Understanding the decline of the western Alaskan Steller sea lion: “An ecological thriller” (John Birks)

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Main collaborator -- Nick Wolf:


2008 Wolf, N. and M. Mangel Multiple hypothesis testing and the declining-population paradigm in Steller sea lions. Ecological Applications (accepted)
• Thank you!

• Nature of the problem

• The need for an approach based on multiple hypotheses

• Our approach

  -- Population model and thinking along sample paths

  -- Parameter estimation

  -- Ecological Detection applied

  -- Pointers towards the hard problems
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Where the Action is Taking Place

Holmes et al. Ecological Applications (2007)
The decline: Census data by year

How do we make sense of what’s happening with 10 data points?
But there are many more data
The decline: Census data by Rookery and Year
The decline: Census data by Rookery and Year

There are actually more than 200 data points—how do we use them?
Why the decline? “The Method of Multiple Working Hypotheses” - T.C. Chamberlain (1890, 1897) -- reprinted in

BOTTOM-UP:
• Not enough food
• Wrong kind of food

TOP-DOWN:
• Predators
• People
• Disease or pollution

Put another way....
It’s the fishery

Mammals / Birds

Target Fish

Fishery

Ianelli et al 2002

![Graph showing pollock catch over the years](image-url)
Walleye Pollock  
Atka Mackerel  
Pacific Salmon  
Pacific Cod  
Arrowtooth Flounder  
Pacific Herring  
Pacific Sand Lance  
Irish Lords  
Cephalopods  
Capelin  
Rockfishes

Theragra chalcogramma  
Pleurogrammus monopterygius  
Oncorhynchus spp.  
Gadus macrocephalus  
Atheresthes stomias  
Clupea pallasi  
Ammodytes hexapterus  
Hemilepidotus spp.  
Class Cephalopoda  
Mallotus villosus  
Family Scorpaenidae

EH Sinclair and TK Zeppelin. Seasonal and spatial differences in diet in the Western Stock of Steller sea lions (Eumetopias jubatus)
It’s the competitors: all roads lead to Stellers

Figure 2. Trends in predator biomass (’000 t) in the Gulf of Alaska, 1964–1997: Pacific halibut, arrowtooth flounder, and Steller sea lion.


cf: The CCAMLR experience, krill surplus, and return of the great whales
It’s the orcas

Mammals / Birds
adults
juveniles

Target Fish

Toothed Whales

Other Fish

Fishery

May 12, 1922]

WHAT BECOMES OF THE FUR SEALS

G. Dallas Hanna
The California Academy of Sciences
27 male or 40 female killer whales switching to a 100% sea lion diet would have been enough to drive the decline. (Williams et al. 2004)
It’s the environment

- Toothed Whales
- Mammals / Birds
  - adults
  - juveniles
- Other Fish
- Target Fish
  - Zooplankton (Euphausiids)
  - Abiotic factors
    - Algae
- Fishery
Food Web

Primary Hypothesis

A  The decline is caused by incidental mortality in the course of fishing operations

A  The decline is caused by removal of target fish by the fishery

B  The decline is caused by an increase in the toothed whales or the prevalence of marine disease

B  The decline is caused by a shift in the mixture of target fish and other fish, which provide different levels of nutrients to the mammals and birds

C  The decline is caused by a shift in the distribution or abundance of zooplankton, thus affecting the resource base for the fish

C  The decline is caused by a shift in abiotic components, either temporally or spatially, that affect the distribution of fish stocks and their accessibility to marine mammals and birds.
There is the problem of the common currency -- the relevant data come from a variety of different sources and in different units. So people tend to study one hypothesis at a time.
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“Problems are not solved by ignoring them” -- William Feller
Previous modeling studies


Estimated time series of missing animals: Blackburn 1990; Loughlin & York 2002; NRC 2003


Spatial patterns, but not temporal: Merrick et al. 1997
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Spatial patterns, but not temporal: Merrick et al. 1997

Conclusions so far: One can get baseline vital rates (pup and non-pup survival and fecundity) but it’s hard to tell which hypothesis is most likely when you’re working with pooled data
What those baseline rates tell us

This year:

\[ \text{# Pups} = \text{Average Fecundity of non-pups} \times \text{# Non-pups} \]

Number Next Year \hspace{1cm} \text{Number This year}

\[ \text{# Non-pups} = \text{Recruitment of pups} \times \text{# Pups} \]
\[ + \text{ Survival of non-pups} \times \text{# Non-pups} \]

In symbols:

\[ J(t) = \phi_0 N(t) \]
\[ N(t + 1) = \rho_0 J(t) + \sigma_0 N(t) = (\rho_0 \cdot \phi_0 + \sigma_0)N(t) \]
Population growth rate

\[ \lambda = \rho_0 \cdot \phi_0 + \sigma_0 \]

With the baseline parameters estimated from previous studies, the population is predicted to grow slowly and steadily, but…

![Graph showing the corresponding reduction in growth rate for different factors](image)
Location, location, location

We are going to make fecundity, recruitment, and survival depend upon location

Example:
Fecundity in year $t$ at rookery $i$ = Baseline Value $\cdot$ Modifier Depending Upon Local Conditions
Our Approach:

1. Formulate alternative hypotheses as one-parameter scaling functions that modify vital rates according to local conditions
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3. Choose a suitable population model and error structure.
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5. Rank effects in terms of strength and statistical support.
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Steps 1-5 provide a general theoretical framework for the declining population paradigm of Graeme Caughley (1994)
The ‘small population paradigm’ and the ‘declining population paradigm’

Small population paradigm is amenable to theory -- stochasticity dominates

“In contrast, the processes relevant to the declining population paradigm are essentially humdrum, being not one but many. So far they have defied tight generalization and hence are of scant theoretical interest”

The small population paradigm has not yet contributed to conserving endangered species because it treats an effect [smallness] as if it were a cause. It provides an answer to only a trivial question: how will will the population persist if nothing unusual happens.

The declining population paradigm is relevant to most problems of conservation. It summons an investigation to discover the cause of the decline and to prescribe its antidote… “The declining population paradigm is urgently in need of more theory”
Hypotheses to explain the decline:

Hypotheses 1, 2, 3: “Food”
Low prey abundance leads to diminished fecundity, pup recruitment, or non-pup survival rates.
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**Hypotheses 1, 2, 3: “Food”**

Low prey abundance leads to diminished fecundity, pup recruitment, or non-pup survival rates.

Tuned parameter: Half-saturation constant

\[ f_F = \text{(Holling Type III functional response)} \]
Hypotheses 4, 5, 6: “Pollock” or “junk food hypothesis”

Too much of the wrong prey (Walleye pollock) leads to diminished fecundity, pup recruitment, or non-pup survival.

Tuned parameter: Exponent of non-pollock prey fraction

\[ f_p = (\text{Power function}) \]
Hypotheses 7, 8: “Boats”
Fishing activities near rookeries lead to diminished pup recruitment or non-pup survival.

Tuned parameter: Poisson mortality rate per unit haul time

\[ f_B = \text{Multiplier} \]

(Exponential)
Hypotheses to explain the decline:

**Hypotheses 9,10: “Seals”**
Predators consume sea lions (depressing recruitment or survival rates) only when more profitable prey (harbor seals) are scarce.

Tuned parameter: Decrement in survival when seals are scarce

\[ f_s = \begin{cases} 0 & \text{Harbor seal density} < S_{\text{crit}} \\ 1 - c & \text{Harbor seal density} \geq S_{\text{crit}} \end{cases} \] (Step function)
Detour: Applying the Classic Diet Breadth Model

Fig. 2. The sequential collapse of marine mammals in the North Pacific Ocean and southern Bering Sea, all shown as proportions of annual maxima.
Assume:

- Harbor seals are preferred prey of Orcas
- In the absence of harbor seals, Orcas will prey upon Stellers
- Therefore harbor seal abundance is in some sense a proxy for the inverse predation rate by Orcas on Stellers
Prey items are ranked by

-- Energy content
-- Handling time
-- Encounter rate

Order by profitability (energy/handling time) per item

Diet chosen to maximize the long-term rate of energy intake

\[ R_k = \frac{\sum_{i=1}^{k} E_i \lambda_i}{1 + \sum_{i=1}^{k} h_i \lambda_i} \]

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• In the absence of harbor seals, Orcas will prey upon Stellers

• Therefore harbor seal abundance is in some sense a proxy for the inverse predation rate by Orcas on Stellers
Key results:

- Items are either completely included or completely excluded from the diet

- Inclusion of item rank n+1 only depends on the encounter rate with more profitable items

\[ \lambda_1 > \frac{E_2}{E_1 h_2 - E_2 h_1} \]

- Study community effects by considering the combination of behavioral ecology and population dynamics

\[ N_i(t + 1) = N_i(t) + r_i N_i(t) \left( 1 - \left( \frac{N_i(t)}{K_i} \right)^a \right) - S_i \left( 1 - e^{-q_i O(t)} \right) N_i(t) \]
The Consequence for the Community of Mammals:
The Consequence for the Community of Mammals:

Suggestion: Estimate harbor seal populations within 300 km of rookeries, separated by declining or growing Steller sea lion populations.
Lower harbor seal populations are associated with decline of Steller sea lions.
A hard problem -- the game between orcas and Stellers

Orca success rate, given the distance a Steller is from the haulout

Steller success rate given the foraging distance from a haulout
The resulting game has a Nash equilibrium

Best orca response to Stellers

Best Steller response to orcas
False attacks make Stellers hungrier and cause them to forage further off shore, where predation risk is greater.
Our Approach:

1. Formulate alternative hypotheses as one-parameter scaling functions that modify vital rates according to local conditions
2. Sort available “local conditions” data by rookery and year
Local conditions: Total non-pollock prey density

Total CPUE (kg/km$^3$, incl. all prey types)
Local Conditions: Pollock fraction, by weight
Local conditions: Fisheries activity within 20 km of rookeries

Within 300 km of rookeries
Local Conditions: Harbor seal density within 300 km of a rookery
Our Approach:

1. Formulate alternative hypotheses as one-parameter scaling functions that modify vital rates according to local conditions.

2. Sort available “local conditions” data by rookery and year.

3. Choose a suitable population model and error structure.

4. Calculate likelihood for all possible values of all parameters (one per hypothesis) simultaneously.
Model structure:

Two-stage population dynamics

\[ J(i,t) = \text{Pups (age < 1 year)} \]
\[ N_{\text{true}}(i,t) = \text{Total Non-pups} \]
\[ N_{\text{obs}}(i,t) = \text{Observed Non-pups} \]
Fecundity: $\phi(i,t)$

Recruitment: $\rho(i,t)$

Survival: $\sigma(i,t)$

Prob. of observation: $p(i,t)$

$s_{true}$ $(i,t)$

$s_{true}(i,t+1)$

$N_{true}(i,t)$

$N_{true}(i,t+1)$

Binomial transitions

$$\Pr\{N_t\} = \sum_{s=0}^{N_t} \left( \frac{N_{t-1}}{s} \right) \sigma_{i,t}^s (1-\sigma_{i,t})^{N_{t-1}-s} \left( \frac{J_{t-1}}{N_t-s} \right) \rho_{i,t}^{N_t-s} (1-\rho_{i,t})^{J_{t-1}-N_t+s}$$

$$\Pr\{J_t\} = \left( \frac{N_t}{J_t} \right) \phi_{i,t}^J (1-\phi_{i,t})^{N_t-J_t}$$
Calculation of local fecundity probability

\[
\phi(i,t) = \phi_0 \cdot f_F(c_1, \text{Food}(i,t)) \cdot f_P(c_4, \text{Pollock}(i,t))
\]

Fecundity: \( \phi(i,t) \)

Recruitment: \( \rho(i,t) \)

Survival: \( \sigma(i,t) \)

Prob. of observation: \( p(i,t) \)

\( N_{\text{true}}(i,t) \)

\( N_{\text{obs}}(i,t) \)

Food

Pollock

Boats

Seals
Calculation of local pup recruitment probability

\[ \rho(i,t) = \rho_0 \cdot f_F(c_2, \text{Food}(i,t)) \cdot f_P(c_5, \text{Pollock}(i,t)) \cdot f_B(c_7, \text{Boats}(i,t)) \cdot f_S(c_9, \text{Seals}(i,t)) \]

Fecundity: \( \phi(i,t) \)
Survival: \( \sigma(i,t) \)
Prob. of observation: \( p(i,t) \)

Recruitment: \( \rho(i,t) \)

\( J(i,t) \)
Calculation of local non-pup survival probability

σ(i,t) = \( \sigma_0 \cdot f_F(c_3, \text{Food}(i,t)) \cdot f_P(c_6, \text{Pollock}(i,t)) \cdot f_B(c_8, \text{Boats}(i,t)) \cdot f_S(c_{10}, \text{Seals}(i,t)) \)

Fecundity: \( \phi(i,t) \)

Recruitment: \( \rho(i,t) \)

Survival: \( \sigma(i,t) \)

Prob. of observation: \( p(i,t) \)

\( N_{true}(i,t) \)

\( N_{true}(i,t+1) \)

\( J(i,t) \)

\( N_{obs}(i,t) \)

Food

Pollock

Boats

Seals
Another Hard Problem:
Characterizing the Observation Error

Fecundity: $\phi(i,t)$
Recruitment: $\rho(i,t)$
Survival: $\sigma(i,t)$

$p(i,t) \sim \text{Beta}(\alpha, \beta)$
(Beta-Binomial error)
We use the Rookeries with Repeat Counts in a Year

<table>
<thead>
<tr>
<th>Year</th>
<th>Hazy</th>
<th>White Sisters</th>
<th>Biali</th>
<th>C. Newenham</th>
<th>C. Ommanney</th>
<th>Coronation</th>
<th>Jacob Rock</th>
<th>Outer (Pye)</th>
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<td>541</td>
<td>649</td>
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<td>784.875</td>
<td>584.625</td>
<td>161.75</td>
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<td>CV</td>
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<td>0.3944941</td>
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</tr>
</tbody>
</table>

Estimate $\alpha$ and $\beta$ using multiple censuses recorded at individual rookeries within a single season (when the only source of variation is observation error).
Beta-binomial density for multiple observations:

\[
\text{Likelihood} \left\{ \alpha, \beta, N_{\text{true}} \mid \text{data} = k_1, k_2, k_3 \ldots k_j \right\} = \prod_{i=1}^{j} \binom{N_{\text{true}}}{k_i} \frac{\Gamma(\alpha + k_i) \Gamma(\beta + N_{\text{true}} - k_i) \Gamma(\alpha + \beta)}{\Gamma(\alpha + \beta + N_{\text{true}}) \Gamma(\alpha) \Gamma(\beta)}
\]

Normalized within \(\alpha/\beta\) plane given \(N_{\text{true}}\):

\[
\text{Likelihood}_{\text{norm}} \{\alpha, \beta \mid \text{data, } N_{\text{true}}\} = \frac{\prod_{i=1}^{j} \frac{\Gamma(\alpha + k_i) \Gamma(\beta + N_{\text{true}} - k_i) \Gamma(\alpha + \beta)}{\Gamma(\alpha + \beta + N_{\text{true}}) \Gamma(\alpha) \Gamma(\beta)}}{\int_{a=1}^{\infty} \int_{b=1}^{\infty} \prod_{i=1}^{j} \frac{\Gamma(a + k_i) \Gamma(b + N_{\text{true}} - k_i) \Gamma(a + b)}{\Gamma(a + b + N_{\text{true}}) \Gamma(a) \Gamma(b)} \, db \, da}
\]

Expectation of Likelihood across \(N_{\text{true}}\):

\[
\text{Likelihood}(\text{data} \mid \alpha, \beta) = \sum_{n = \max(k)}^{\infty} \frac{\prod_{i=1}^{j} \frac{\Gamma(\alpha + k_i) \Gamma(\beta + n - k_i) \Gamma(\alpha + \beta)}{\Gamma(\alpha + \beta + n) \Gamma(\alpha) \Gamma(\beta)}}{\int_{a=1}^{\infty} \int_{b=1}^{\infty} \prod_{i=1}^{j} \frac{\Gamma(a + k_i) \Gamma(b + n - k_i) \Gamma(a + b)}{\Gamma(a + b + n) \Gamma(a) \Gamma(b)} \, db \, da}
\]
The bottom line...

The MLE values of $\alpha$ and $\beta$ are around 6 and 2, respectively, resulting in a mean sighting probability of 75%.
Keeping Our Eye on the Prize

Objective: We want to find the values of the link parameters that give the highest Likelihood (the probability of observing all the reported SSL counts), given the Local Conditions Matrix and a particular model formulation.
Model Likelihood = Probability of getting the observed sequence of censuses at all rookeries, given the local conditions matrices, the model structure, and a set of parameters in the vital rate functions

Method of calculation: Path integration
**Model Likelihood** = Probability of getting the observed sequence of censuses at all rookeries, given the local conditions matrices, the model structure, and a set of parameters in the vital rate functions

Method of calculation: Path integration
Actually, it’s a bit more complicated...

\[
L\left\{c_1, c_2, \ldots, c_{10} \mid \text{data} \right\} = \sum_{N_{\text{true}}(i, t_{\text{start}})} \left[ \Pr\left\{N_{\text{true}}(i, t_{\text{start}}) \right\} \prod_{\text{all censuses}} \Pr\left\{N_{\text{obs}}(i, t), J(i, t) \mid N_{\text{true}}(i, t_{\text{start}}), c_1, c_2, \ldots, c_{10}, \alpha, \beta, \text{etc.} \right\} \right]
\]
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2. Sort available “local conditions” data by rookery and year
3. Choose a suitable population model and error structure
4. Calculate likelihood for all possible values of all parameters (one per hypothesis) simultaneously
5. Rank effects in terms of strength and statistical support
6. Think about what to do next
After much computing the marginal likelihoods emerge
The scaling functions for the supported hypotheses, given the MLE parameters, and their confidence intervals.
Summary:

Our motivation: Space-time plot of missing production relative to the pre-decline vital rates
Summary:

Our motivation: Space-time plot of missing production relative to the pre-decline vital rates

Our result: Space-time plot of the missing production according to the supported hypotheses
The big picture 1985-2005:
Conclusions

“The totality of causes of phenomena is inaccessible to the human mind. But the need to seek causes has been put into the soul of man”
L Tolstoy, War and Peace (Volume IV, Part Two, line 1)
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• Looking at the data at a local scale tells us things we could not see otherwise.
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- Ecology teaches us to expect many causes for declines, so allowing multiple hypotheses to compete should be the standard approach for such questions.
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- Looking at the data at a local scale tells us things we could not see otherwise.

- Ecology teaches us to expect many causes for declines, so allowing multiple hypotheses to compete should be the standard approach for such questions.

- Testing one hypothesis at a time, is likely -especially if there are lots of data -- to be fraught with danger
For Steller sea lions:

It is food, both quantity and quality (but mostly quality): Strongest effect is pollock fraction → Pup recruitment

Predation on non-pups (age 1+) may also contribute

• But --is it too much pollock or too little of something else?

More field work is needed.
A result that neither environmentalists nor NMFS likes

Who manages regimes shifts?  Whom do you sue when one happens?
Adaptive management and the search for mechanism are feasible:

Designate the areas around some of the rookeries as experimental zones in which to make fishery quotas contingent upon the results of pre-fishing season survey trawls:

- Rookeries around which fishing is not affected by the pre-season survey information (control type 1).
- Rookeries around which no fishing occurs (control type 2)
- Rookeries around which fishing is reduced or prohibited if the total prey biomass in the pre-season zone is below a critical threshold (determined by $c_1$).
- Rookeries around which a directed pollock fishery occurs if the pre-season survey suggests pollock fraction is above a critical threshold (determined by $c_5$).
A resolution to the killer whale controversy

Figure B. Four different types of interactions between killer whales and Steller sea lions are predicted for a given haulout depending on whether the proposed model is correct, whether the local density of harbor seals is below the diet-expansion threshold, and whether the observer is looking close to the haulout or far from it.