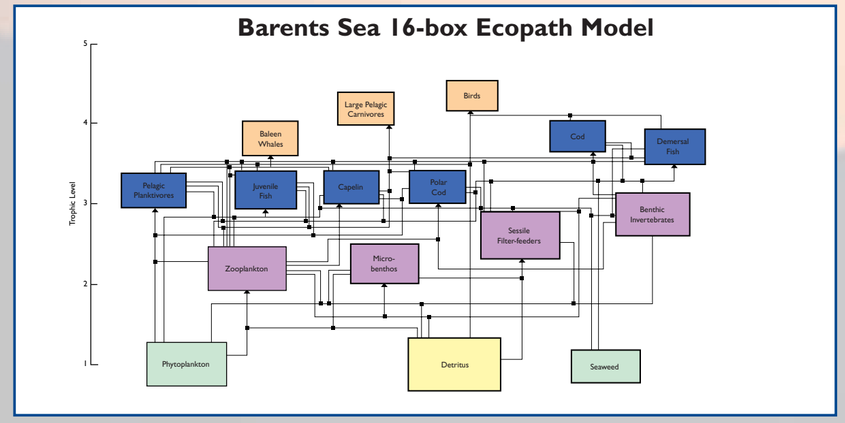
CONSEQUENCES OF ALTERNATIVE ASSUMPTIONS ON MARINE MAMMAL FEEDING BEHAVIOUR

Julia Blanchard, Steven Mackinson, John Pinnegar, Robert Scott and Mark Bravington

CEFAS
The Centre for Environment, Fisheries & Aquaculture Science

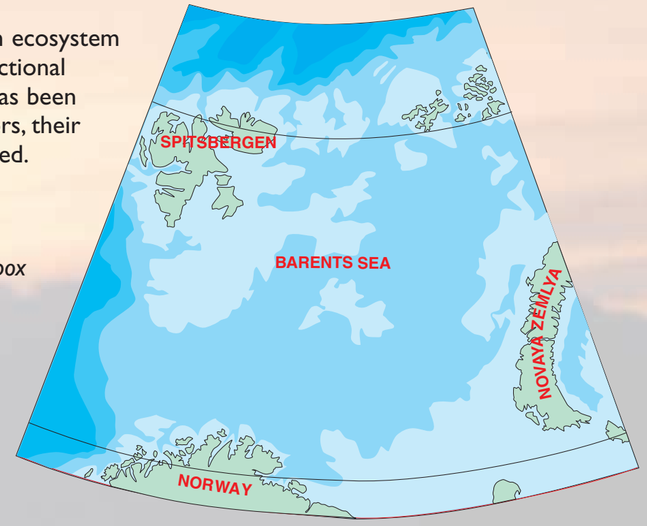
Aim

Compare how assuming different feeding behaviours of marine mammals affect ecosystem model (Ecosim) predictions. i.e. functional responses (see Box1)



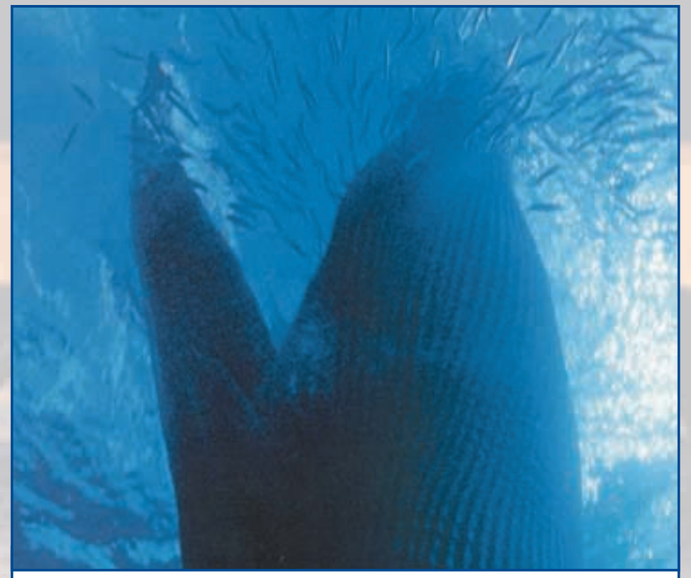
Why do it?

Whether marine mammals compete with fisheries is an important issue scientifically. In ecosystem models, formulating the way that predators respond to changes in prey availability (functional response) is critical for predicting the mortality imposed by those predators. Ecosim has been proposed as a useful tool for exploring interactions[1] between marine-mammal predators, their prey and fisheries. However, its utility for addressing such questions remains to be tested.



What we did

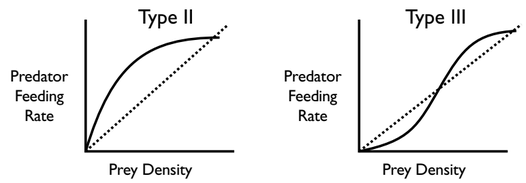
1. Constructed a 41-box Barents Sea model using Ecopath with Ecosim. *Simplified 16-box model used here (opposite)*
2. Determined how Ecosim considers functional responses
3. For alternative functional responses, we compared the predicted effects of two harvesting scenarios (involving baleen whales or cod) on other components in the system



Sei whale feeding on pelagic fish
(courtesy of the BBC: bbc.co.uk/nature/programmes/tv/blueplanet/)

BOX 1. How do marine mammals respond to changes in prey abundance?

- Holling's[9] functional response equations describe how a predator's feeding rate changes with prey abundance.
- When a particular prey is reduced to low densities, a Type III functional response predicts lower predation pressure on that prey because the predator switches to a more abundant substitute.



Modelling functional responses

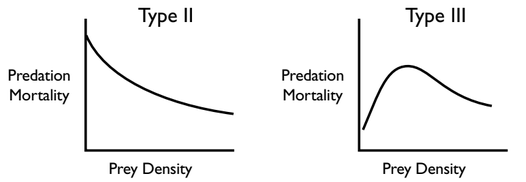
- Most ecosystem and multispecies models use a modified version of the Type II functional response[10].
- Type III functional response are often more difficult to incorporate into complex population dynamics models[11] and hence are less widely used.

What is known about marine mammals?

- Many marine mammals are opportunistic feeders[2, 3].
- At low prey abundance some marine mammals switch to a more abundant prey[4, 5,6].
- This is thought to be the case for minke whales and harp seals in the Barents Sea[7,8].

How could model specifications affect predictions on marine mammals' feeding?

- If many marine mammals exhibit a Type III functional response (i.e. switching), then assuming a Type II functional response could greatly over-estimate the effect such predators might have on depleted prey stocks.

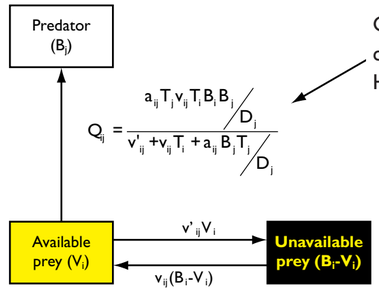


Prey groups denoted with subscript i
Predator groups denoted with subscript j
$\mathbf{B_i}$ Total prey biomass
$\mathbf{V_i}$ Available prey biomass
$\mathbf{B_i - V_i}$ Unavailable prey biomass
$\mathbf{B_j}$ Total predator biomass
$\mathbf{Q_{ij}}$ Consumption of prey i by predator j per unit time
$\mathbf{a_{ij}}$ Rate of effective search for prey i by predator j
$\mathbf{v_{ij}}$ Prey vulnerability parameter representing flow rate from unavailable to available behavioural state
$\mathbf{v'_{ij}}$ Prey vulnerability parameter representing flow rate from available to un-available behavioural state
By default $v_{ij}=v'_{ij}$
$\mathbf{D_j = 1 + h_j a_{ij} T_j V_{ij}}$ is the effect of handling time as a limit to consumption rate
$\mathbf{T_i}$ time spent foraging by i
$\mathbf{T_j}$ time spent foraging by j

[1] What is Ecosim? Ecosim is a dynamic simulation tool for ecosystem modelling, that uses key initial parameters from a mass-balance food web model built using the Ecopath approach [12].

BOX 2. How Ecosim incorporates functional responses

Prey can be in two 'behavioural states': Available and Unavailable. This represents a'foraging arena' concept where not all prey are vulnerable to all predators.



Consumption rate by predators (Q_{ij}) is calculated using a generalisation of a Holling Type II functional response.

Consumption rate can be limited in two ways relating to time management of predators and prey. Thus, functional responses are an 'emergent' feature.

Factors limiting consumption rate

1. **Handling time is the inverse of the max prey biomass eaten per unit time by a predator**
   - When handling times are very short, consumption is NOT limited, and is proportional to prey biomass
   - When handling times are long, consumption rate is limited, SATIATION of the predator (Type II response)
2. **Effective search rate and vulnerability are modified by time spent foraging**
   - Changes in an individual's consumption rate result from changes in prey densities as well as their own density (due to effects of intraspecific competition). In trying to maintain constant consumption rate, they adjust time spent foraging
   - Foraging time adjustments have opposing trade-offs. Increased forage time means higher food intake rate (increased effective search rate), but also higher predation loss (increased flow to vulnerable state)
   - **Type III functional response** curves for predators result from prey behaviour (changes in their search rate and consequent exposure to predation risk), NOT as a result of change in predator search tactics

CONSEQUENCES OF ALTERNATIVE ASSUMPTIONS ON MARINE MAMMAL FEEDING BEHAVIOUR

Simulation Scenarios

Three Ecosim model formulations were considered:

1. No limitation to consumption rate. Consumption proportional to prey biomass
2. Handling time for whales long. Consumption rate limited; satiation of the predator (Type II response)
3. Foraging time adjustments for whales and their prey included. Consumption limited through prey behaviour.

Two harvest scenarios were considered:

- Scenario 1: Fishing mortality (F) of 'Baleen Whales' was increased ten-fold (from 0.0012)
- Scenario 2: Fishing mortality (F) of 'cod' was doubled (from 0.14)

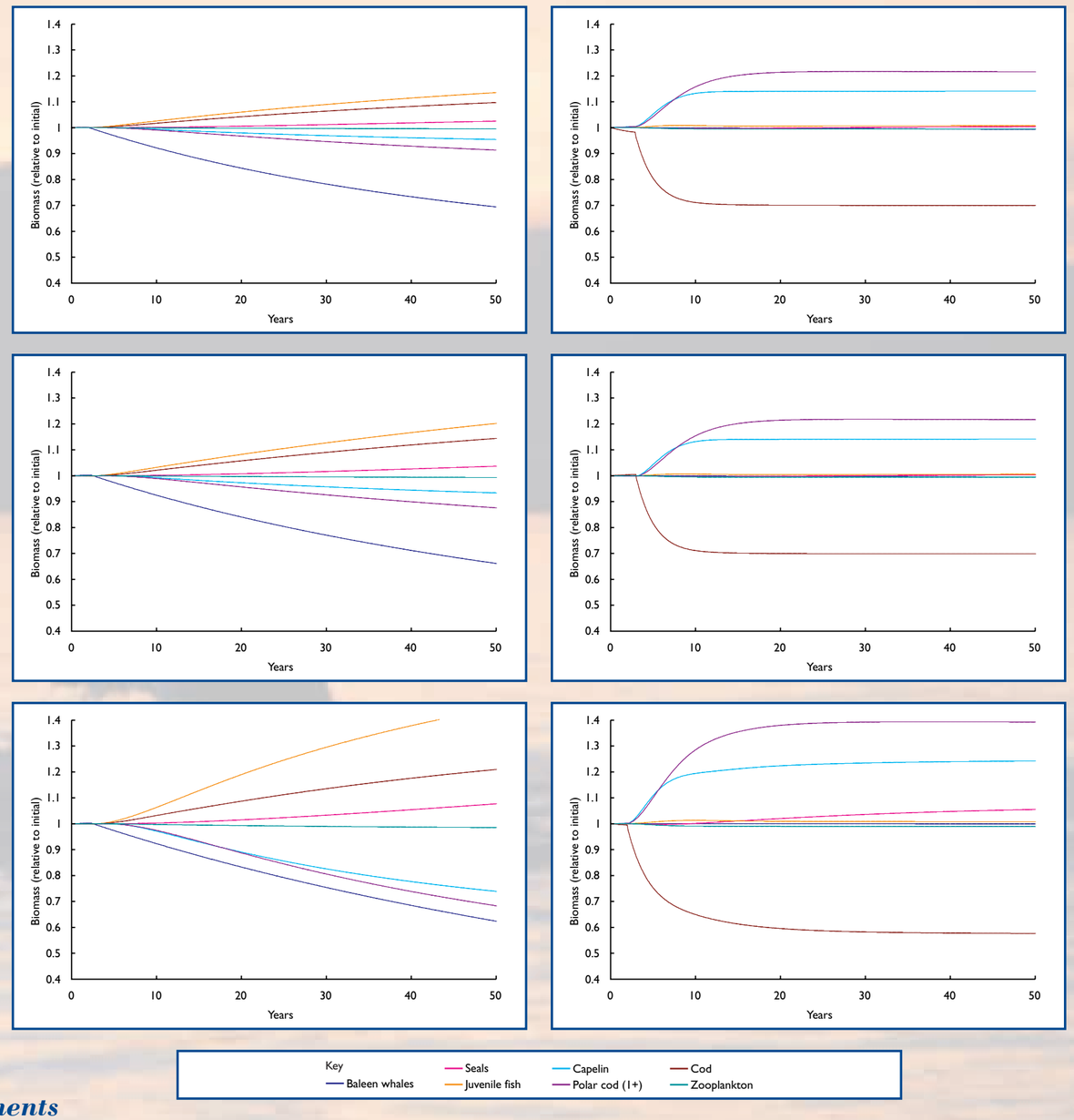
Each scenario covered a period of 50 years. Vulnerabilities (v_{ij}) for all groups were set at 0.4

Discussion

- Marine mammals responded to perturbations more slowly than did fish, as expected due to longer generation times.
- Accounting for handling time limitation in baleen whales (sensu a Holling type II response) resulted in very similar predictions (in terms of magnitude) compared to a model where predation rate was proportional to available prey density. This agrees with field observation data that suggests most consumers are rarely able to achieve satiation.
- When foraging time adjustments for whales and their prey were implemented, whale consumption was limited through prey behaviour and system responses were greater in magnitude.
- Indirect responses of other predators (competitors) in the system can result in counter-intuitive responses in prey stocks (i.e. 'trophic cascades' and 'keystone predation' effects).
- Type III functional response curves of predators consumption rate result from prey behaviour NOT as a result of change in predator search tactics. Functional responses are not hardwired. They 'emerge' depending on how predators and prey are assumed to manage their foraging time.
- Our 16-box model is likely to be over-aggregated in terms of the number of functional components, therefore the effect one group might have on another (e.g. marine mammals on fish stocks) could be greatly overestimated (underestimation of dampening effects)[13].

The way forward

- Using a derived model, outside of the Ecosim interface, we plan to consider how to incorporate prey switching as direct consequence of predator search rate (a_{ij}), rather than prey behaviour as is currently implemented.
- We plan to use new tools currently being developed within Ecosim in continuing to formulate various representations of functional responses for marine mammals
- We intend to use our more detailed 41 compartment model for future analyses



Acknowledgements

The authors would like to thank the International Fund for Animal Welfare (IFAW) for funding this project, and the project steering committee John Harwood, Justin Cooke, Vassili Papastavrou, John Reynolds and Andy Payne. We thank Carl Walters and Villy Christensen for informative discussion regarding the structure, functioning and capabilities of Ecosim.

References

1. IWC 2001, *J. Cetacean Res. Manage.* 3 (Suppl) p. 63. **2. Beddington et *al.* 1985,** *Marine Mammals and Fisheries.* 354 pp. **3. Skaug et *al.* 1997,** *J. Northw. Atl. Fish.* 22: 91-104. **4. Ohizum et *al.* 2000,** *Mar. Ecol. Prog. Series* 200: 265-275. **5. Bailey & Ainley 1982,** *Fish. Res.* 1: 163-176. **6. Tollit et *al.* 1997,** *Can J. Zool.* 75: 1508-1518. **7. Schweder et *al.* 2000,** *NAMMCO Sci. Publ.* 2: 120-133. **8. Nilssen et *al.* 2000,** *NAMMCO Sci. Publ.* 2: 9-27. **9. Holling 1965,** *Mem. Entomolec. Soc. Can.* 45: 1-60. **10. Whipple et *al.* 2000,** *Fish and Fisheries.* 1:22-40. **11. Liermann & Hilborn 2001,** *Fish and Fisheries.* 2:33-58. **12. Christensen et *al.* 2000,** *Ecopath with Ecosim: A User's Guide.* 130 pp **13. McCann et *al.* 1998,** *Nature.* 395: 794-798.

The Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK. http://www.cefas.co.uk