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

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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 × 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.uaa.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 matrilines. 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.

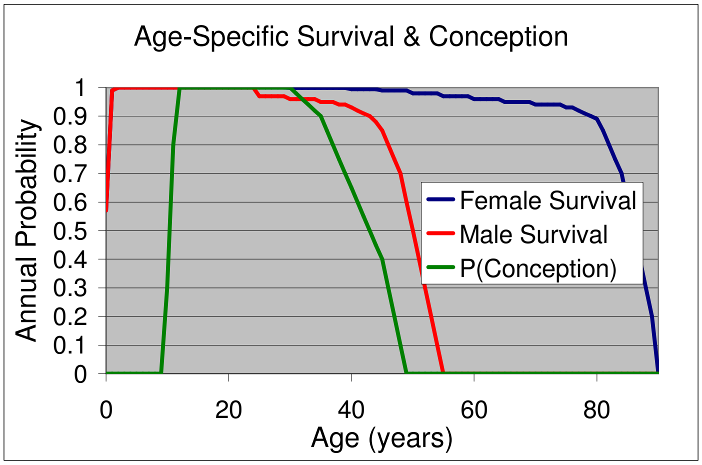


Figure 1. Baseline annual probabilities of survival and conception for a population of transient killer whales unlimited by prey availability.

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	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 (kcals)	FMRConstant	405.39
	Field Metabolic Rate Exponent(kcals)	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 (kcals/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 (kcals/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 a 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

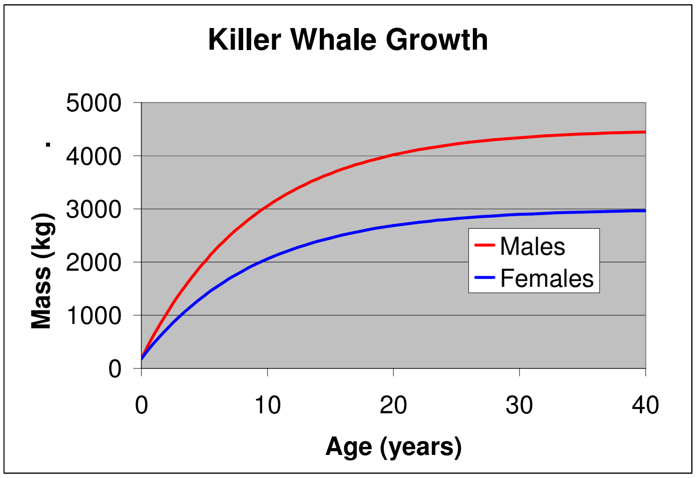


Figure 2. Von Bertalanffy growth model of age-specific target mass for transient killer whales.

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.

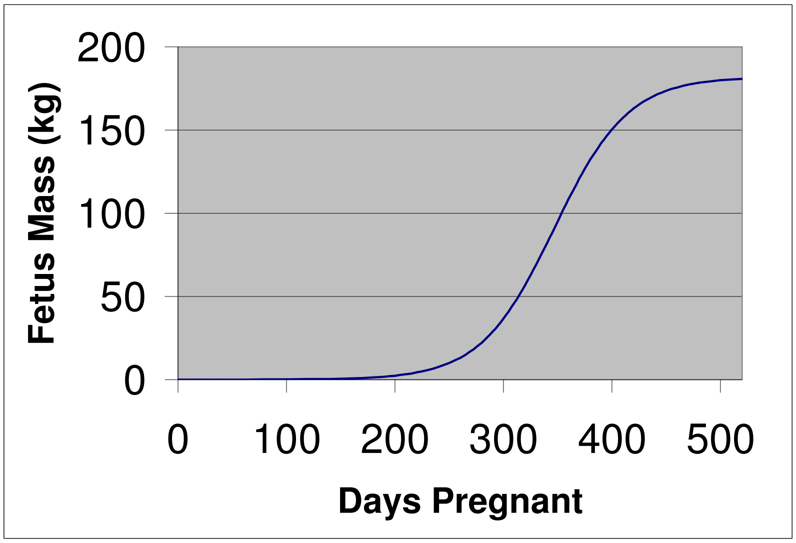


Figure 3. Fetal growth in model killer whales.

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.

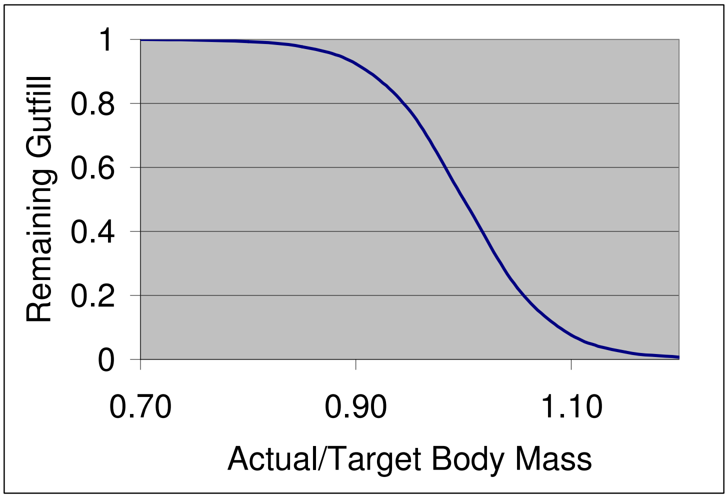


Figure 4. Proportion of remaining stomach volume (beyond that needed for maintenance metabolism) that will satiate an individual killer whale in relation to body condition (actual mass/target mass).

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.

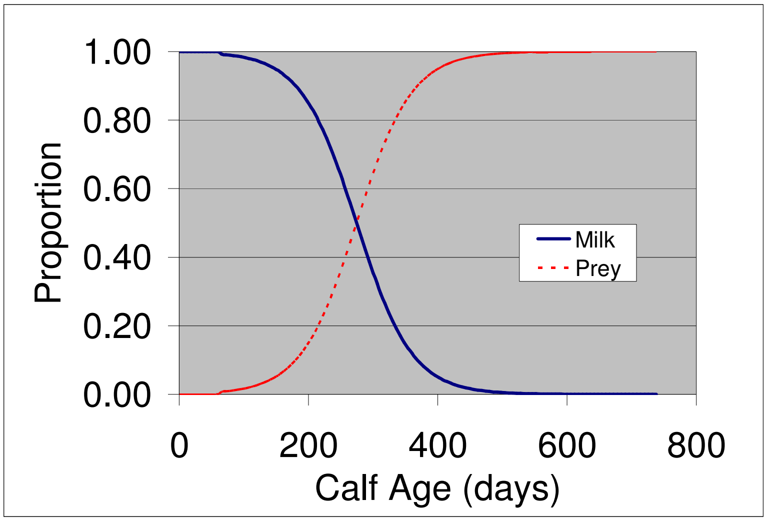


Figure 5. Logistic model of calf diet describing age-related transition from milk to prey.

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.

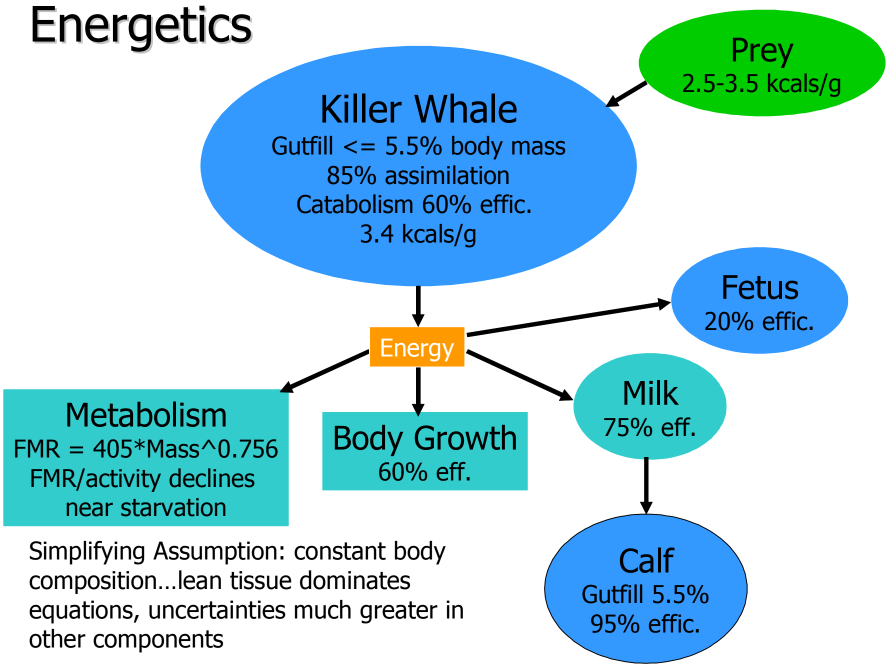


Figure 6. Energetic model by which prey are converted into energy for metabolism, body growth and reproduction of individual killer whales.

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

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

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

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

Group 2

Whale ID	Counters
3	1→ 20

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

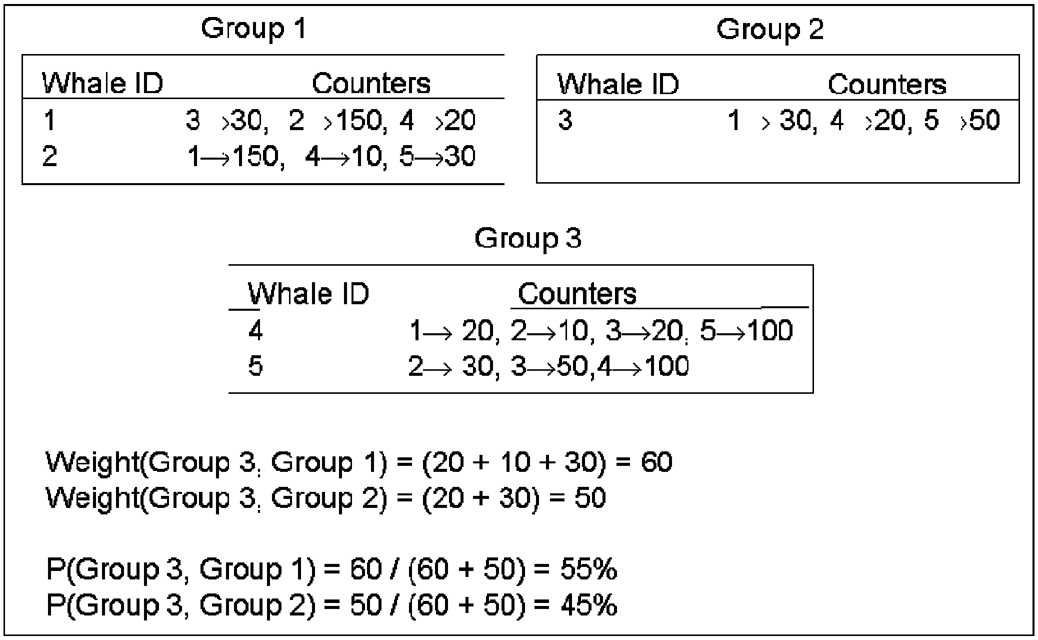
If the calf is in the same exact group the next time step then those counters will be incremented to 2. If at some point in the future a new whale joins the calf’s group then a similar suite of new counters will be created for that whale that are initialized to 1. When a whale dies the counters are removed. 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

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

Group 2

Whale ID	Counters
3	1→30, 4→20, 5→50

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.

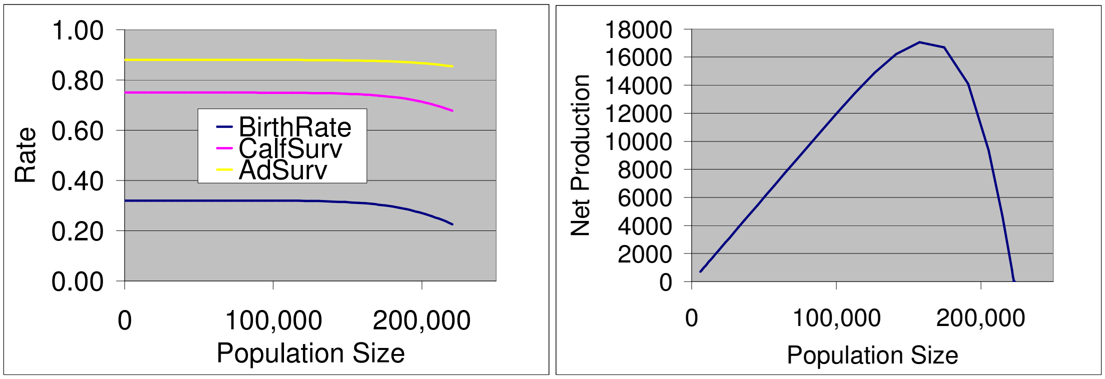


Figure 8. General density-dependent properties of vital rates (left) and net productivity (right) of model prey populations.

Group-size Dependent Prey Vulnerability

While relatively little is know 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 × 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:

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

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.

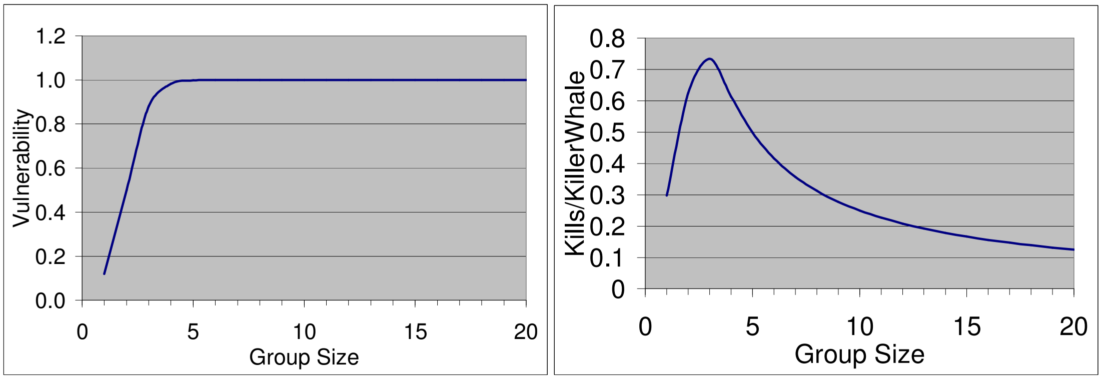


Figure 9. The left graph shows the modeled relationship between the vulnerability (probability of being killed given an encounter with a group of transient killer whales) of a vulnerable prey type (e.g., harbor seals) and the effective size (adult equivalents) of the hunting group, while the right graph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

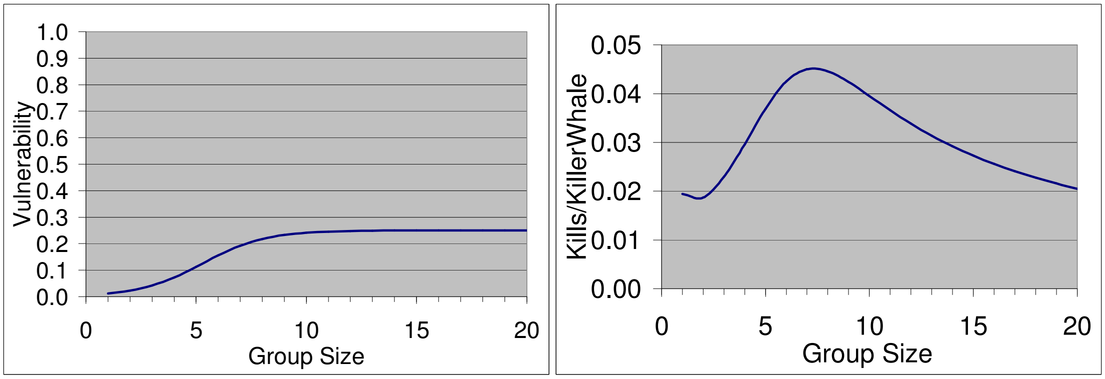


Figure 10. The left graph shows the modeled relationship between the vulnerability (probability of being killed given an encounter with a group of transient killer whales) of a difficult-to-kill prey species (e.g., gray whale) and the effective size (adult equivalents) of the hunting group, while the 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 × 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/ .

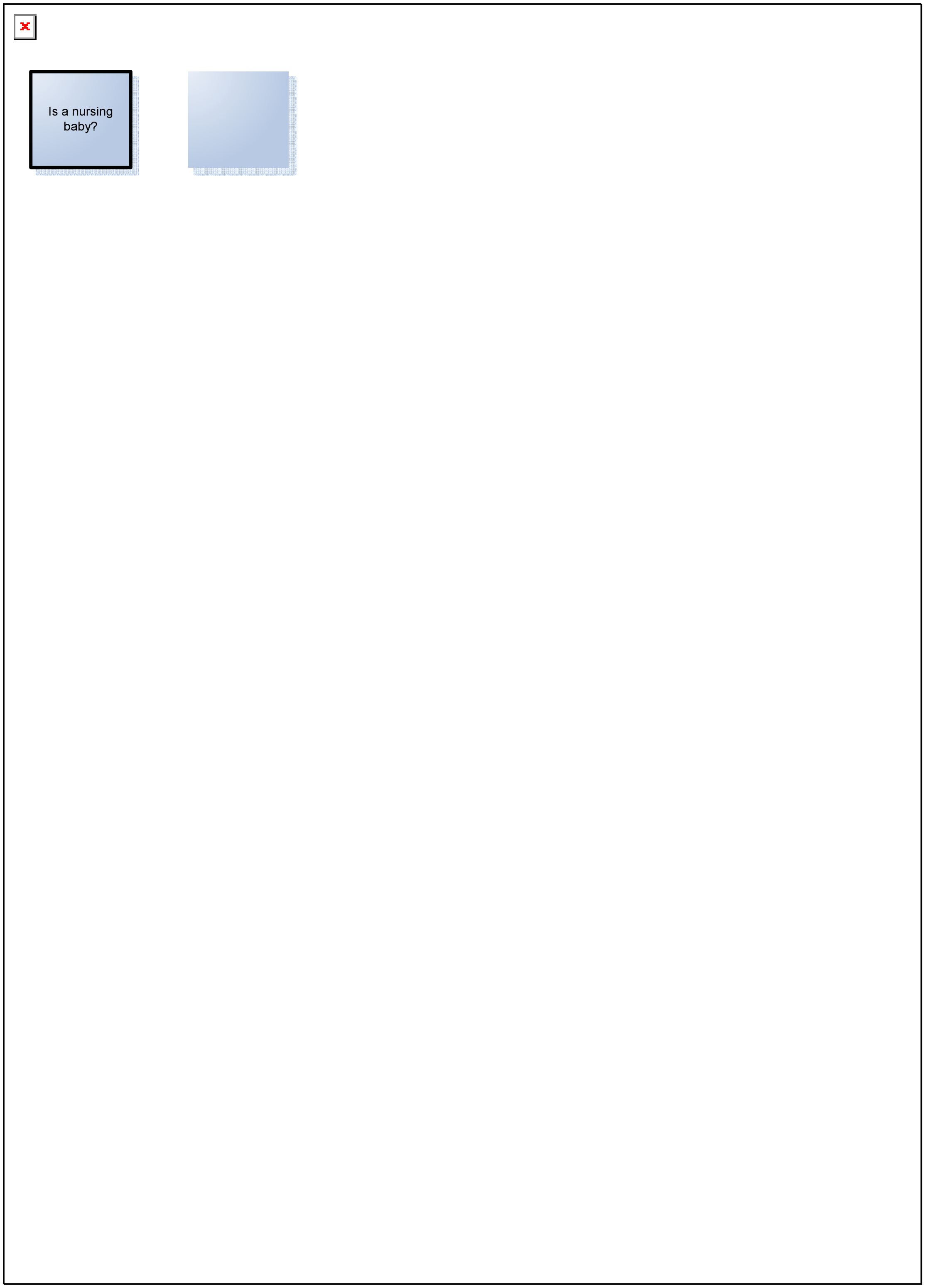


Figure 11. Model execution of daily routines is illustrated with a flow diagram. Object shapes denote actions taken at either group, individual or model level.

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 (λ~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 ~ 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 <3.00E-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 4.00E-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

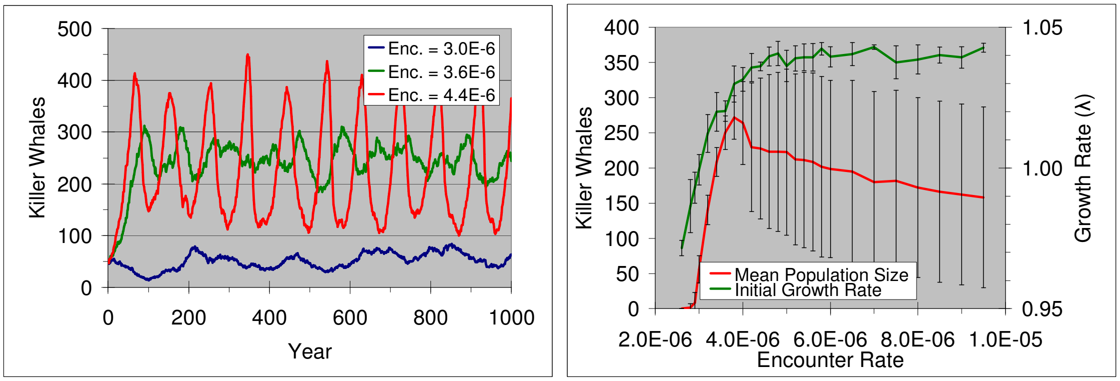


Figure 12. Three trajectories are shown (left) for different assumed encounter rates between hunting groups of killer whales and individual prey. The initial (maximum) growth rate of the killer whale population in the first 50 years of simulations, and the mean abundance of killer whales (SD in error 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

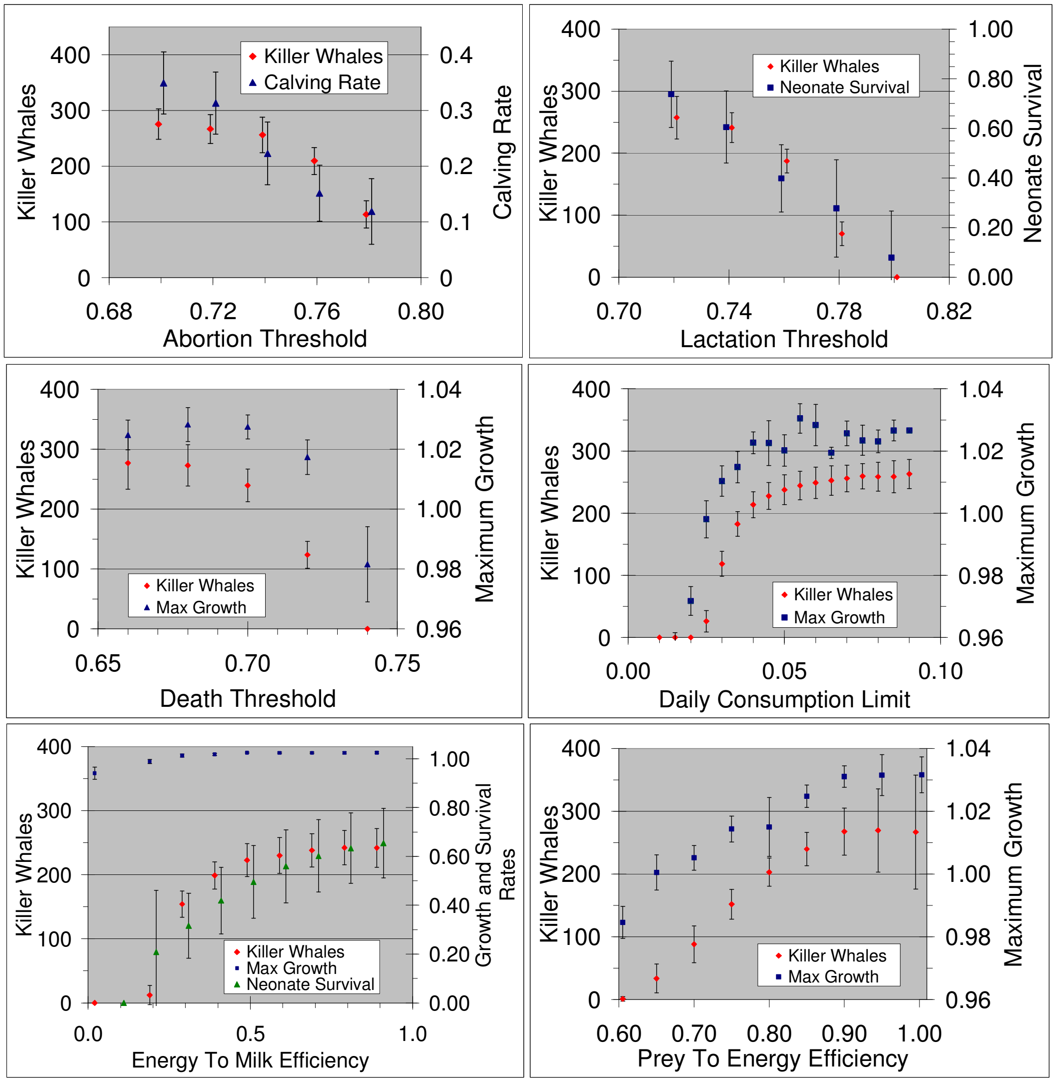


Figure 13. Sensitivity of killer whale numbers in the final 800 years of 1000-year simulations, maximum population growth in the initial 50 years, and other key output variables are shown as key input parameters were varied (5 replicates each, error bars = SD). Thresholds at which killer whales aborted 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

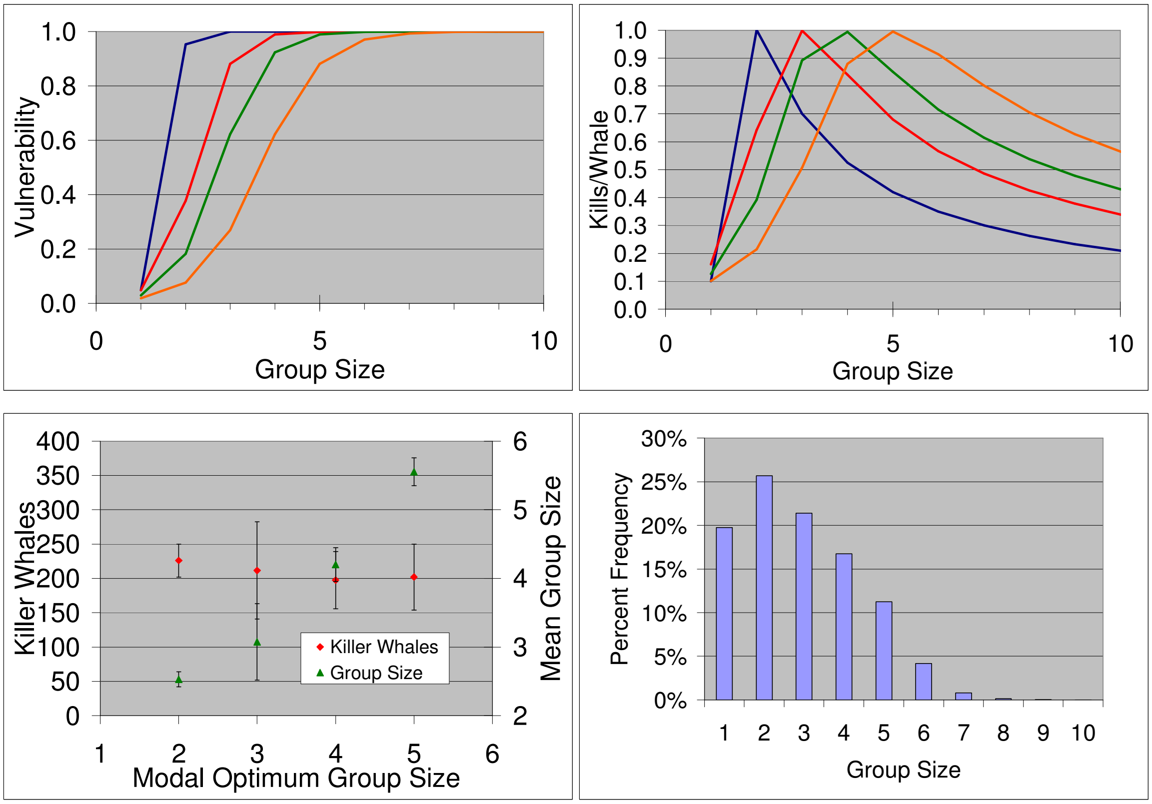


Figure 14. The logistic functions relating killer whale group size to a maximum vulnerability (probability of killing given an encounter) of prey (top left) produce expected payoffs in consumable prey per group member (top right, scaled to the maximum value with colors to match curves at top left). Simulations 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 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.

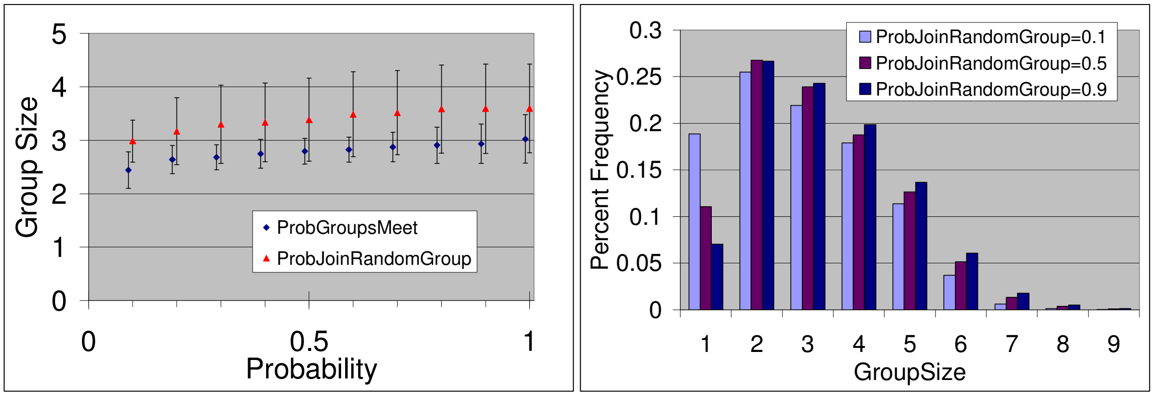


Figure 15. For an optimum hunting group size of 3, parameters controlling the daily probability of meeting and considering joining another group of killer whales (ProbGroupsMeet), and the probability that it would be a random group or a group of relatives (ProbJoinRandomGroup) had positive effects on 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).

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 λ=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 λ=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

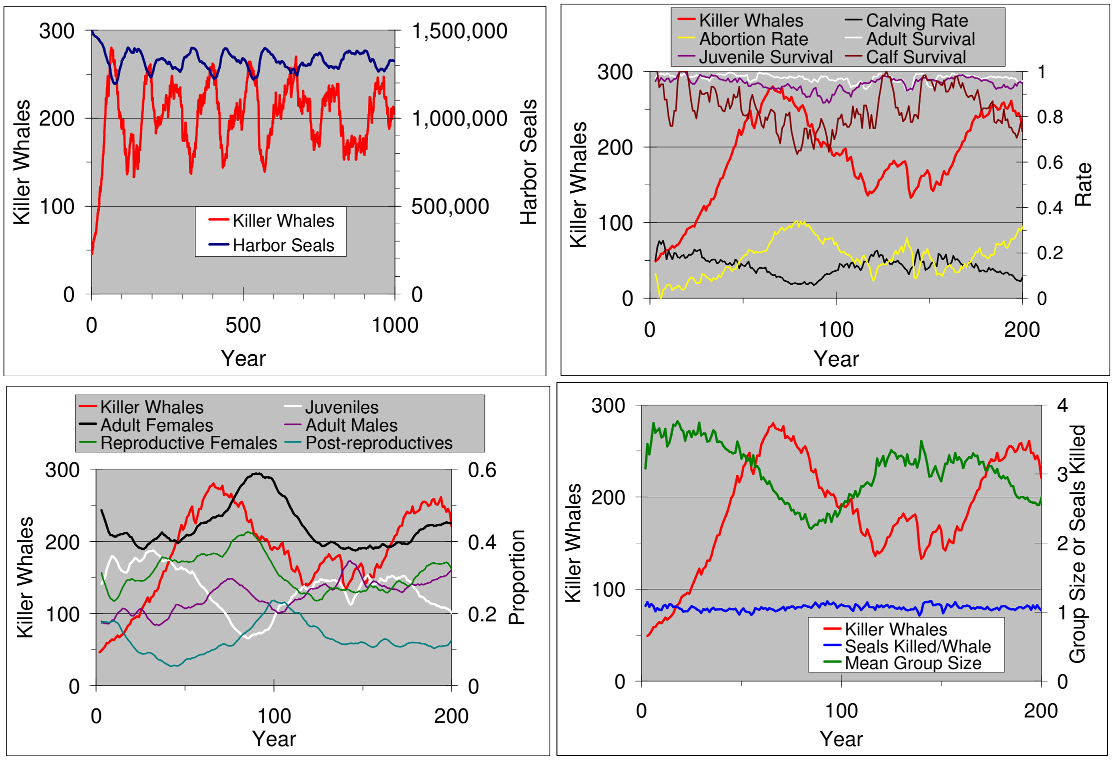


Figure 16. A typical simulation of transient killer whales and a superabundant, single prey population of harbor seals shows fluctuating population size of predators and prey (top left) over 1000 years. Changing vital rates (top right; rates are 5-year running averages), age structure (bottom left), 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

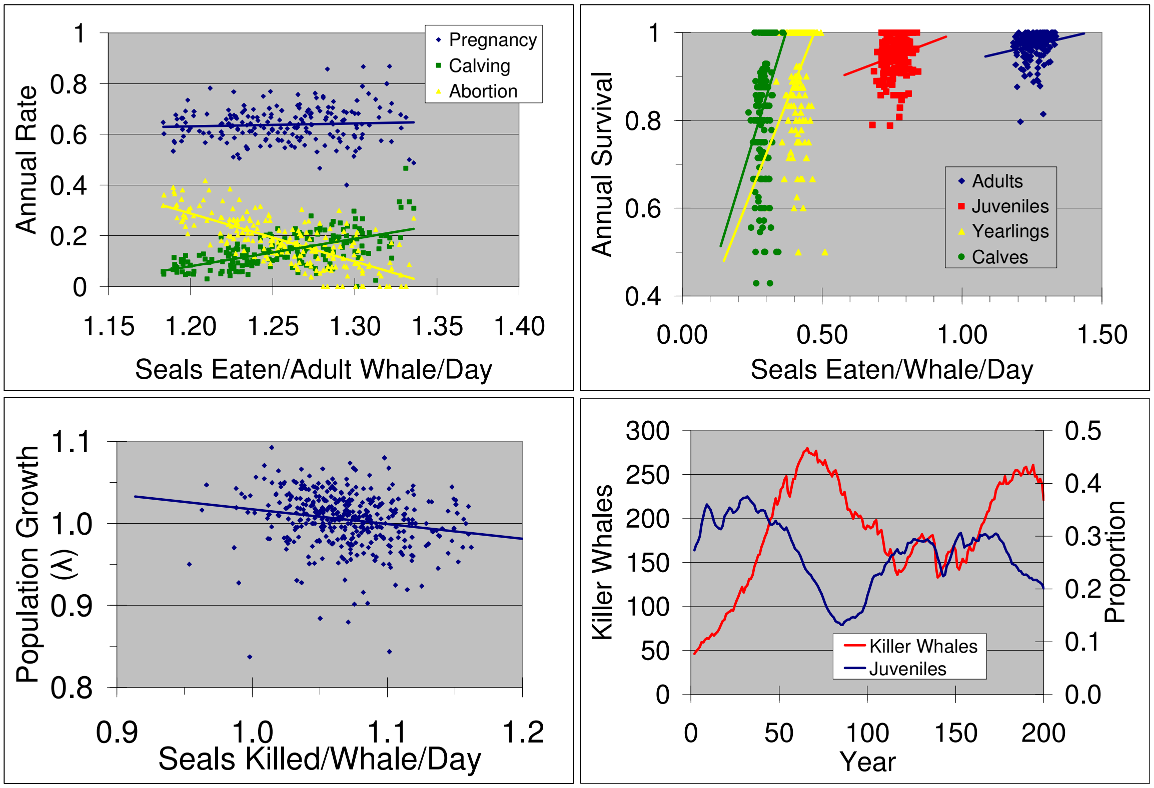


Figure 17. Scatterplots from the first 200 years of a simulation of killer whales preying on a single, superabundant prey population of harbor seals. Calving rates were positively and abortion rates negatively correlated with the number of seals eaten/adult (>10 years) killer whale/day (top left; reproductive 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*.

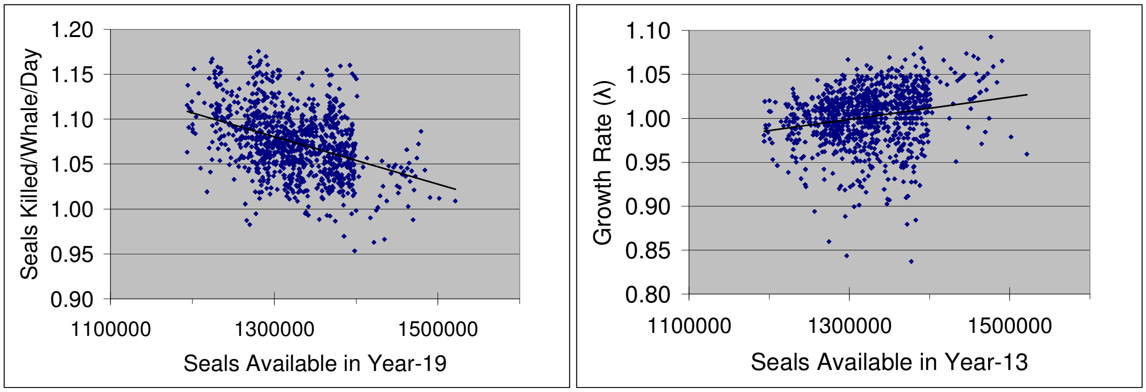


Figure 18. Functional (left) and numeric (right) responses of killer whales to prey abundance were more dependent on absolute abundance than the seals/killer whales ratio, with anti-regulatory properties indicated by long time lags.

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 × expected encounter rate × 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.

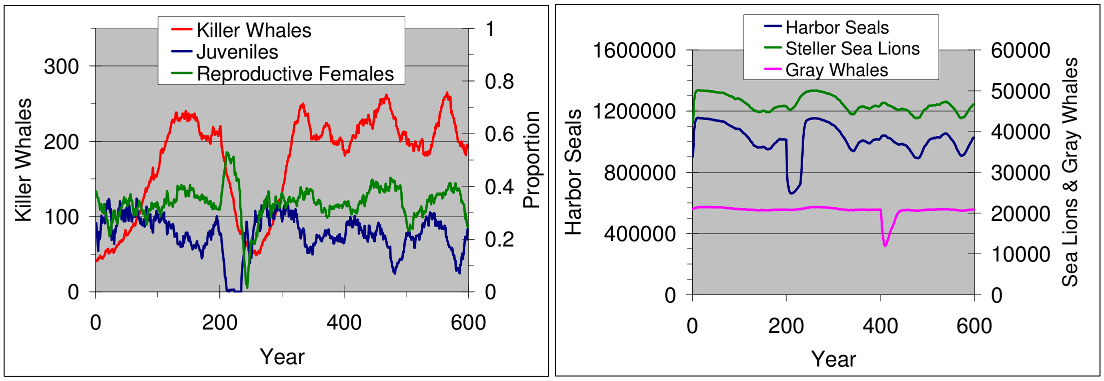


Figure 19. Simulation of a 3-species prey community (see text) over 600 years in which a 30-year "regime shift" reducing the carrying capacity of harbor seals by ~60% begins in year 200, and a harvest of 12,000 gray whales occurs in years 400-409.

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 affects 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 ~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 (Dalhleim 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, (Rice 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.