Agent-Based Modeling of the Dynamics of Mammal-eating Killer Whales and Their Prey: Not Your Lynx-Hare Cycle

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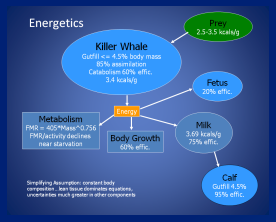
Abstract

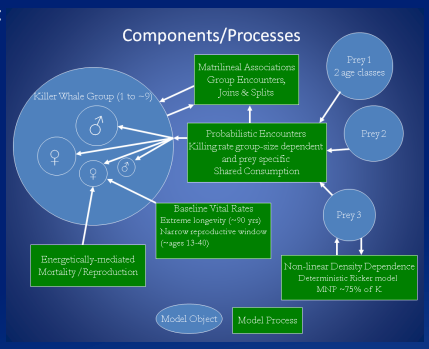
The role of mammal-eating ("transient") killer whales *Orcinus orca* in the decline of various marine mammal populations in Alaska is controversial and potentially important in their recovery. Classical predator-prey models are insufficient to describe the dynamics of a single predator on the number of prey types known for these predators, and there are few data that could be used to parameterize such models. We developed an agent-based model of killer whales with plausible energetics and behavior, calibrated and validated the model against published expectations for killer whale consumption rates, group dynamics and demography, and explored the emergent properties of single-prey and 3-prey models using small, abundant seals as primary prey, a generic small population of "sea lions" and seasonally available "large whales". The single-prey model gave results that were intuitively responsive to underlying parameters, but were sensitive to killing rates, much as expected in classical predator-prey models. The dynamics showed long time lags (~ 30 years) between troughs of prey and predator numbers and highly variable predator age structure. In scenarios where the importance of seasonally available large whales was manipulated, the large whales had the potential to augment killer whale numbers somewhat, but had minimal effect on the overall dynamics of either predators or alternate prey when reduced by a simulated harvest. Perturbing the carrying capacity of the primary, small prey created strong numeric shifts in killer whale population size and consequent indirect effects on both alternate prey. No predictive inference is suggested for these models due to the absence of more realistic elements (e.g., spatial structure, explicit prey-switching, more realistic prey structure) than we used, but the models do suggest that we expect more complicated numerical dynamics than have thus far been considered in discussion of the impact of killer whales on their mammalian prey.

The Model: Individual energetics, group level interactions

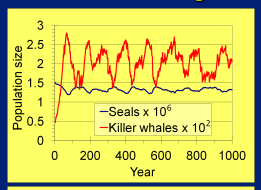
Model execution in daily time-steps:

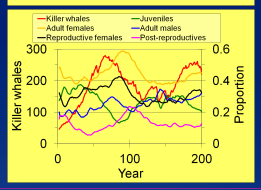
- Group formation (joining/splitting of relatives)
- Encounter and consumption of prey
- Adjust prey population for predation and DD
- Adjust KW body mass
- Apply energetically mediated mortality
- Apply probabilistic demographic events





Emergent Properties: Single-Prey Scenario

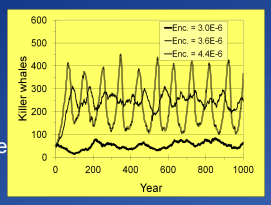




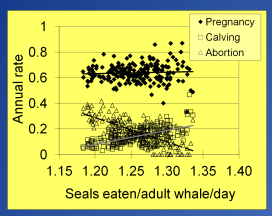
- Prey (generic "Seals") numbers and encounter rates chosen to create moderate KW fluctuations
- Peaks and troughs at intervals ~50-100 yrs
- Lags between clear troughs of prey and predators were ~16-38 yrs (mean=31)
- Lags driven by declines in juvenile recruitment and narrow reproductive window for females
- Recovery of prey usually coincided with weak reproductive class (13-40 yrs) of female killer whales
- Individual consumption rates (seals/KW) were negatively correlated with killer whale population growth due to decline in proportion of small-bodied juveniles as prey declined

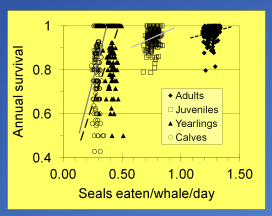
Calibration/Validation: Single-prey scenario

- Single, superabundant prey (seals) sufficient to support roughly 200-300 killer whales
- Replicated runs of 1000 years from initial population of 50 killer whales
- Model sensitivity to predator efficiency (killing rates, metabolic efficiency) similar to classic difference equation predator-prey models: progression from low predator numbers to higher numbe and relative stability to increasing oscillations (right)



- Population growth rate, survival and reproductive parameters similar to published rates of "resident" killer whales

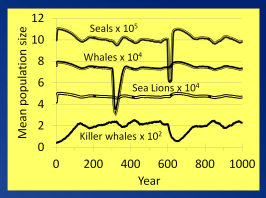


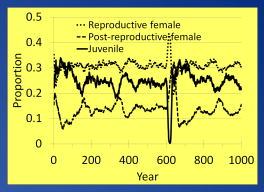


- Consumption-dependent demographic responses (above) match those expected/observed in other large mammals (Juv response > adult)
- Group size and composition similar to observations, and consistent with optimum sizes parameterized in model
- Consumption rates similar to those published (not surprising, given shared origin)

A 3-prey scenario: Seals, Sea Lions, Whales

- Starting with a primary prey population of "Seals", small population of "Sea Lions", and seasonally available large "Whales"
- Increasing the preference/vulnerability for large, vulnerable whale calves had little effect on equilibrium numbers of other prey, and only a small effect on killer whale numbers, even if impact on seasonally available whales was high
- A scenario where highly preferred whales were reduced by half (harvest beginning in year 300 at right) had small effect on killer whales, or alternate prey
- An ecological "regime shift" reducing the carrying capacity of primary prey by 40% for 20 years (year 600 at right) caused a collapse in killer whale recruitment and a sharp decline in killer whale abundance that reached a nadir 54 years after the onset of the seal decline and 30 years after seals had recovered; full recovery took over a century





Conclusions

- No specific predictive ability is implied, but some general patterns emerged from these agent-based simulations that suggest areas for future simulations and field research
- The long life-span and narrow reproductive window of killer whales is unique among large predators, and simulations show their predator-prey dynamics might entail long-term instabilities in numbers and age structure with much longer time lags than for other predators
- Indirect effects of prey reductions on alternate prey did not occur without strong direct effects on killer whale abundance, though the absence of realistic spatial structure or other mechanisms for prey-switching could influence this

Acknowledgements

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