Predicting Population Level Risk Effects Of Predation From The Responses Of Individuals
A Case Study On Harbour Porpoises In Scottish Waters

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MacLeod et al. (2014) Ecology
Background

• It has long been accepted that predators can affect prey populations by killing individual animals.
• This is known as direct mortality.
• It is easy to measure and study at the population level and strong theoretical framework for understanding its impacts.
• However, it is becoming increasingly clear that even the risk of predation can affect prey populations.
• Such effects are known as indirect, or risk, effects.

Creel and Christianson (2007) TREE
Background

Background

Background

• **Indirect or Risk Effects:** More difficult to study at population level; currently no theoretical framework to understand or predict them.

• This makes them difficult to take into account when deciding on conservation and management strategies.

*Creel et al. (2007) Sci.*
# Individual-based Starvation-Predation Trade-off Theory

<table>
<thead>
<tr>
<th>Starvation Risk</th>
<th>Predation Risk</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>Low</td>
<td>$HF_{LP}$</td>
<td>$HF_{HP}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No particular impact on energy stores</td>
<td>Reduce energy stores (become lighter for size to reduce predation risk – more manoeuvrable)</td>
</tr>
<tr>
<td>High</td>
<td>Low</td>
<td>$LF_{LP}$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>Increase energy stores (become heavier for size to reduce starvation risk)</td>
<td>Reduce energy stores regardless of starvation risk (become lighter for size, but increased risk of starvation)</td>
</tr>
</tbody>
</table>

Conceptual Framework To Predict Population Level Effects From Individual Responses

MacLeod et al. (2014) Ecol.
In eastern Scotland ~65% of recorded porpoise deaths due to dolphins.

~0% porpoises killed by dolphins in rest of Scotland (or southern North Sea).

Sandeels are a key prey species for porpoises, especially in spring months.

**Study System**

*Harbour Porpoise – Sandeels – Bottlenose Dolphin*

- **Blue:** Porpoises killed by dolphins.
- **Red:** Porpoises which died from starvation.
- **Black:** Other causes of death

*MacLeod et al. (2014) Ecol.*
Study System

Harbour Porpoise – Sandeels – Bottlenose Dolphin

Co-Efficient Of Weight Difference (kg)

Sandeel Spawning Stock Biomass (SSB - Tons)

MacLeod et al. (2014) Ecol.
A Thermo-Energetic Model Of Starvation in Cetaceans

Model quantified using only data from ‘healthy’ porpoises killed by dolphins

Et+1 = Et - (EQ/CE)

Et = (Lcm WDt) * LiC * LiE

Qtm = (Tbm - Ta) * (2πLmk) * ln(r_o/r_bm)

T_LCL = Tbm - Q_admr ln(r_o/r_bm) / 2πLmk

D_{t+1} = ((E_{(t+1)} / Li_E) * Li_C) / L_{cm} W

MacLeod et al. (2014) Ecol.
A Thermo-Energetic Model Of Starvation in Cetaceans

Seasonal variation in recorded deaths from starvation from Eastern Scotland from strandings programme (1992-2006)

GAM model with Poisson distribution: EDF: 1.75; DE: 76.2%, p<0.0001
Seasonal variation in starvation survival times based on modelled seasonal variations in blubber thickness for ‘healthy’ harbour porpoises killed by bottlenose dolphin.
Combining Predation And Starvation Risk

MacLeod et al. (2014) Ecol.
Population Level Mortality

Starvation And Sandeels

A.

Sandeel Spawning Stock Biomass (Tonnes)

Recorded deaths

MacLeod et al. (2014) Ecol.
Is Increased Starvation Mortality In Addition To Other Causes Of Death?

In western Scotland, other causes of death are the main contributor to the relationship with sandeel abundance (junk food hypothesis?)

MacLeod et al. (2014) Ecol.
In eastern Scotland, same number of deaths from other causes, but additional deaths from predation (regardless of sandeels). However, at low sandeels, additional deaths due to starvation. This is the population level effect predicted from the individual trade-off based framework.

MacLeod et al. (2014) Ecol.
Conclusions

• Individual-based trade-off theory can be used create a framework for predicting population level predation risk effects (non-lethal effects).

• From one example, we predicted that species subject to starvation-predation trade offs will suffer additional deaths from starvation at low food availability - **BUT** only when high levels of predation present.

• When tested on a wild system of Harbour Porpoises – Sandeel - Bottlenose Dolphin, this is exactly what we find.

• At the lowest sandeel abundances (recorded so far), predation risk effect results in an increased in recorded mortality of ~20%.

• Is this extra mortality sufficient to influence population dynamics? Do strandings data reflect what is happening across populations as a whole?
Conclusions

<table>
<thead>
<tr>
<th>Low Predation Environment</th>
<th>High Predation Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Porpoise population abundance measured at these two points</strong></td>
<td><strong>Porpoise population abundance measured at these two points</strong></td>
</tr>
<tr>
<td><strong>No additional mortality from starvation</strong></td>
<td><strong>No additional mortality from starvation</strong></td>
</tr>
<tr>
<td><strong>No additional mortality</strong></td>
<td><strong>17% additional mortality</strong></td>
</tr>
<tr>
<td><strong>No additional mortality</strong></td>
<td><strong>23% additional mortality</strong></td>
</tr>
</tbody>
</table>

Spawning Stock Biomass Of Sandeels (from http://www.ices.dk/advice/icesadvice.asp)

**Predict:** Pop Fine (Southern North Sea)  
**Predict:** Pop Decline (Northern North Sea)
Conclusions

• Main decline in density is in region where high predation and high starvation risk overlap (as predicted by the theoretical framework).

• Therefore, this framework can potentially provide important information for predicting how populations will change over time as environmental conditions change.

• Similar individual-based frameworks should also apply to other species and systems (e.g. seabirds, turtles, fisheries?)
Acknowledgements

• **Jennifer Learmonth** (prepared and verified the porpoise strandings data set used as part of the BIOCET Project).

• **Scottish Strandings Reporting Scheme** (collection of all the porpoise data/necropsies etc).

• **BIOCET Project** (funding for collecting/analysing porpoise strandings data).

• **John Speakman** (advice on energetics, thermoregulation and starvation).