea lion	37,191	1201	0.032
Northern fur seal	888,120	60062	0.068
Harbor seal	43,488	3175	0.073
Spotted seal	59,214	1724	0.029
Sea otter	58,026	5787	0.100

Figure 1. Locations of sightings of transient killer whales during surveys from 2001-30. Below the map is a figure showing relative density of transient killer whales by area.

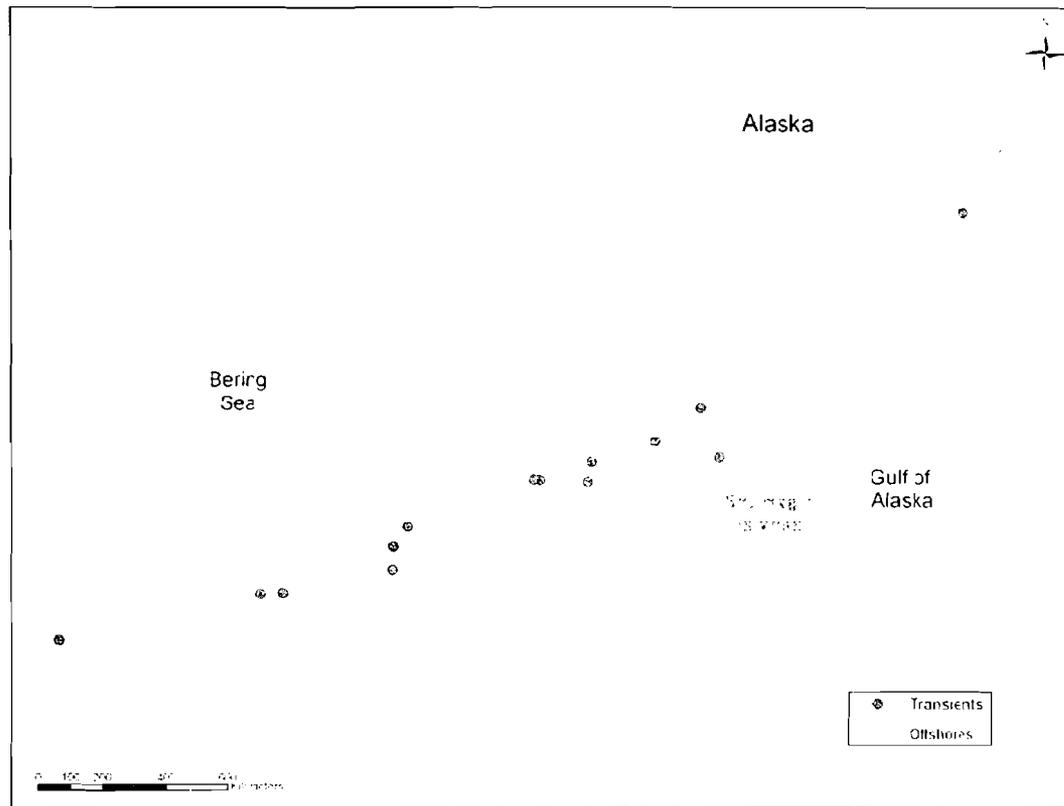


Figure 2. Map of North Pacific with labels of place names mentioned in the text.

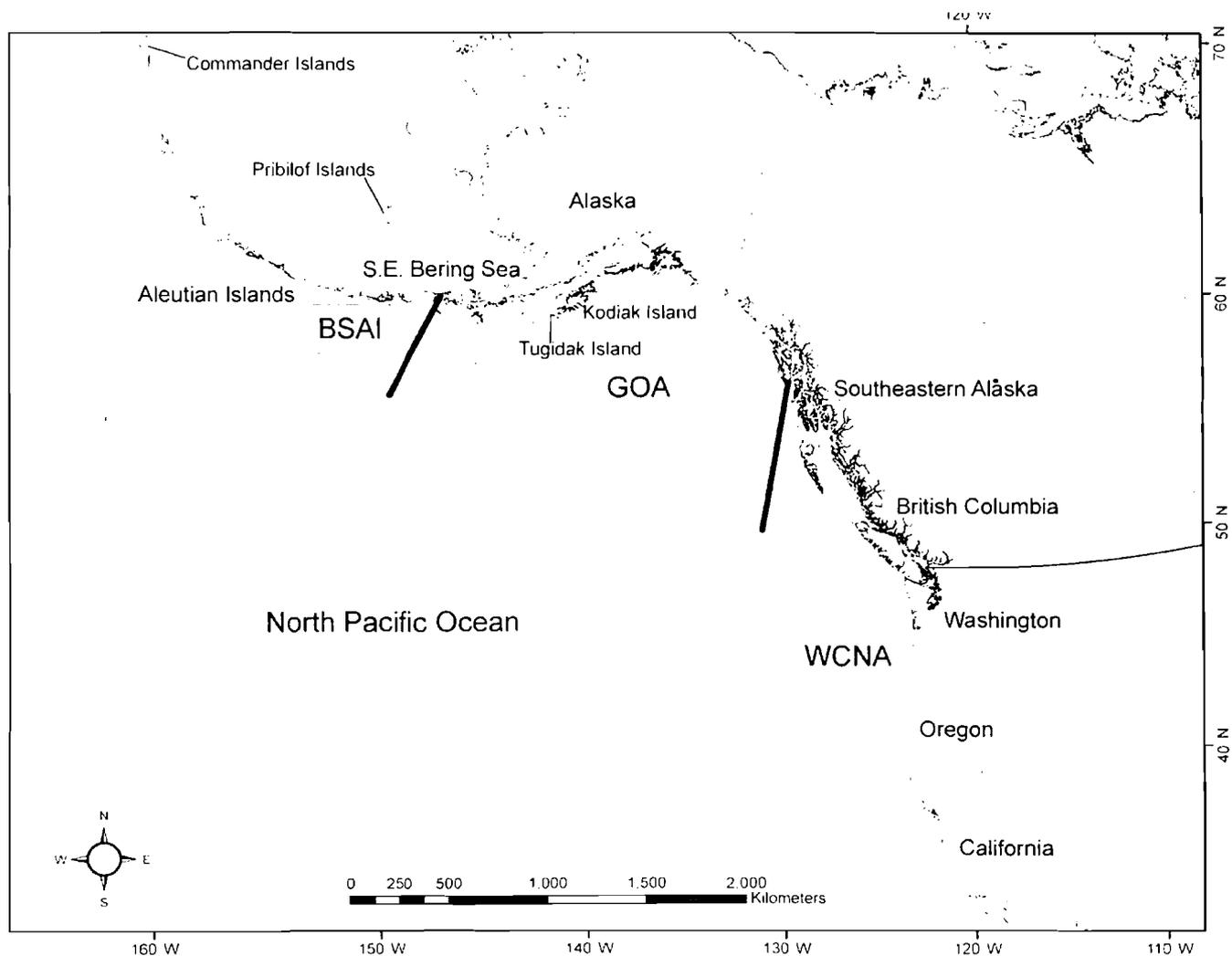
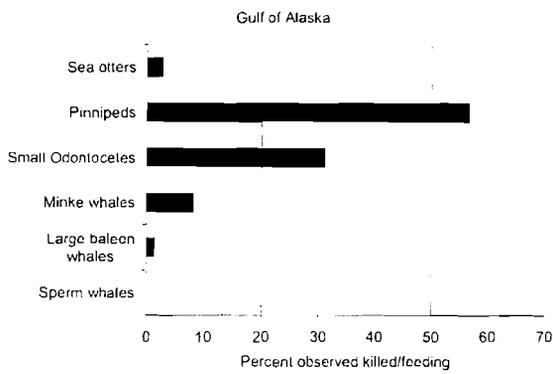
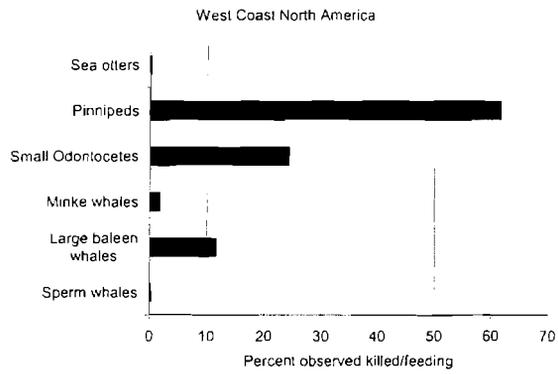


Figure 3. Percent of observations of marine mammal prey killed or eaten by killer whales in the three regions considered in the eastern North Pacific. From Wade *et al.* (submitted).

A.



B.

C.

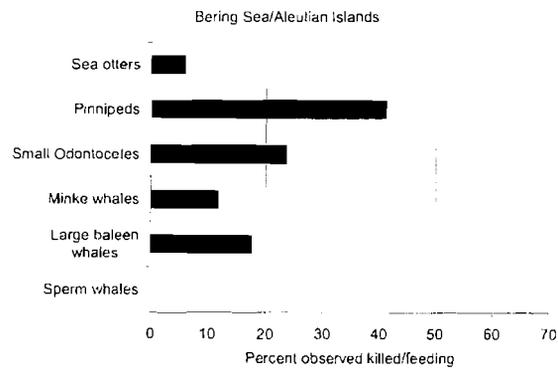
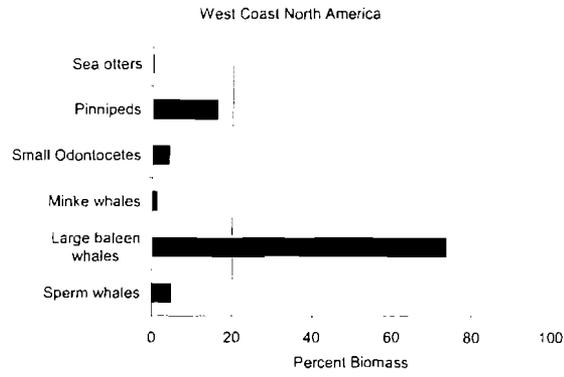
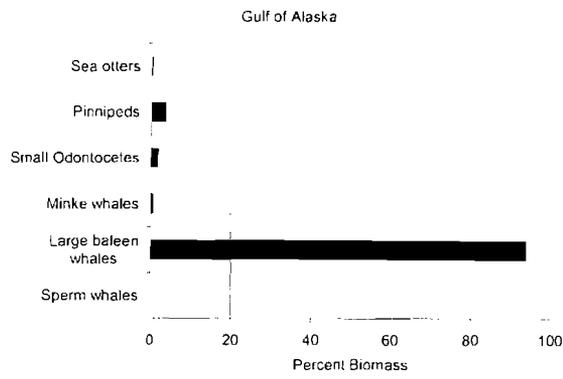


Figure 4. Percent biomass currently represented by potential marine mammal prey of killer whales in the three regions. From Wade *et al.* (submitted).
A.



B



C

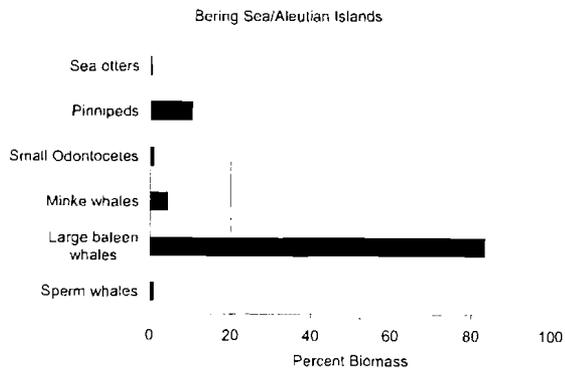
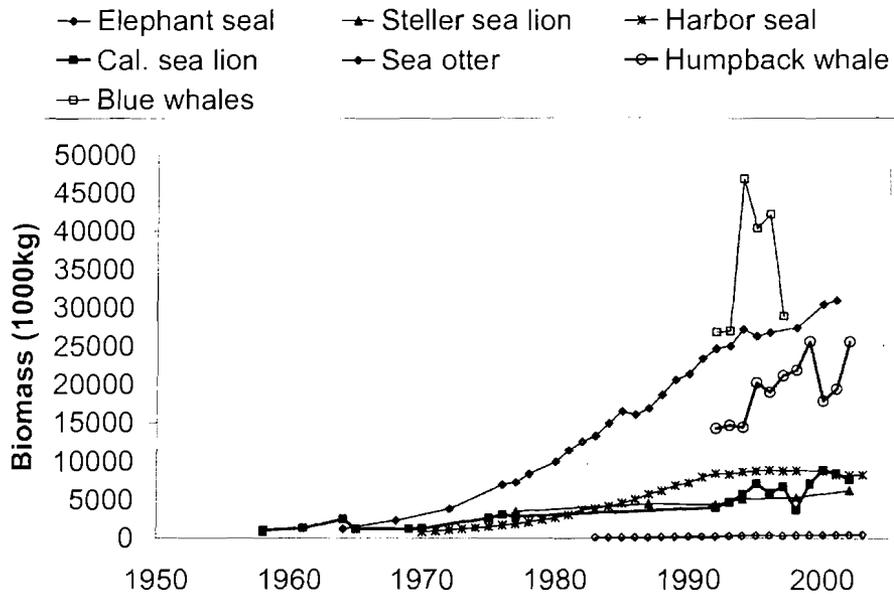


Figure 5. Trends in biomass of marine mammals from the West Coast of North America region. Panel B is identical to Panel A, but is shown at a larger scale so the species at lower biomass can be seen. From Wade *et al.* (submitted).

A.



B.

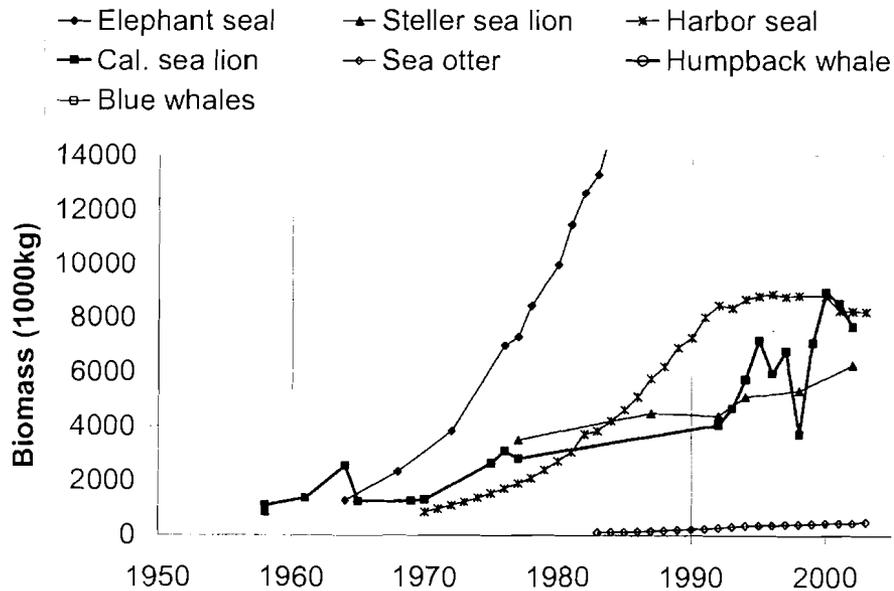
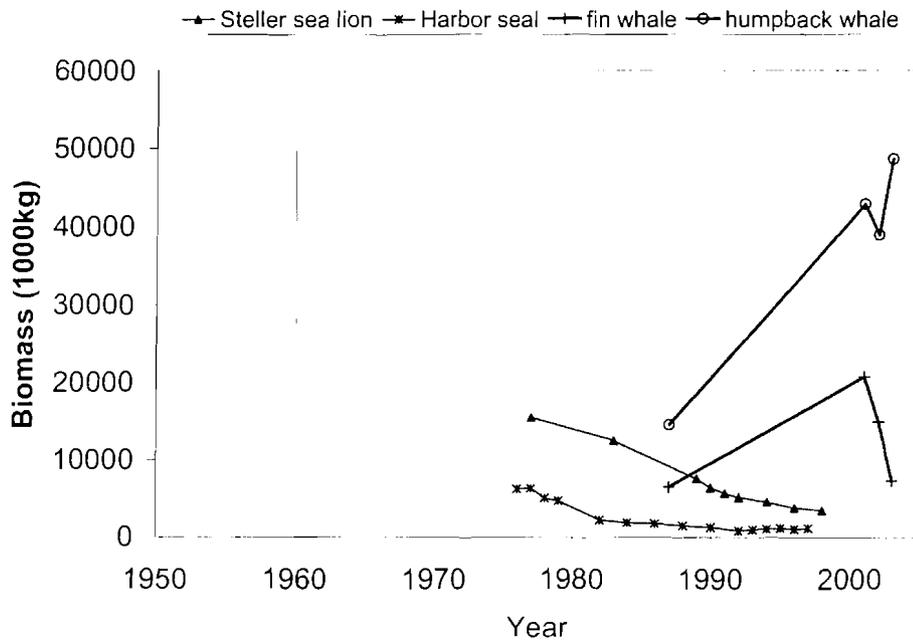


Figure 6. Trends in biomass of marine mammals from the Gulf of Alaska region. Panel B is identical to Panel A, but is shown at a larger scale so the species at lower biomass can be seen.



B.

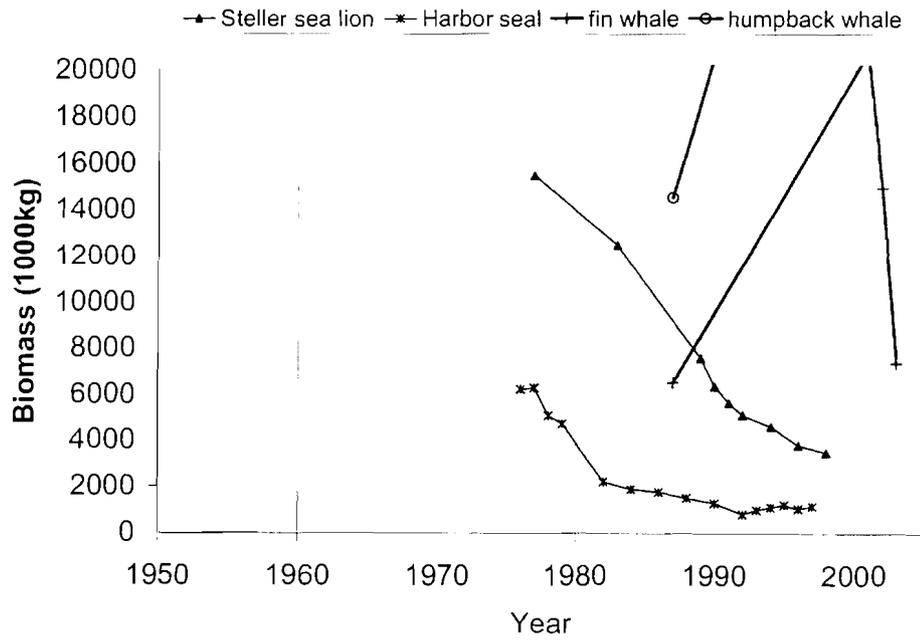
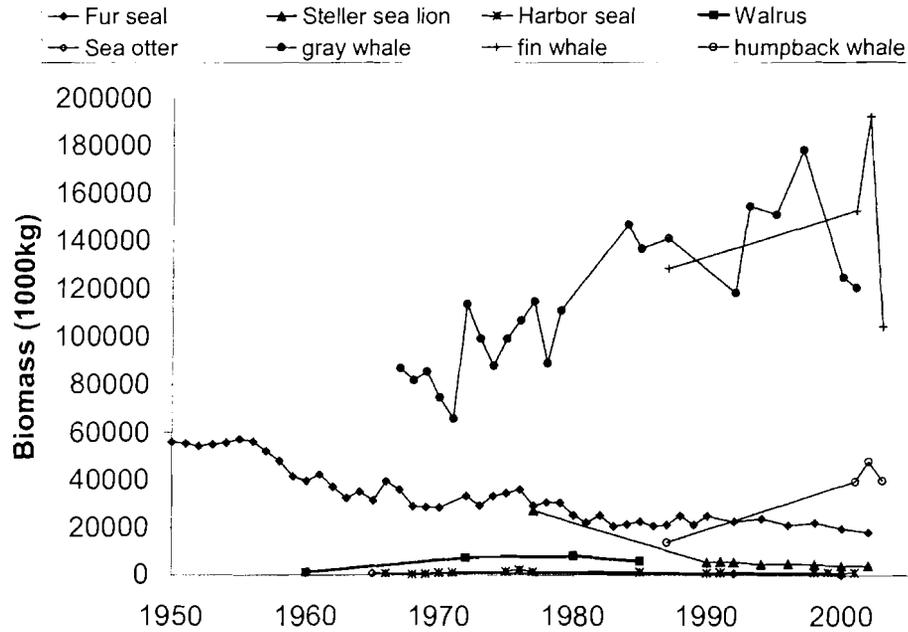


Figure 7. Trends in biomass of marine mammals from the Bering Sea/Aleutian Islands region. Panel B is identical to Panel A, but is shown at a larger scale so the species at lower biomass can be seen. From Wade *et al.* (submitted).

A.



B.

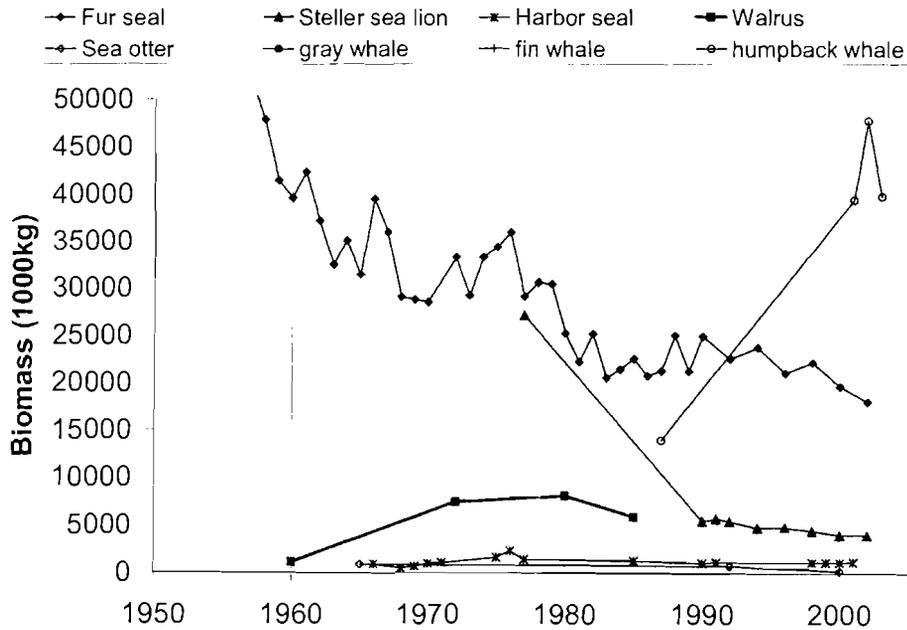
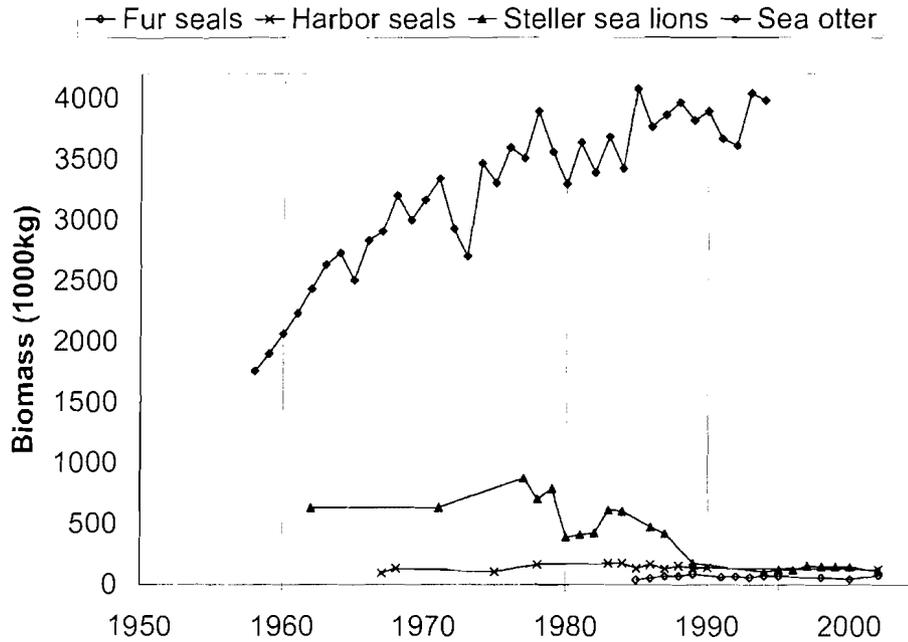


Figure 8. Trends in biomass of marine mammals from the Commander Islands. Panel B is identical to Panel A, but is shown at a larger scale so the species at lower biomass can be seen. From Wade *et al.* (submitted).

A.



B.

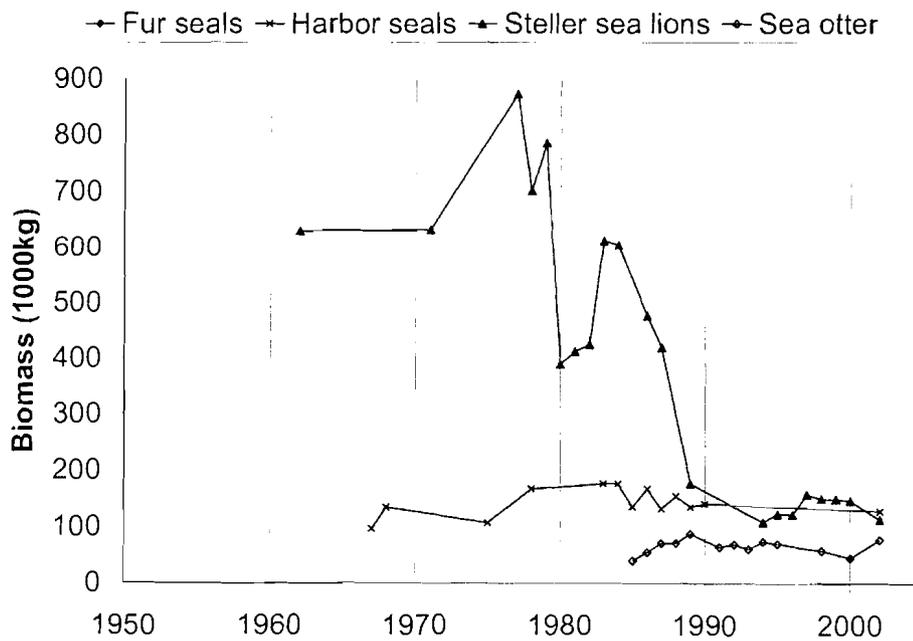
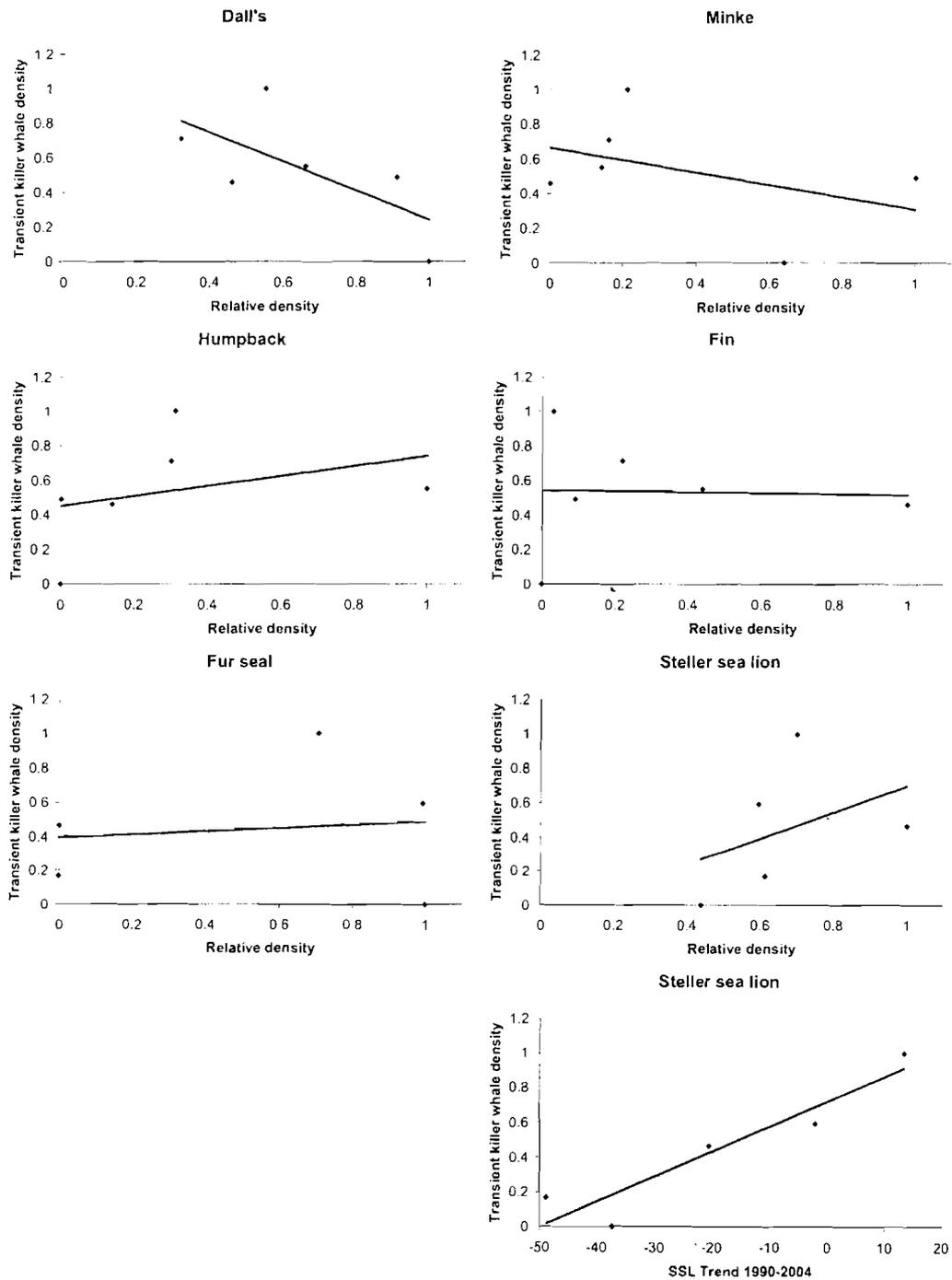


Figure 9. Correlations between transient killer whale density and the density of various marine mammal species in the Aleutian Islands and Gulf of Alaska. Cetacean and fur seal density estimates are from Zerbini *et al.* (unpublished *a*), Zerbini *et al.* (unpublished *b*), and Zerbini (unpublished). Note that the bottom panel is the correlation between transient killer whale density and the trend of Steller sea lions from 1990-2004, by area (Sea lion trend and abundance data from F. Lowell, pers. comm.).



MARINE MAMMAL COMMISSION
4340 EAST-WEST HIGHWAY, ROOM 905
BETHESOA, MD 20814

22 March 2005

Mr. Garth Griffin
Chief, Protected Resources Division
National Marine Fisheries Service
525 NE Oregon Street, Suite 500
Portland, OR 97232-2737

Dear Mr. Griffin:

The Marine Mammal Commission, in consultation with its Committee of Scientific Advisors on Marine Mammals, has reviewed the National Marine Fisheries Service's proposed rule (69 Fed. Reg. 76673) to list Southern Resident killer whales as a threatened species under the Endangered Species Act (ESA). The proposal is based on the Service's 2004 status review of Southern Resident killer whales. In turn, the outcome of the status review reflects the results of a recent workshop on cetacean taxonomy held in April-May 2004, which was sponsored jointly by the Service and the Commission.

The proposed listing is premised on three findings. First, North Pacific resident killer whales are a distinct, unnamed subspecies of killer whales, based on genetic, morphological, acoustic dialect, and behavioral differences between them and transient killer whales. Second, Southern Resident killer whales are a distinct population segment (DPS) of the North Pacific resident subspecies. To qualify as a DPS under the policy guidance published jointly by the National Marine Fisheries Service and the Fish and Wildlife Service in 1996 (61 Fed. Reg. 4722), the population must be considered both "discrete" in relation to the remainder of the species to which it belongs and "significant" to that species. Southern Resident killer whales are considered discrete based on genetics (both mtDNA and nuclear microsatellites), spatial distribution (summer range does not overlap the nearest neighboring group of resident killer whales), and behavior. They are considered to be significant for similar reasons—notably because Southern Resident killer whales are genetically and behaviorally unique and are the only resident killer whales in the California Current ecosystem along the west coasts of Washington, Oregon, and California. Third, Southern Resident killer whales appear to be at least threatened under the ESA, i.e., likely to become an endangered species in the foreseeable future.

Based on the above, the Marine Mammal Commission supports the Service's proposal to list Southern Resident killer whales under the ESA. However, the Commission finds the Service's preliminary determination that Southern Resident killer whales are "threatened" rather than "endangered" to be internally inconsistent, as well as inconsistent with the available data and ESA listing determinations for other species. At the end of page 76678, the proposed rule states, "the BRT [Biological Review Team] was concerned about the viability of the Southern Resident DPS and concluded that it is at risk of extinction...." Three paragraphs later the proposed rule states that "[t]his DPS is not presently in danger of extinction throughout all or a significant portion of its

Mr. Garth Griffin
22 March 2005
Page 2

range.” The latter conclusion appears to be based on a recent, slight increase in abundance (from 80 in 2001 to 85 animals in 2004). Nevertheless, the population remains small, has experienced a significant recent reduction that has yet to be explained, and is highly susceptible to catastrophic events such as oil spills and disease outbreaks because of its social structure and limited range adjacent to highly urbanized coastal areas.

Furthermore, population viability analyses conducted for the status review indicate that, even under optimistic conditions, Southern Resident killer whales have a 0.1-3.0 percent chance of extinction in 100 years. Under pessimistic conditions, the probability of extinction increases to 39-67 percent. This level of extinction risk indicates that Southern Resident killer whales should be listed as endangered under the ESA, particularly in light of their small population size, the lack of information regarding the factors controlling population fluctuations, and the possibility that necessary conservation measures might meet with local resistance.

Finally, the proposed rule does not include a measure to designate critical habitat for Southern Resident killer whales. Critical habitat designation provides a basis for ensuring that ESA section 7 consultations are conducted in the event that actions are proposed that could cause adverse modifications of critical habitat. This is an important tool for protecting habitat essential for recovery and conservation. The Commission notes that the ESA allows critical habitat designations to be separated from listing actions when the critical habitat of the species “is not then determinable.” The Marine Mammal Commission recommends that, in the case of Southern Resident killer whales, the Service proceed with a critical habitat designation as quickly as possible inasmuch as habitat degradation may be a primary cause for the current depletion of the population.

Please let me know if you have any questions about these recommendations or wish to discuss our comments.

Sincerely,



David Cottingham
Executive Director

cc: Laurie Allen

MARINE MAMMAL COMMISSION
4340 EAST-WEST HIGHWAY, ROOM 905
BETHESDA, MD 20814

14 August 2006

Ms. Donna Darm
National Marine Fisheries Service
Protected Resources Division
1201 NE Lloyd Boulevard, Suite 1100
Portland, OR 97232-1274

Dear Ms. Darm:

The Marine Mammal Commission, in consultation with its Committee of Scientific Advisors on Marine Mammals, has reviewed the National Marine Fisheries Service's 15 June 2006 *Federal Register* notice describing proposed critical habitat for the southern resident killer whale stock. The Service has done a commendable job of describing and weighing the issues involved in the designation of the stock's critical habitat. The recommendations and comments that follow are intended to support the proposed rule and related conservation efforts.

RECOMMENDATIONS

The Marine Mammal Commission recommends that the National Marine Fisheries Service establish critical habitat for the southern resident stock of killer whales as described in the *Federal Register* notice of 15 June 2006. In addition, the Commission recommends that the Service—

- recognize natural sound characteristics as an essential feature or primary constituent element of southern resident killer whale critical habitat;
- investigate all potential connections between sources of sound disturbance and actions authorized, funded, or carried out by the federal government to determine if a nexus exists, thereby allowing the Service to avail itself of all conservation tools under the Endangered Species Act, particularly section 7 consultations;
- implement a precautionary approach with regard to management of contaminants to prevent them from entering the Puget Sound environment;
- designate critical habitat for the southern resident killer whale stock up to the shoreline, rather than limit it to waters more than 20 feet deep; and
- initiate its investigation of winter habitat use by southern resident killer whales as soon as possible.

The *Federal Register* notice excludes 18 military sites from critical habitat designation based on the importance of those sites to military readiness activities in time of war. The sites comprise about four percent of the total area under consideration, and military activities in those areas are subject to the jeopardy standard under the Endangered Species Act. The Marine Mammal Commission recognizes the importance of military readiness. At the same time, the Commission encourages the Service to work with the Navy to monitor activities in the excluded areas and advise it of steps that should be taken to minimize potential destruction or adverse modification of killer whale habitat,

including but not limited to indirect effects of anthropogenic sound both within the excluded areas and more broadly. In that regard, a well-conceived monitoring program that is initiated as soon as possible—preferably before designation of critical habitat and before any activities are undertaken in those regions—would be useful. The results of such work could inform decisions concerning similar exclusions in the future.

RATIONALE FOR RECOMMENDATIONS

The Marine Mammal Commission offers the following explanation and discussion of its recommendations.

Sound as an essential feature of critical habitat

The best available scientific evidence indicates that resident killer whales use—and presumably depend on—sound for navigation, foraging, and communication. These functions are essential for physical growth, reproduction, survival, and, ultimately, population growth. It therefore seems indisputable that the whales in this stock require an environment that does not significantly interfere with their use of sound for these vital functions. The introduction of human-generated sound into the marine environment may affect killer whales by causing hearing loss or serious injury (probably an infrequent worst case involving exposure to high-intensity or high-energy sounds) or, more likely, masking or disturbance. For example, a paper by Morton and Symonds (2002) provides convincing empirical evidence that introduced noise can cause killer whales to abandon certain habitat. Those kinds of effects, although less serious in the short term, may nonetheless constitute a significant impediment to recovery of the southern resident stock if the introduced sounds persist over time, causing continuous or long-term disruption of natural habitat-use patterns and vital functions. For those reasons, the Marine Mammal Commission recommends that the National Marine Fisheries Service recognize natural sound characteristics as an essential feature or primary constituent element of southern resident killer whale critical habitat. Doing so is entirely consistent with the regulatory definition provided in the *Federal Register* notice, which states that essential features may include such things as food, water, air, or light (which, like sound, is a form of energy) and which also recognizes that such requirements include “habitats that are protected from disturbance.”

A federal nexus for management of sound

To minimize their effects, the human activities producing sounds that may disturb killer whales should be managed in a comprehensive and precautionary manner. Vessel traffic may be the single most important source of disturbance. For example, whale-watching vessels may have significant effects because of the noise they generate and their proximity to the whales, and such vessels should be managed cautiously, even in the absence of demonstrated effects. Similarly, large commercial vessels may have significant effects because they likely introduce the most acoustic energy into Puget Sound waters. In addition, military vessels using certain types of sonar may introduce episodic, high-intensity sound into the environment. The *Federal Register* notice indicates that the Service has not identified a nexus between the federal government and many of the vessel

types that may cause sound-related disturbance. The Marine Mammal Commission recommends that the Service carefully investigate all such potential connections to determine if such a nexus exists, thereby allowing the Service to avail itself of the conservation tools under the Endangered Species Act, particularly section 7 consultations. U.S. Coast Guard licensing procedures, for example, may provide such a nexus. The conservation tools made available may prove important in addressing activities that not only generate sound but also pose other risks to killer whales. For example, large vessels also pose risks related to collisions or introduction of contaminants via fuel spills or discharge of ballast or bilge water.

Precautionary management of contaminants

The *Federal Register* notice identifies water quality as an essential feature of critical habitat, and the Commission concurs with that finding. Southern resident killer whales carry significant concentrations of contaminants that may be affecting their immune or reproductive systems. The *Federal Register* notice also states that the Service presently “lack[s] sufficient information about the relationships among the sources of contaminants, their movement through the food chain, and their impact on killer whales....” This statement characterizes the state of knowledge regarding the effects of contaminants on marine mammals generally, and much work remains to be done to investigate the nature and significance of such effects. The Commission encourages the Service to continue its ongoing work and initiate such new work as may be needed, including careful assessment and monitoring of contaminant sources, tracking of contaminants through the food chain, and assessment of dose-specific impacts on individual animal health. Until cause-and-effect relationships are better understood, the Marine Mammal Commission recommends a precautionary approach with regard to management of contaminants by preventing them from entering the Puget Sound environment. We recognize that there are many good reasons for taking such an approach in addition to improving the prospects for recovery of killer whales. To a considerable degree, killer whales serve as sentinels that can help draw attention to unseen health hazards for people and many other organisms. Cooperative efforts with the Environmental Protection Agency, the National Pollutant Discharge Elimination System, the new Puget Sound Partnership, and the State of Washington are an important step toward improving marine environmental health for the benefit of many forms of life. This is particularly critical in view of the projected 25 to 30 percent increase in human population in Washington State by 2025, much of which will be in coastal counties that border Puget Sound or drain into the Sound via surrounding watersheds.

Water depths used by killer whales

The *Federal Register* notice indicates that critical habitat will be limited to waters more than 20 feet deep because killer whales, which can reach almost 30 feet in length, may not be able to maneuver in shallow waters. The Commission does not concur with that assumption and believes that the existing evidence (including evidence cited in the *Federal Register* notice) indicates that killer whales are indeed able to use waters shallower than 20 feet. For example, killer whales use shoreline rocks and beaches for rubbing in British Columbia and beach themselves to capture pinniped prey in the Southern Hemisphere. Killer whales have been observed preying on stingrays in waters so shallow that they had to turn onto their sides to maneuver and even stranded themselves, returning

Ms. Donna Darm
14 August 2006
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to the water by thrashing their tails (Visser 1999). In addition, as stated in the *Federal Register* notice, killer whales foraging in Puget Sound take advantage of channels and shorelines that constrict movement and force prey to congregate. Even if killer whales could not enter waters less than 20 feet in depth, human activities in shallow waters might displace nearby whales and alter their habitat-use patterns. For example, shallow-water aquaculture facilities using acoustic harassment devices such as those used in the areas studied by Morton and Symonds (2002) could cause such disturbance. Finally, creating a requirement for mariners, managers, and enforcement personnel to parse the nearshore environment along a 20-foot isobath would unnecessarily constrain and complicate regulatory efforts. For all of those reasons, the Marine Mammal Commission recommends that the Service designate critical habitat as extending up to the shoreline.

Wintering areas

The *Federal Register* notice indicates that available information is not sufficient to identify areas outside of Puget Sound used by southern resident killer whales during winter months. The notice also states that the Service will increase its efforts to study habitat-use patterns outside of the Sound to identify areas that should be designated as critical habitat. Clearly it is possible, if not likely, that habitats used by killer whales in the winter will prove to be as important as summer habitats for recovery of the population. It is essential that winter habitats be identified and given appropriate protection. The Marine Mammal Commission therefore recommends that the Service initiate its investigations of winter habitat use by southern resident killer whales as soon as possible.

Please contact me if you have questions about these recommendations or wish to discuss them.

Respectfully,



Timothy J. Ragen, Ph.D.
Acting Executive Director

cc: Frank Stone, Ph.D.
Usha Varanasi, Ph.D.

References

- Morton, A. B., and H. K. Symonds. 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia. *ICES Journal of Marine Science* 59:71–80.
- Visser, I. N. 1999. Notes: Benthic foraging on stingrays by killer whales (*Orcinus orca*) in New Zealand waters. *Marine Mammal Science* 15:220–227.

MARINE MAMMAL COMMISSION
4340 EAST-WEST HIGHWAY, ROOM 905
BETHESDA, MD 20814

2 March 2007

Mr. Garth Griffin, Chief
Protected Resources Division
National Marine Fisheries Service
1201 NE Lloyd Boulevard., Suite 1100
Portland, OR 97232

Dear Mr. Griffin:

The Marine Mammal Commission, in consultation with its Committee of Scientific Advisors on Marine Mammals, has reviewed the National Marine Fisheries Service's proposed recovery plan for the southern resident stock of killer whales (*Orcinus orca*). The Service has done a commendable job of assessing the status of the stock, evaluating factors that are likely to impede recovery, proposing recovery measures to address those factors, and identifying research activities necessary to inform and support recovery measures. The recommendations and comments that follow are intended to support the proposed recovery plan.

RECOMMENDATIONS

Based on its review of the proposed recovery plan for the southern resident stock of killer whales, the Marine Mammal Commission recommends that the National Marine Fisheries Service—

- revise the delisting and downlisting criteria to be more explicit and measurable;
- revise biological criterion 2 to be more precautionary with respect to numbers of reproductive males and females that would be required before consideration of downlisting or delisting;
- assign high priority to monitoring of population status in view of its importance for detecting changes in status, evaluating threats, and assessing the effectiveness of recovery actions;
- also assign high priority to monitoring and evaluation of the effectiveness of recovery actions; and
- clarify the relationships among specific delisting or downlisting criteria, recovery measures, and research and monitoring activities to ensure internal consistency in the recovery program.

RATIONALE

Delisting and downlisting criteria

The logic behind the proposed delisting and downlisting criteria is generally well developed. However, in a number of cases, the criteria would be improved by making them as explicit, measurable, and reliable as possible.

Certain criteria could be improved by specifying the period of time involved in their measurement. For example, the fourth bullet under biological delisting criterion 2 requiring “no significant increase in mortality rate for any sex or age class” and threats delisting criteria A.1, A.3, and D.3 should be clarified to indicate the relevant time frame for the observations, including collection of baseline information. For example, it would be useful to indicate if mortality would have to be monitored for 1 year, 5 years, 10 years, or some other time period before a finding of no significant impact could be reached. In this case, it might also be useful to indicate what constitutes a “significant” increase in mortality. In the same manner, it would be helpful to indicate the period of consideration for whale-watching impacts (e.g., a year, a decade) and how those impacts would be measured (e.g., number of vessels, noise levels, changes in behavior or distribution).

Similarly, delisting criterion B.2 should be clarified to indicate the amount of time that would have to elapse since the last removal or human-caused death before the southern resident stock could be considered for delisting. For example, would a year without a death be sufficient, or 10 years, and so on? In this regard, it is worth noting that ship strikes were implicated in the deaths of two southern resident killer whales in 2006. Presumably those deaths would fall under “other activities” and thus be considered under criterion B.2.

Other proposed criteria are not sufficiently measurable to be useful for indicating when delisting or downlisting should occur. For example, threats delisting criteria A.2, C.1, and E.5 all refer to “knowledge” as a requirement for recovery, but it is not clear how knowledge would be assessed or measured to determine that it was sufficient to consider the population for delisting or downlisting. An example of specific knowledge related to foraging might be determination of foraging patterns when the whales are outside of Puget Sound. Examples of possible measures for assessing disease might be gained from stranded animals or from photo-based assessment of animal condition. Similarly, criteria A.3 and D.3 both indicate a need for reduction in impacts, but it is not clear how much reduction is necessary. For example, would any reduction suffice or would a reduction need to be of sufficient magnitude to allow recovery?

Both threats-based downlisting criteria 1 and 2 are vague and leave too much room for interpretation. Here, too, it is not clear how “understanding” or “progress” will be measured or what level of “improvement” or “progress” will be necessary to merit downlisting. Without clarification of these criteria, it seems quite likely that downlisting decisions will be made solely on the biological criteria without consideration of potential threats to the population.

A number of delisting criteria require that management and research actions are effective, but it is not clear how effectiveness will be measured. Examples include criterion A.2, which seems to focus on the need for effective ecosystem-based fisheries management, A.4, B.1, E.1, E.2, and E.4. These criteria all could be revised or clarified to provide explicit measures of effectiveness. For oil spills, for example, effectiveness might be judged based on written plans, coordination meetings among respondents, stockpiling of response supplies and equipment, conducting drill exercises, identification of key habitat areas and development of measures to protect them, and so on. Efforts to assess the effectiveness of management actions also should take into account likely future conditions to ensure that they are up to the task.

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Finally, delisting criterion E.1 was not clear to us. The plan should be modified to clarify what is meant by “oil spill response plan wildlife brand section of NWACP.”

Although we believe that the delisting and downlisting criteria are comprehensive with regard to topics covered, we also believe they could be made more explicit and measurable. For that reason, the Marine Mammal Commission recommends that the delisting and downlisting criteria be revised accordingly.

Demographic considerations

Delisting and downlisting criteria also need to be reliable indicators of recovery. We question whether demographic criterion 2 reflects sufficient recovery for downlisting or delisting. Our concern is focused particularly on the number of males per pod. Mate selection by southern resident killer whales appears to follow the pattern exhibited by northern resident whales: mating only occurs between and not within matrilineal pods (e.g., a male from J pod would not mate with females from J pod but would mate with females from K or L pods). This behavior is thought to reduce the potential deleterious effects of inbreeding. However such effects could still accrue if very few reproductive males or females were present in one or more pods. For example, in recent years J and K pods each have had only one reproductive male; as a result, all the reproductive females from L pod were able to mate only with one of those two males. Clearly, those two males from J and K pods could contribute substantially to the genetic composition of the next generation of L pod animals, increasing the risks of inbreeding if one or both males carry detrimental alleles. In this regard, it is interesting to note that L pod has declined in recent years, while J and K pods (which had access to seven reproductive males from L pod) have increased. Although a variety of factors could have led to those disparate trends, it is clear that the demographic and social structure of the population is critical for sustained recovery. The Service recognizes the importance of demographic and social structure and explicitly addresses relevant concerns in biological delisting criterion 2 (“Available information on social structure, calf recruitment, survival, population age structure, and gender ratios of the Southern Resident DPS ... are indicative of an increasing or stable population”). This criterion focuses primarily on the demographic structure of the population and specifically requires “representation from at least three pods; at least two reproductive age males in each pod or information that fewer males are sufficient; and a ratio of juveniles, adults, post-reproductive, male and female individuals similar to the Northern Resident population model.”

Although it is clear that demographic structure is an important determinant of recovery potential, it is not clear that the standards set by biological criterion 2 for both delisting and downlisting are sufficient to promote and sustain recovery. In particular, it is not clear that the presence of two reproductive males in each pod is sufficient to support the reproductive rate necessary for recovery and avoid the deleterious impacts of inbreeding. Given the long calving interval and low number of reproductive females in the population, it is conceivable that very few mature males could impregnate a sufficient number of females to maintain the current reproductive rate. It is not clear, however, that opportunities for mating (i.e., contact between pods with available reproductive males and females) always result in successful mating (e.g., females may refuse mating attempts and some males may have low sperm quality or other such limitations). To address this

uncertainty, as well as inbreeding risks, the quantitative measures under criterion 2 should be revised to require sufficient numbers of reproductive males and females in each pod to support the reproductive rate necessary for recovery and avoid the deleterious effects of inbreeding. Further research will be necessary to determine "sufficient numbers," such as genetic research to determine the pedigree of extant killer whales and estimate the frequency with which individual males successfully mate with multiple females from other pods. Until such research has been conducted, the Marine Mammal Commission recommends that the recovery plan be revised to be more precautionary with respect to numbers of reproductive males and females that would be required to merit downlisting or delisting. To the extent possible, such default values should be derived from population viability analyses based on known demography, genetics, and population trends.

Priorities for Research and Monitoring

With regard to the setting of research priorities, we believe two areas warrant greater emphasis than indicated in the draft plan. The first pertains to monitoring of population status, which is given priority 2 or 3. Such monitoring is essential to detect changes in status in a timely fashion, evaluate the effects of risk factors, and guide recovery actions. One could reasonably argue that monitoring itself does not lead directly to recovery and therefore should not be given greater priority than actual recovery actions. At the same time, however, the recovery process will occur over a period of time and will almost certainly be dependent upon information about the status and trends of the population to guide recovery efforts. Whether the plan assigns a priority of 1, 2, or 3 to monitoring, we cannot realistically expect an effectively managed recovery program without such monitoring. For that reason, the Marine Mammal Commission recommends that during the implementation of the recovery plan, the National Marine Fisheries Service give high priority to the level of monitoring deemed necessary to guide recovery efforts.

The same arguments apply to evaluating the effectiveness of recovery actions, and the Marine Mammal Commission also recommends that the National Marine Fisheries Service give high priority to these activities. We do not advocate excessive focus on research alone, and the Service will have to weigh recovery and research activities carefully, but we believe evaluation of the effectiveness of recovery actions is important. In particular, the Service should monitor the effectiveness of (1) fisheries management actions to promote the recovery of salmon populations and thus ensure that adequate prey is available for the southern resident stock, (2) management actions to eliminate incidental or direct mortality of southern resident whales, (3) measures to reduce the level of disturbance to the population by whale-watching vessels, and (4) measures to reduce the levels of contaminants in Puget Sound and, through bioaccumulation, in the whales.

Linking delisting and downlisting criteria, recovery measures, and research

Although all recovery plan measures and research activities appear to be relevant, how and to what extent they will promote or help document recovery is not always evident. For example, it is not obvious how the management of atypical southern residents (recovery measure 4.1) will contribute to the recovery of the population. Also, the priority levels assigned to recovery and research activities do not always appear to be internally consistent. For example, research activities

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focused on southern resident diet (B.2), prey availability (B.6.1), and oceanography (B.8) were assigned priority 1. However, the relevant recovery action (1.1) to “rebuild depleted populations of salmon and other prey to ensure an adequate food base for recovery of the Southern Residents” was assigned lower priority, which seems inconsistent. As another example, preventing and responding to oil spills (2.1.1 and 2.1.2) were assigned priority 1, but the relevant research activity (B.6.4, “Determine risks from other human-related activities”) was assigned priority 2. These apparent mismatches in priority assignments may be justified, but a review of the relationships among delisting or downlisting criteria might reveal some inconsistencies that warrant reconsideration or highlight recovery measures or research activities that might otherwise be overlooked. For example, delisting criterion B.2 requires that there be no incidental or deliberate deaths associated with fisheries or other activities, but no recovery measures or research activities are included in the recovery plan to ensure that this criterion is met— although the Service clearly has programs in place to monitor and manage incidental mortality associated with commercial fisheries.

To ensure internal consistency in the recovery program, the Marine Mammal Commission recommends that the National Marine Fisheries Service review and clarify the relationships among specific delisting or downlisting criteria, recovery measures, and research and monitoring activities. Such clarification should help the Service make and justify decisions regarding research and recovery priorities.

Again, we believe that the Service has done a commendable job preparing this draft recovery plan, and we hope you will find our recommendations and comments helpful as you finalize the plan. Please contact me if you have any questions.

Sincerely,



Timothy J. Ragen, Ph.D.
Executive Director



MARINE MAMMAL COMMISSION

15 January 2010

Ms. Donna Darm
Assistant Regional Administrator
Protected Resources Division
National Marine Fisheries Service
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Seattle WA 98115

Dear Ms. Darm:

The Marine Mammal Commission, in consultation with its Committee of Scientific Advisors on Marine Mammals, has reviewed the National Marine Fisheries Service's 29 July 2009 proposed rule (74 Fed. Reg. 37674) and corresponding environmental assessment of measures to protect killer whales (*Orcinus orca*) in Washington's inland waters. The rule is intended to reduce the effects of vessel traffic on the whales, including the effects of whale-watching activities. It would be issued under the authority of the Endangered Species Act and the Marine Mammal Protection Act and primarily would establish a distance limit for vessels approaching whales, a "no-go" zone off San Juan Island, and a prohibition against positioning vessels in the path of whales. The Commission supports each of these elements of the proposed rule but questions whether they will be sufficient to protect killer whales from the adverse effects of vessel traffic and whale-watching. The Commission offers the following recommendations and rationale.

RECOMMENDATIONS

The Marine Mammal Commission recommends that the National Marine Fisheries Service implement all of the regulations described in the 29 July 2009 *Federal Register* to increase protection of killer whales, particularly the endangered southern resident stock, from vessel impacts in Washington's inland waters. In addition, the Marine Mammal Commission recommends that the Service—

- analyze and include additional regulatory provisions to establish stand-by zones at some distance beyond the 200-yard approach limit (e.g., beyond 400-600 yards) and limit the number of vessels (e.g., 10) that can be present between that boundary and the 200-yard approach limit at any one time;
- consider and include the safe operating procedures described later in this letter as part of any final rule governing vessel operations in the vicinity of killer whales in the inland waters of Washington State;
- adopt a regulatory speed limit of either seven knots or, at a minimum, a "slow safe speed" requirement (as defined in 33 U.S.C. § 2006 and the International Regulations for Preventing Collisions at Sea 1972 (see 33 U.S.C. § 1602)) within 400 yards of killer whales;
- develop a monitoring plan to assess compliance with and evaluate the effectiveness of the vessel approach regulations included in the final rule and describe that plan in the associated preamble;
- include implementation of a "no-go" zone off the west coast of San Juan Island; and

- move quickly to initiate discussions with Canada to develop comparable management strategies for killer whales throughout the inland waters of both Washington State and British Columbia. Among other things, the Service should seek comparable regulations, monitoring, enforcement, and outreach, assuming that these are not already in place.

RATIONALE

The most apparent effects of vessel traffic on killer whales include disturbance from the presence of the vessels and their associated noise, the risk of vessel strikes on the whales, and the masking of sounds important to the whales for navigation, foraging, or communication. Each of these effects has the potential to influence the behavior of the whales and to reduce their chances of survival and reproduction (directly in the case of ship strikes). Such effects would impede population recovery and conservation. The most common killer whales in the inland waters of Washington are members of the southern resident stock, which the Service has listed as endangered. This population numbers fewer than 100 animals, is vulnerable to several human-related risk factors, and has experienced significant declines in recent years that have not been fully explained by science. This killer whale stock clearly needs protection.

Approach Limits and Stand-by Zones

Vessel traffic is likely the most common and significant source of disturbance for southern resident killer whales. Commercial and recreational whale-watching vessels may be particularly harmful because, by intent, they operate close to the whales. Voluntary guidelines (i.e., Be Whale Wise) developed in collaboration with stakeholders were intended to keep the whale-watching vessels well away from the whales and thereby limit disturbance. However, vessel operators violate the guidelines on a frequent basis. In 2006 Soundwatch, a stewardship program of The Whale Museum in the Pacific Northwest, documented 1,281 cases in which vessels failed to follow the guidelines, and the frequency of non-compliance has increased since 1998. Such observations provide more than enough impetus for regulation of whale-watching activities, as reflected in the proposed rule.

Multiple factors may influence the extent to which whales are disturbed by approaching vessels. Such factors include the closeness and number of vessels, their configuration around the whales, the nature and level of noise from their engines, weather, bathymetry, proximity to shore, location, etc. The environmental assessment indicates that the mean number of commercial and recreational whale-watching boats following a given group of whales within ½ mile increased from 5 boats in 1990 to an average of about 20 boats for the years 1998 through 2006. On any given day, that number may be much higher. According to the assessment "...107 vessels followed one Southern Resident pod (Lien 2000); 76 boats simultaneously positioned around a group of 18 whales from K pod (Baird 2002); and up to 500 vessels came out on the weekends to view a group of whales from L pod in Dyes Inlet during the fall of 1997." Such fleets of vessels, most of which are motorized, must create considerable underwater noise. Furthermore, depending on the configuration of those vessels around the whales, they could form a barrier that impedes the whales'

movements. Under such circumstances, it is not hard to imagine that the whales would be at least distracted, if not disturbed, likely leading to physiological stress and changes in their behavior (e.g., increased respiratory intervals, prolonged transitions between activity states, decreased resting and foraging, increased directional changes). Such effects could in turn impose energetic costs and have population-level consequences (Lusseau et al. 2009).

Two of the three main measures of the proposed rule should help ensure that vessels maintain a reasonable distance from the whales. The first is the 200-yard limit for vessels approaching a whale or group of whales. Clearly, the relationship between distance and effects on the whales cannot be described exactly. But the Service reasonably included this measure based on evidence that it would reduce (1) the risk of vessel strikes, (2) disturbance of biologically important behavior, and (3) masking. The second measure prohibits vessel operators from positioning in the path of whales so that the whales either have to come close to the vessels or change their course. The Marine Mammal Commission supports these measures and recommends that the National Marine Fisheries Service implement all of the regulations described in the 29 July 2009 *Federal Register* notice to increase protection of killer whales, particularly the endangered southern resident stock.

Even with those measures, the Commission believes that more protection is needed. Because large numbers of vessels (as described earlier) sometimes aggregate in an area to watch a killer whale or a group of killer whales, the Service also should consider the use of stand-by zones to limit the number of vessels allowed to approach whales at any one time. The Service has included such measures in whale-watching guidelines on the East Coast. For example, in the Northeast Region and the Stellwagen Bank National Marine Sanctuary, guidelines include both a "Close Approach Zone" (equivalent to the approach limit) and a "Stand-by Zone" at some additional distance from the whales. Both zones limit the number of vessels allowed to be present within a particular distance. In addition, a vessel can remain in the Close Approach Zone only for a limited time if additional vessels are waiting in the Stand-by Zone. The Service's environmental assessment did not evaluate Stand-by zones and they are not included in the proposed rule. However, because such zones provide a mechanism to limit the number of boats near the whale(s), they also provide a mechanism to limit the amount of associated disturbance. The Marine Mammal Commission therefore recommends that the National Marine Fisheries Service analyze and include additional regulatory provisions to establish stand-by zones at some distance beyond the 200-yard approach limit (e.g., beyond 400-600 yards) and limit the number of vessels (e.g., 10) that can be present between that boundary and the 200-yard approach limit at any time. The Service also should consider limiting the time a vessel can remain at the 200-yard limit if other vessels are waiting in the stand-by zone. The Commission understands that such zones may be difficult to implement and enforce, but believes that they could be implemented successfully with sufficient outreach, self-policing, and additional enforcement as necessary.

Best Practices and Safe Operating Procedures

In addition, the Commission believes that the Service should use this rule to promote a number of other best practices and safe operating procedures. The Service need only review its own guidelines and rules in other parts of the country to identify them. Whale-watching guidelines in the

Northeast, Be Whale Wise guidelines in the Northwest, and North Atlantic right whale approach regulations all include safe operating procedures that could increase significantly the level of protection beyond that conferred by the currently proposed rule. These include (1) posting a dedicated lookout to assist the vessel operator in monitoring the location of all marine mammals; (2) avoiding sudden changes in speed and direction; (3) approaching and leaving stationary whales at no more than idle or "no wake" speed, not to exceed seven knots; (4) maintaining communication among multiple vessels at a site (via VHF channels 9, 13, or 16 for hailing) to coordinate viewing; (5) monitoring the presence of obstacles (vessels, structures, fishing gear, or the shoreline) to safe navigation; (6) putting engines in neutral if whales approach within 100 feet of a vessel and not re-engaging propulsion until the whales are observed to be clear of the area; and (7) ceasing whale-watching activities before dark by returning to port at least 15 minutes before sunset. All of these are commonsense measures that reduce the likelihood of striking or interfering with a whale or group of whales, and their application clearly is warranted by the southern resident killer whale stock's endangered status. Therefore, the Marine Mammal Commission recommends that the National Marine Fisheries Service consider and include the safe operating procedures discussed here as part of any final rule governing vessel operations in the vicinity of killer whales in the inland waters of Washington State.

Speed Limits

Vessel speed limits deserve special consideration because they provide an obvious mechanism to reduce the probability of vessel strikes, interference with the whales' use of sound for multiple kinds of behavior (e.g., communication, foraging), and adverse physiological responses by the whales. The current voluntary guidelines recommend speeds of less than seven knots when a vessel is within 400 yards of the nearest whale. Nonetheless, documented instances in which vessels failed to follow the speed guidelines increased from 13 in 2003 to 139 in 2006 (Tables 3.1 and 3.2 and Figure 3-9 in the assessment). The Service analyzed the effects of such a regulation in its environmental assessment and concluded that a speed regulation would result in only small reductions in risks associated with vessel strikes or auditory masking and would likely provide only small biological benefits to the whales. The Service also asserts that a speed restriction would be difficult to enforce without vessel tracking technology as it would need to measure both speed and distance from the whales.

The Commission disagrees with the Service's reasoning and conclusion regarding speed limits. In some cases, the benefits to the whales might be small. However, if increasing speed increases the noise introduced into the marine environment, and increasing noise increases the probability of masking, then slowing vessels should reduce the potential for significant masking effects. Perhaps more important, excessive speed increases the risk of injury or death from vessel strikes, and the loss of even a single whale would have serious consequences for the recovery and conservation of the southern resident stock. Those potential consequences, together with the extraordinary frequency of interactions between whales and vessels in these waters and the minor costs to vessel operators from reducing speed near whales, all argue that speed limits would provide important additional protection with little associated cost and therefore should be included in this rule. To do otherwise is to place the stock at unnecessary risk.

Although the Commission agrees that precise measurement of both vessel speeds and distances from whales is challenging, surely the more egregious violations could be identified with existing technology. In fact, regulated slow speed zones are enforced in multiple areas of the country for many reasons, including protection of marine mammals (e.g., manatees in Florida, large whales off the northeast Atlantic coast, right whales in various parts of the U.S. Atlantic coast, and humpback whales in Alaska waters¹). In addition, the fact that the Service's environmental assessment referenced violations of the voluntary guideline for speed near whales implies that the Service has some degree of confidence in assessments of speed near whales. Implementation and enforcement of a speed limit also could be enhanced by education of the public and commercial whale-watching community. The results may not be total compliance, but they would likely reduce the probability of a serious accident. For all these reasons, the Marine Mammal Commission recommends that the National Marine Fisheries Service adopt a regulatory speed limit of either seven knots or, at a minimum, a "slow safe speed" requirement (as defined in 33 U.S.C. § 2006 and the International Regulations for Preventing Collisions at Sea 1972 (see 33 U.S.C. § 1602)) within 400 yards of killer whales.

Monitoring Compliance with and Assessing the Effectiveness of the Final Regulations

The Service has been working with researchers and organizations such as Soundwatch to monitor compliance with whale-watching guidelines. The Commission supports such partnerships, particularly for the purpose of monitoring compliance, which is likely to become more difficult in the foreseeable future. As discussed in the environmental assessment, human population growth is expected to result in increased commercial and recreational vessel traffic in Washington's inland waters. Registration figures for recreational boating bear this out—the number of boats is increasing and likely will continue to increase (National Marine Manufacturers Association 2005). More recreational vessels and more people engaged in whale-watching will likely lead to more interactions between vessels and killer whales. The effects on the whales also will increase if whale-watching is not well managed. To ensure good management, the Service must develop and implement a monitoring program that (1) assesses vessel compliance and (2) confirms that the new regulations are sufficient. If compliance is poor and the new regulations prove inadequate, the Service must identify a process for determining what additional regulations are necessary. To that end, the Marine Mammal Commission recommends that the National Marine Fisheries Service develop a monitoring plan to assess compliance with and evaluate the effectiveness of the vessel approach regulations and that this plan be included in the final rule and described in the associated preamble.

No-go Zone

The Commission supports the implementation of a "no-go" zone along the west side of San Juan Island. This area is thought to be particularly important for killer whale foraging, particularly

¹The Alaska humpback whale approach regulations (66 Fed. Reg. 29502, May 31, 2001) require vessels to operate at a slow, safe speed when near a humpback whale. "Safe speed" has the same meaning as the term is defined in 33 U.S.C. § 2006 and the International Regulations for Preventing Collisions at Sea 1972 (see 33 U.S.C. § 1602), with respect to avoiding collisions with humpback whales.

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for Chinook salmon. Although disturbance by whale-watching vessels has been implicated as an important factor in the decline of this stock, so too has the decline in Chinook salmon populations, which appear to be the most important prey for southern resident killer whales. Creating a no-go zone at this site makes sense because (1) the area is frequented by the whales, which means the risk of a vessel strike may be increased, (2) the area appears to be important for foraging and its protection helps address a major risk factor, and (3) limiting vessel traffic in this area may reduce the likelihood of masking, which could confound the whales ability to forage successfully. For these reasons, the Marine Mammal Commission recommends that the National Marine Fisheries Service include the implementation of a no-go zone off the west coast of San Juan Island.

Cooperation with Canadian Authorities

Statistics in the environmental assessment indicate that both U.S. and Canadian commercial whale-watching operators violate the guidelines, including parking in the path of approaching whales, operating inshore of whales, operating under power within 100 yards of whales, and operating at high speeds near the whales. Of the 1,281 guideline violations in 2006 (referred to earlier in this letter), 30 percent were by commercial whale-watching operators. Of that 30 percent, more than two-thirds involved Canadian operators, although—in fairness—the Commission understands that more whale-watching operators are from Canada and violation rates are comparable.

The take prohibitions of the Marine Mammal Protection Act (16 U.S.C. § 1372(a)(2)(A)) and Endangered Species Act (16 U.S.C. § 1538(a)(1)(B)) and corresponding regulations apply unambiguously to all persons or vessels, regardless of their nationality or country of registry, in waters or on lands under the jurisdiction of the United States. Once finalized, the regulations that are the subject of this rulemaking will be binding on Canadian commercial whale-watching operators and recreational boaters when they are operating in the area set forth in section 224.103(e)(1) of the regulations. The Service will need to consider how best to pursue enforcement actions against Canadian vessel operators that are based in Canadian ports but enter U.S. waters and violate the regulations.

However, protecting the whales only in U.S. waters will not be sufficient to ensure the recovery and conservation of this stock. The observations that Canadian operators also violate whale-watching guidelines and the fact that the whales use the Canadian waters of northern Puget Sound mean that the Service must work with its Canadian counterparts to protect southern resident killer whales in Canadian waters as well.

The Commission understands that Canadian and U.S. officials already cooperate to a degree on matters pertaining to the protection of southern resident killer whales. The Commission also is aware of similar cooperation between the countries on management efforts related to other marine mammals (e.g., sea otters). So a precedent for international cooperation exists. Such cooperation seems essential and, in view of existing violations, warrants expanding. With that in mind, the Marine Mammal Commission recommends that the National Marine Fisheries Service initiate discussions with Canada to develop comparable management strategies for killer whales throughout

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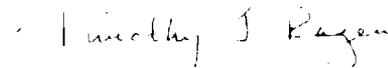
the inland waters of Washington State and British Columbia. Among other things, the Service should seek comparable regulations, monitoring, enforcement, and outreach.

A Precautionary Approach

The National Marine Fisheries Service has primary responsibility for protecting the southern resident killer whale stock in Washington's inland waters. As is always the case in management of endangered species, meeting this responsibility will require making some difficult decisions based on uncertain information. However, most of the measures discussed in this letter would result in relatively little cost to boaters who wish to approach killer whales in this region. In contrast, failing to impose the necessary measures could come with a serious cost to the stock and associated ecosystem. The loss of a single whale from a vessel strike could have important consequences. As noted previously, the southern resident killer whale stock consists of fewer than 100 individuals, faces a number of risks from human activities, and has experienced sharp declines in recent years that scientists have not yet been able to explain fully. Surely this is a situation where any uncertainty regarding potential adverse effects should be managed in a precautionary manner.

Please contact me if you have questions about the Commission's recommendations.

Sincerely,



Timothy J. Ragen, Ph.D.
Executive Director

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