

StrathE2EPolar version 1.0.0: Ecology model description.

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WORK IN PROGRESS – ROUGH DRAFT TO BE COMPLETED

Introduction

The StrathE2EPolar ecology model builds on the earlier fully documented StrathE2E2 (Heath et al. 2021), version 3.3.0, by adding additional state variables and horizontal spatial differentiation to represent the role of sea ice in the system. This document provides an overview of the essentials of StrathE2E2 and describes the features which extend it to include ice, in particular:

- Time-varying horizontal spatial driving data to represent sea ice and snow,
- Representation of nutrient, algae and detritus ecology in sea ice and its connection to the rest of the food web,
- Dynamics of maritime mammals (polar bears),
- Ice-dependency in the feeding and migrations of birds, pinnipeds, cetaceans and maritime mammals,
- Seasonal immigration and emigration from the model domain by birds, pinnipeds, cetaceans and maritime mammals,

Brief summary of the StrathE2E2 model

Table 1. Ecology model state variables and spatial hierarchy in StrathE2E2

Differentiated by horizontal zone and sediment habitat	Differentiated by horizontal zone and water column layer	Differentiated by horizontal zone with modelled vertical distribution	Differentiated by horizontal zone only
Sediment bacteria and labile detritus	Nitrate	Omnivorous zooplankton	Suspension/deposit feeding benthos
Refractory sediment detritus	Ammonia	Carnivorous zooplankton	Carnivore/scavenge feeding benthos
Pore-water nitrate	Suspended bacteria and detritus	Larvae of suspension/deposit feeding benthos	Planktivorous fish
Pore-water ammonia	Phytoplankton	Larvae of carnivore/scavenge feeding benthos	Demersal fish (divided into fishery quota-limited and non-quota components)
Fishery discards		Larvae of planktivorous fish	Migratory fish

Corpses		Larvae of demersal fish	Pinnipeds
Macrophytes (confined to inshore rock habitat)			Seabirds
			Cetaceans

Key equations in StrathE2E2

The general equation for the rate of change of a food web component (X) in StrathE2EPolar given a set of k prey types (N_k) and a set of j predator types (Y_j), is essentially the same as in StrathE2E2:

$$\frac{dX}{dt} = A \sum_k U_{X(N_k)} - \sum_j U_{Y_j(X)} - \varepsilon(t)X - \delta X^2 + F_X - H(t)X - D(t)X + R_X \quad \text{eqn 1}$$

- $U_{v_1(v_2)}$ Flux of ingestate to a predator (v_1) from prey (v_2). ($v_1, v_2 = X, N$ or $v_1, v_2 = Y, X$)
- A Assimilation efficiency. Ingestate not assimilated ($(1 - A) \sum_k U_{X(N_k)}$) is divided equally between a flux to dissolved ammonia, and a flux to detritus.
- $\varepsilon(t)$ Temperature, and hence time-dependent basal metabolic rate coefficient (generates a flux from body mass to ammonia)
- δ Density dependent mortality coefficient (generates a flux from body mass to a detritus category). δ is normalised to the area or volume of a zone or layer, depending on the food web component (X), so that the mortality rate scales with concentration rather than the mass.
- F_X Vertical advection and diffusion fluxes affecting the food web component
- $H(t)$ Harvest ratio (time-dependent rate of biomass capture by fisheries)
- $D(t)$ Time-dependent developmental export rate for the food web component X . For $X =$ adult stages, $D(t)X$ represents the flux of spawning products to the egg, larval and juvenile (ELJ) stage. For $X =$ ELJ stages, $D(t)X$ represents the settlement flux to adults. For food web components lacking demographic structure, $D(t) = 0$
- R_X Recruitment flux to the food web component X . For $X =$ adult stages, R_X is equal to the settlement flux from the ELJ stage. For $X =$ ELJ stages R_X is equal to the flux of spawning products from the adults. For food web components lacking demographic structure, $R_X = 0$

General equation for the flux of ingestate to a predator (v_1) from prey (v_2) is:

$$U_{v_1(v_2)} = \frac{v_1 \cdot v_2 \cdot \rho_{v_1(v_2)} \cdot U_{max_{v_1}}}{v_2 + h_{v_1}} \quad \text{eqn 2}$$

- $\rho_{v_1(v_2)}$ Preference of the predator v_1 for the prey class v_2 . For a given predator class, the sum of the preference coefficients over all prey classes = 1.
- $U_{max_{v_1}}$ Temperature, and hence time-dependent maximum uptake rate of the predator v_1
- h_{v_1} Half-saturation constant for uptake of prey by the predator v_1 (temperature independent). Within the model code, h is normalised to the area or volume of a zone or layer, depending on the food web component (X), so that half saturation is expressed in terms of concentration rather than the mass.

For phytoplankton ($v_1 =$ phytoplankton ($X = P$)), the assimilation efficiency $A = 1$, temperature dependent basal metabolic rate coefficient $\varepsilon = 0$, and there is no demographic structure so $D(t) = 0$ (and hence $R_X = 0$). The uptake of prey ($v_2 =$ dissolved nutrient N_k) has a light-dependent term:

$$U_{P(N_k)} = \text{Min} \left\{ 1, \frac{L(t)}{L_{max}} \right\} \frac{P \cdot N_k \cdot \rho_{P(N_k)} \cdot U_{maxP}}{N_k + h_P} \quad \text{eqn 3}$$

$L(t)$ Time-dependent light intensity
 L_{max} Saturation light intensity for nutrient uptake

Food uptake plankton, benthos and fish in StrathE2E2 follows the Michelis Menten form outlined above. Uptake of prey by the top-predators (birds, pinnipeds and cetaceans), follows the predator-density dependent Beddington-DeAngelis functional form (Beddington, 1975; DeAngelis *et al.*, 1975) with an additional parameter γ :

$$U_{v_1(v_2)} = \frac{v_1 \cdot v_2 \cdot \rho_{v_1(v_2)} \cdot U_{maxv_1}}{v_2 + \gamma v_1 + h_{v_1}} \quad \text{eqn 4}$$

Representing horizontal structure, seabed habitats and sediment processes

We define two depth-zones of seabed in StrathE2E2 – an inshore/shallow/well-mixed zone and an offshore/deep/seasonally-stratified zone. We use the terms ‘inshore’ and ‘offshore’ to refer to these zones though it should be noted that, in reality, shallow well-mixed areas of a model region can be located over isolated offshore banks as well as adjacent to the coast. However, we assume that for the purposes of the model the inshore zone constitutes a contiguous, horizontally homogeneous body of water.

The inshore zone comprises a single water column layer connected vertically to a seabed sediment layer. The latter is divided horizontally into four habitats defined by sediment properties. The offshore zone has two vertically connected water column layers (upper and lower), with the lower being connected to seabed sediment habitats as in the shallow zone. The offshore zone upper layer and the shallow zone are horizontally connected to represent advection and mixing.

Resolving different types of sediments

The extents of seabed habitats in each zone are defined by their area-proportion of the seabed. One habitat in each zone is reserved for exposed rock, and the other three are configurable for any combination of sediment types defined by layer thickness, median grain size, porosity, hydraulic conductivity and natural disturbance rate. Data on sediment porosity and hydraulic conductivity are scarce, so the model code includes an option to impute these from median grain size values using default or user-supplied parameters.

Modifications of StrathE2E2 to create StrathE2EPolar

Time-varying ice and snow-related driving data

Additional state variables and guilds to represent ice ecology

Additional guild to represent maritime mammals

Representing ice-dependency in the feeding ecology of birds, pinnipeds, cetaceans and maritime mammals

Prey consumption functional responses

The Holling Type-II equation (Holling, 1959) is widely used to describe the per capita uptake rate (g) of prey (v_2) by a consumer (v_1), in terms of a search rate (c) and a time for processing (b):

$$g(v_1) = \frac{c \cdot v_2}{1 + c \cdot b \cdot v_2} \quad \text{eqn 7}$$

This form can be reconfigured as the Michaelis-Menten equation in terms of a prey half-saturation coefficient $h = \frac{1}{c \cdot b}$, and a maximum per capita uptake rate by the predator $U_{max} = \frac{1}{b}$.

$$g(v_1) = \frac{v_2 \cdot U_{max} v_1}{v_2 + h v_1} \quad \text{eqn 8}$$

Incorporating a preference term, the general equation for the flux of ingestate to a predator (v_1) from prey (v_2) is then:

$$U_{v_1(v_2)} = \frac{v_1 \cdot v_2 \cdot \rho_{v_1(v_2)} \cdot U_{max} v_1}{v_2 + h v_1} \quad \text{eqn 9}$$

where $\rho_{v_1(v_2)}$ is the preference of the predator v_1 for the prey class v_2 . For a given predator class, the sum of the preference coefficients over all prey classes = 1. This particular form of preference coefficient is adopted because of the high degree of taxonomic aggregation in the functional guilds of the model (Heath, 2012).

In common with many other aquatic food web models (Gentleman *et al.*, 2003), the Holling Type-II / Michaelis-Menten form is used as the basis for predator-prey relationships in StrathE2E2 and StrathE2EPolar. However, the Holling Type-II does not incorporate any regulatory mechanism and hence food chain models based solely on this function exhibit neutral stability or instability. For this reason, the StrathE2E models include quadratic (density-dependent) loss terms for most trophic guilds to represent, for example, competition for an un-modelled resource (e.g. space for sessile taxa), cannibalism (intra-guild predation in the context of our model based on trophic guilds), or incidence of disease epidemics. Other authors have referred to this mathematical process as 'interference' (McCann *et al.*, 1998; Polis & Holt, 1992).

An alternative to mortality regulation is to invoke consumer density-dependence of per capita uptake rate, which suppresses responsiveness by regulating the flux between prey and consumers. This model form is intended to represent sharing of resources, behavioural interference between consumers to their mutual impairment, enhanced escape reactions by prey, sheltering in refuges with increasing predator density (Hill & Weissburg, 2013), or the foraging of predators in a patchy prey environment (Anderson, 2010; Cosner *et al.*, 1999). There are many observational and experimental examples of top-down forced prey behavioural responses to predators of this type, with evidence that they lead to impacts on basal resources – and hence a *de facto* cascade effect (Griffin *et al.*, 2011; Schmitz *et al.*, 2004; Trussell *et al.*, 2006). An established adaptation of the familiar Michaelis-Menten

uptake function to confer consumer density-dependent regulation by specifying an additional parameter (γ) is the Beddington-DeAngelis equation (Beddington, 1975; DeAngelis *et al.*, 1975):

$$g_{v_1} = \frac{v_2 \cdot Umax_{v_1}}{h_{v_1} + v_2 + \gamma \cdot v_1} \quad \text{eqn 10}$$

In StrathE2EPolar we adopt this form to represent the consumption of food by the high trophic level predators in the model ecosystem (birds, pinnipeds, cetaceans and maritime mammals). This is justified particularly on the grounds that, more than any other guilds in the ecosystem, their foraging behaviour involves cooperative groups of individuals actively seeking out dense patches of prey.

Effects of temperature on uptake function parameters

We expect $Umax_{v_1}$ to be temperature-dependent since it depends only on the handling time which should decrease with temperature (so $Umax_{v_1}$ increases). However, we expect the half saturation coefficient to have negligible temperature sensitivity since it depends upon both the search rate and the handling time and these should vary in opposite direction with temperature – search rate should increase with temperature but handling time decrease.

We represent the temperature dependency of $Umax_{v_1}$ by a monotonic Q_{10} function. The Q_{10} is appropriate for individual species only within their normal temperature range of occurrence; over a wider range the response is typically dome-shaped with declining uptake rates at higher temperatures. However, the model guilds are an adaptive assemblage of species each with different temperature tolerances, so the collective response is not necessarily dome shaped until physiologically damaging temperatures are encountered.

Ice-dependency of uptake function parameters

We expect ice cover and extent to influence search rates, but not handling times. Hence, half saturation coefficients should be dependent on ice but maximum uptake rates parameters should not.

The half saturation coefficient is a measure of the efficiency of a predator at catching prey, and empirical evidence suggests that efficiency occurs at some optimum ice conditions for any given predator. For example, polar bears have an optimum ice cover for efficient prey capture (REFS), with lower efficiency (higher half saturation coefficient) towards 100% cover and 0% cover.

We define an ice-dependency function which scales an optimum (minimum) value of prey half saturation according to ice conditions:

$$q_{ice} = \begin{cases} (0 - opt_{ice})^2, & opt_{ice} > 0.5 \\ (1 - opt_{ice})^2, & opt_{ice} \leq 0.5 \end{cases}$$

$$d_{ice} = \frac{(ice - opt_{ice})^2}{q_{ice}}$$

$$mult_{hs} = 1 + d_{ice} \cdot (s_{ice} - 1)$$

$mult_{hs}$ is a U-shaped function which has a minimum value of 1.0 at the optimum ice conditions and a maximum of s_{ice}

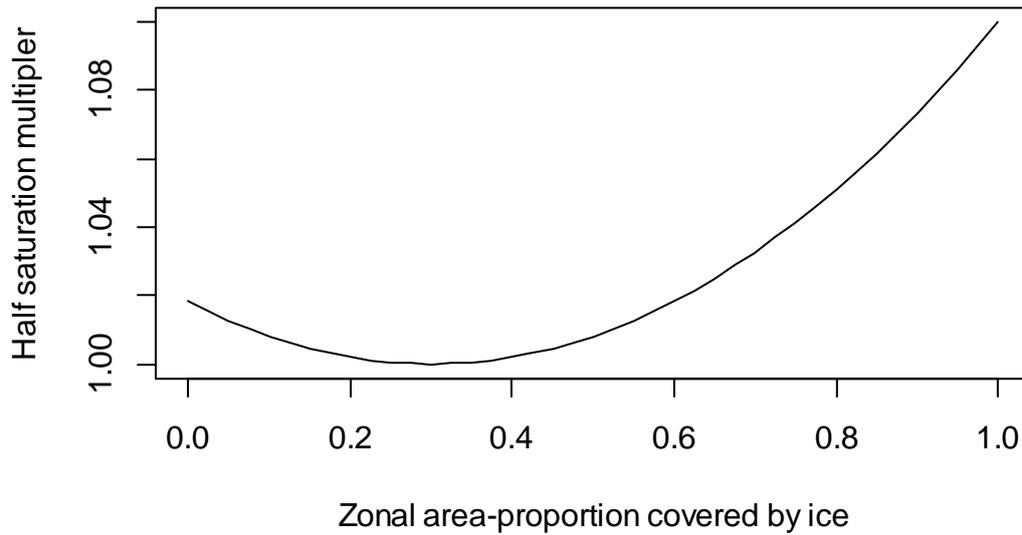


Figure xx. Example of the U-shaped function $mult_{hs}$ with respect to the zonal area-proportion covered by ice (i.e. $(1 - \text{area proportion of exposed sea surface})$), for parameter values: $opt_{ice}=0.3$, $s_{ice}=1.1$

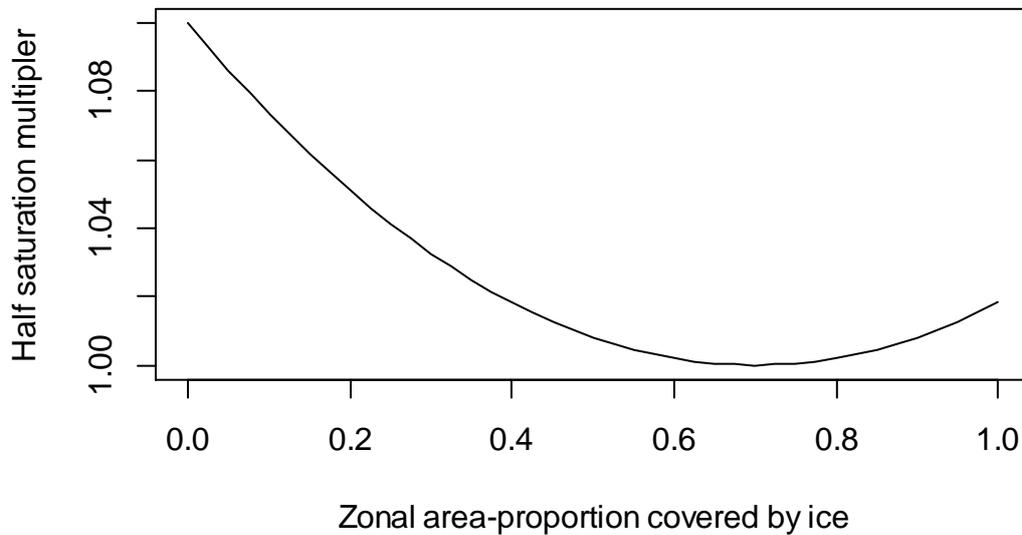


Figure xx. Example of the U-shaped function $mult_{hs}$ with respect to the zonal area-proportion covered by ice (i.e. $(1 - \text{area proportion of exposed sea surface})$), for parameter values: $opt_{ice}=0.7$, $s_{ice}=1.1$

Representing ice-dependency in active horizontal migrations of birds, pinnipeds, cetaceans and maritime mammals

Spatially resolved models which include fish and top predators must address the role of active migrations. Some models treat movement as a non-dynamic or 'clockwork' data-driven process, but this is clearly limiting for scenario experiments which aim to explore the properties of the system outside the envelope of observed driving conditions. Movement fundamentally affects regionally-integrated encounter rates between predators and their prey, and hence productivity (Nathan *et al.*, 2008), so needs to be modelled as a dynamic property. However, the motivations for active migrations are many and complex, including time and state-dependent interplays between the feeding, need-to-breed, predator avoidance and environmental tolerances, which are very poorly understood (Berdahl *et al.*, 2016). Individual based methods are an attractive modelling option, but are computationally costly and complicated to integrate with eulerian representations of lower trophic levels (Kay *et al.*, 2017).

As a first order approximation we can assume that active predators are at least motivated by feeding, and are monitoring their environment in an attempt to optimise their distribution in relation to preference-weighted prey concentrations. We achieve this in the model by adopting a ratio-dependent behaviour scheme in which the grazer population attempts to maintain a spatially uniform value of the ratio of their own concentration to the preference-weighted concentration of their prey. The implication of this is that, by means of short-time scale processes such as random searching which are not represented in the model, the grazers are able to monitor concentration gradients in both their prey and their conspecifics, and distribute themselves accordingly (Berdahl *et al.*, 2016). Ratio-dependent behaviour such as this has been widely adopted in ecological models to represent the distribution of grazers (Anderson, 2010; Arditi & Ginzburg, 1989, 2012; Cosner *et al.*, 1999).

Implementation in StrathE2E2

Planktivorous, demersal and migratory fish, and birds and mammals, were assumed to be capable of active horizontal movements, completely independent of hydrodynamics. Given the spatial scale of the horizontal compartments in the model, the time-scales for active horizontal redistributions of biomass were assumed to be much longer than the intrinsic daily resolution. Hence, the migrations of these guilds needed to be represented as directed rate processes (horizontal fluxes between spatial compartments) rather than being tightly bound to the distributions of prey as for the vertical migrators.

For each migrating guild, the flux of biomass between spatial compartments was parameterised to be proportional to the horizontal gradient of prey-to-predator biomass density ratio, so that predators migrated towards the zone where the prey-predator biomass ratio was highest. Prey density was estimated as the preference-weighted sum over all prey guilds for each predator.

The gradient in prey : predator density ratio (R_Y) is given by:

$$R_Y = \ln \left(\frac{\left(\frac{\sum_i \left(\frac{pref_i \cdot X_{i,offshore}}{A_{offshore}} \right)}{\left(\frac{Y_{offshore}}{A_{offshore}} \right)} \right)}{\left(\frac{\sum_i \left(\frac{pref_i \cdot X_{i,inshore}}{A_{inshore}} \right)}{\left(\frac{Y_{inshore}}{A_{inshore}} \right)} \right)} \right) = \ln \left(\frac{\left(\frac{\sum_i (pref_i \cdot X_{i,offshore})}{Y_{offshore}} \right)}{\left(\frac{\sum_i (pref_i \cdot X_{i,inshore})}{Y_{inshore}} \right)} \right) \quad \text{eqn 1}$$

provided that:

$$\sum_i (pref_i \cdot X_{i,offshore}) > 0 \text{ and } \sum_i (pref_i \cdot X_{i,inshore}) > 0, \text{ and } Y_{offshore} > 0 \text{ and } Y_{inshore} > 0$$

Otherwise,

$$R_Y = -R_{Ylim} \text{ if:}$$

$$Y_{inshore} = 0 \text{ and } \sum_i (pref_i \cdot X_{i,inshore}) > 0, \text{ or } \sum_i (pref_i \cdot X_{i,offshore}) = 0 \text{ and } \sum_i (pref_i \cdot X_{i,inshore}) > 0$$

$$R_Y = +R_{Ylim} \text{ if:}$$

$$Y_{offshore} = 0 \text{ and } \sum_i (pref_i \cdot X_{i,offshore}) > 0, \text{ or } \sum_i (pref_i \cdot X_{i,inshore}) = 0 \text{ and } \sum_i (pref_i \cdot X_{i,offshore}) > 0$$

Otherwise,

$$R_Y = 0$$

Here, $X_{i,offshore}$ and $X_{i,inshore}$ are the masses (mMN) of the prey guild i in the offshore and inshore zones respectively, $Y_{offshore}$ and $Y_{inshore}$ are the corresponding masses of the predator, $pref_i$ is the preference of the predator Y for each prey type i , and $A_{offshore}$ and $A_{inshore}$ are the surface areas of the offshore and inshore zones.

R_{Ylim} is a fixed value of R_Y to achieve the extreme eventualities of recolonization of a zone devoid of Y provided that food is present, or evacuation of Y from a zone where food becomes absent. In reality these conditions can never be met provided that positive non-zero values are provided for the initial values of the state variables in the model.

Then, the directed migration fluxes (mMN.d⁻¹) from the offshore to the inshore zone ($M_{Y,offshore-inshore}$), and conversely from the inshore to the offshore zone ($M_{Y,inshore-offshore}$) are given by:

$$M_{Y,offshore-inshore} = \begin{cases} Y_{offshore} \cdot \frac{k_Y}{A_{offshore}} \cdot R_Y^2, & R_Y < 0 \\ 0 & \text{otherwise} \end{cases} \quad \text{eqn 2}$$

$$M_{Y,inshore-offshore} = \begin{cases} Y_{inshore} \cdot \frac{k_Y}{A_{inshore}} \cdot R_Y^2, & R_Y > 0 \\ 0 & \text{otherwise} \end{cases} \quad \text{eqn 3}$$

where k_Y is a predator-specific scaling coefficient.

Incorporating ice-dependency into migrations in StrathE2EPolar

Some of the predator guilds in the model (birds, pinnipeds, cetaceans and maritime mammals (bears and foxes)) are associated with, or excluded by sea ice, the areal extent of which is which is continually varying with time. This requires some additional consideration in equation 1.

For prey terms ($X_{i,offshore}$ and $X_{i,inshore}$) the relevant area for deriving density ($\text{mMN}\cdot\text{m}^{-2}$) is still the full area of the offshore and inshore zones, regardless of ice areal extent. Thus, for example, if ice algae and phytoplankton mass remain constant but ice extent changes, then the two prey types remain equally attractive to a potential consumer. However for the predator terms ($Y_{offshore}$ and $Y_{inshore}$), the relevant area of their habitat ($A_{offshore-predhabitat}$ and $A_{inshore-predhabitat}$) depends in ice properties (Table X).

Table X. Relevant areas for computing ice-dependent predator densities in equation 1

Guild	Relevant habitat areas $A_{offshore-predhabitat}$ and $A_{inshore-predhabitat}$ for estimating predator density	Justification
Birds	Time-varying exposed sea surface area	Birds must breed on land or the ice, but can only forage in exposed water. As ice extent expands within a zone we expect this to repel birds.
Pinnipeds	Time-varying exposed sea surface area	Ringed and Bearded seals have a strong affinity for ice and can maintain breathing holes allowing them to forage below solid ice. Harp seals (by far the most abundant pinniped) are ice-associated and forage near the ice edge during April – July but migrate to open water during the rest of the year. They spend at least 53% of the year in areas with less than 40% ice coverage ((Polar Biology 27(5):281-298 (2004); Front. Ecol. Evol. 3:29.(2015))Nordøy et al., 2008, PolarBiol. 31,1119–1135.). Walrus have an affinity for ice but also spend time on the shoreline, and forage mainly in inshore waters. Generalising across the species is difficult but ultimately most pinnipeds have an affinity for ice. As ice extent expands within a zone then, for feeding purposes, we expect this to repel pinnipeds.
Cetaceans	Time-varying exposed sea surface area	Cetaceans require access to open water in order to breathe at all times. As ice extent expands within a zone we expect this to repel cetaceans.
Maritime	Time-varying ice-extent area	Maritime mammals are essentially

mammals	confined to the land or ice although bears can swim and feed a short distance from the ice edge. As ice extent expands within a zone we expect this to attract maritime mammals.
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Here, we define ice-extent (I_E) as being the area of a zone where the ice-cover p_i is greater than a minimum threshold (15%). Conversely, we refer to the ice-free area (I_F) as being the area where ice-cover is less than the minimum threshold. The exposed sea surface area is then given by $I_F + (I_E \cdot (1 - \overline{p_{I(E)}}))$.

The introduction of these time-varying terms ($A_{offshore_predhabitat}$ and $A_{inshore_predhabitat}$) in equation 1 yields

$$R_Y = \ln \left(\frac{\left(\frac{\sum_i \left(\frac{pref_i \cdot X_{i,offshore}}{A_{offshore}} \right)}{Y_{offshore}} \right)}{\left(\frac{\sum_i \left(\frac{pref_i \cdot X_{i,inshore}}{A_{inshore}} \right)}{Y_{inshore}} \right)} \right) = \ln \left(\frac{\left(\frac{\sum_i (pref_i \cdot X_{i,offshore})}{(Y_{offshore})} \right) \cdot \frac{\rho_{offshore_predhabitat}}{\rho_{inshore_predhabitat}}}{\left(\frac{\sum_i (pref_i \cdot X_{i,inshore})}{(Y_{inshore})} \right)} \right) \text{ eqn 4}$$

where $\rho_{offshore_predhabitat}$ and $\rho_{inshore_predhabitat}$ are the area-proportions of the offshore and inshore zones respectively constituting feeding habitat for the given predator guild:

$$\rho_{offshore_predhabitat} = \frac{A_{offshore_predhabitat}}{A_{offshore}} \text{ eqn 5}$$

$$\rho_{inshore_predhabitat} = \frac{A_{inshore_predhabitat}}{A_{inshore}} \text{ eqn 6}$$

This formulation requires some additional conditions:

R_Y is valid provided that:

$$\sum_i (pref_i \cdot X_{i,offshore}) > 0 \text{ and } \sum_i (pref_i \cdot X_{i,inshore}) > 0, \text{ and}$$

$$Y_{offshore} > 0 \text{ and } Y_{inshore} > 0, \text{ and}$$

$$\rho_{offshore_predhabitat} > 0 \text{ and } \rho_{inshore_predhabitat} > 0.$$

Otherwise,

For birds, pinnipeds and cetaceans:

$R_Y = -R_{Y_{lim}}$ if:

$$Y_{inshore} = 0 \text{ and } \rho_{inshore_predhabitat} > 0 \text{ and } \sum_i (pref_i \cdot X_{i,inshore}) > 0, \text{ or}$$

$$\rho_{inshore_predhabitat} > 0 \text{ and } \sum_i (pref_i \cdot X_{i,offshore}) = 0 \text{ and } \sum_i (pref_i \cdot X_{i,inshore}) > 0, \text{ or}$$

$$\rho_{offshore_predhabitat} = 0 \text{ and } \rho_{inshore_predhabitat} > 0.$$

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$R_Y = +R_{Y_{lim}}$ if:

$Y_{offshore} = 0$ and $\rho_{offshore_predhabitat} > 0$ and $\sum_i(pref_i \cdot X_{i,offshore}) > 0$, or
 $\rho_{offshore_predhabitat} > 0$ and $\sum_i(pref_i \cdot X_{i,inshore}) = 0$ and $\sum_i(pref_i \cdot X_{i,offshore}) > 0$, or
 $\rho_{inshore_predhabitat} = 0$ and $\rho_{offshore_predhabitat} > 0$.

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For maritime mammals:

$R_Y = -R_{Y_{lim}}$ if:

$Y_{inshore} = 0$ and $\sum_i(pref_i \cdot X_{i,inshore}) > 0$, or
 $\sum_i(pref_i \cdot X_{i,offshore}) = 0$ and $\sum_i(pref_i \cdot X_{i,inshore}) > 0$, or
 $\rho_{offshore_predhabitat} = 0$

$R_Y = +R_{Y_{lim}}$ if:

$Y_{offshore} = 0$ and $\rho_{offshore_predhabitat} > 0$ and $\sum_i(pref_i \cdot X_{i,offshore}) > 0$, or
 $\rho_{offshore_predhabitat} > 0$ and $\sum_i(pref_i \cdot X_{i,inshore}) = 0$ and $\sum_i(pref_i \cdot X_{i,offshore}) > 0$, or
 $\rho_{inshore_predhabitat} = 0$ and $\rho_{offshore_predhabitat} > 0$.

Otherwise,

$R_Y = 0$

In these exceptions we distinguish between birds, pinnipeds and cetaceans on the one hand, and maritime mammals on the other. The latter cannot access an offshore zone without an offshore ice platform, but can foraging inshore from a land-base if necessary. Birds, pinnipeds and cetaceans are not so constrained.

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