

## A POSSIBLE FRAMEWORK IN WHICH TO CONSIDER PLAUSIBLE MODELS OF THE ANTARCTIC MARINE ECOSYSTEM FOR EVALUATING KRILL MANAGEMENT PROCEDURES

A.J. Constable  
Australian Antarctic Division  
Department of Environment and Heritage  
Channel Highway, Kingston 7050  
Tasmania, Australia  
Email – andrew.constable@aad.gov.au

### Abstract

CCAMLR is developing a management procedure for the krill fishery, including the evaluation of candidate management procedures in a simulation framework, using plausible models of the Antarctic marine ecosystem. This paper develops a framework for erecting such models. It discusses the general model requirements and presents a conceptual framework for allowing flexibility in dealing with biological, spatial and temporal scales. The body of the paper is concerned with conceptualising an element of the ecosystem to account for the varying qualities of data and knowledge and for exploring the consequences of uncertainty.

### Résumé

La CCAMLR met en place actuellement une procédure de gestion de la pêche de krill qui comportera, entre autres, l'évaluation des procédures de gestion proposées dans une structure de simulation au moyen de modèles plausibles de l'écosystème marin de l'Antarctique. Ce document développe une structure pour l'élaboration de ces modèles. Il discute des exigences générales des modèles et présente une structure conceptuelle permettant une certaine flexibilité en ce qui concerne les échelles biologique, spatiale et temporelle. Le document traite de la conceptualisation d'un élément de l'écosystème pour expliquer les diverses qualités des données et des connaissances et pour explorer les conséquences de l'incertitude.

### Резюме

АНТКОМ разрабатывает процедуру управления промыслом криля, включая в систему моделирования оценку возможных процедур управления, на основе правдоподобных моделей морской экосистемы Антарктики. В данной статье разрабатывается основа для создания таких моделей. В ней рассматриваются общие требования к модели и представлена концептуальная структура, обеспечивающая гибкость при использовании биологических, пространственных и временных масштабов. В тексте статьи затрагивается проблема концептуализации элемента экосистемы с целью учета различного качества данных и знаний, а также изучения последствий неопределенности.

### Resumen

La CCRVMA está desarrollando un procedimiento de ordenación para la pesquería de krill, incluida la evaluación de los procedimientos propuestos mediante simulaciones que utilizan modelos verosímiles del ecosistema marino antártico. Este documento formula un marco para la construcción de tales modelos. Se discuten los requerimientos generales de los modelos y se presenta un marco conceptual para trabajar con flexibilidad dentro de las escalas biológicas, espaciales y temporales. El grueso del documento trata de conceptualizar un elemento del ecosistema para considerar la calidad variable de los datos y del conocimiento, y estudiar las consecuencias de la incertidumbre.

Keywords: ecosystem model, uncertainty, management strategy evaluation, management procedure, krill, CCAMLR

## Introduction

CCAMLR has been implementing the precautionary approach to managing the krill fishery in the Southern Ocean since 1991 (CCAMLR, 1991; Constable et al., 2000; Kock, 2000). A work plan has been adopted by CCAMLR to assist in the development of an ecosystem-based management procedure for krill (CCAMLR, 2001). This has entailed the Scientific Committee of CCAMLR defining small-scale management units (SC-CAMLR, 2002), agreed in 2002 (CCAMLR, 2002), to begin to review how the CCAMLR Ecosystem Monitoring Program could provide information to assist with management of the krill fishery (SC-CAMLR, 2003), and now to begin to evaluate proposals aiming to (i) manage the krill fishery at scales smaller than the ocean-wide sectors used to date and (ii) provide for conservation of the wider ecosystem.

The agreed work plan includes evaluating candidate management procedures. Plausible computer simulation models of the Antarctic marine ecosystem are to be developed for testing these candidates in a simulation environment. In this way, the robustness of a management procedure in achieving its objectives despite uncertainties in knowledge can be evaluated prior to implementation in the natural world (de la Mare, 1998; Cooke, 1999; Smith, 1993). This approach, often known as management strategy evaluation (MSE) (Smith et al., 1999), is now applied in many fisheries.

Constable (2002) described the important elements for developing a management procedure for the krill fishery. The main task at present is to develop plausible models of the Antarctic marine ecosystem in which management procedures can be evaluated. These management procedures will involve the monitoring and assessment of ecosystem effects of krill fishing and the potential implementation of spatial and temporal harvest controls. As a result, the simulations use ecosystem models that are able to simulate harvest controls at various spatial and temporal scales as well as being able to monitor and assess different components of the ecosystem at relevant scales.

This paper develops a framework for constructing plausible Antarctic marine ecosystem models to enable the evaluation of candidate management procedures for the krill fishery. Rather than developing a specific ecosystem model, the aim of the framework is to have available a variety of functions and representations of different components of the ecosystem. While not all management procedures require the same model detail to examine their robustness to uncertainties, it will be important to have the facility to examine the robustness of

management procedures to structural uncertainties as well as parameter uncertainties. The framework is intended to retain realism while not sacrificing computing time for unnecessary model complexity (Fulton et al., 2003).

## Model framework

Andrewartha and Birch (1984) provided a rationale for modelling the dynamics of populations, including how a population is impacted by its environment (other populations as well as the physical environment). This approach is used here to link different taxonomic/biological groups and for incorporating physical environmental models and functions.

A flexible framework is used to explicitly decide how best to represent a taxon in the model, which may differ conceptually between taxa. Some taxa will need to be represented in some detail in order to simulate field monitoring and the local-scale effects of fishing, while others might be simulated in a very general way in order to save simulation time while maintaining realism in the important ecosystem responses. As such, this approach allows for differences in the representation of the different taxa, which takes account of the very different levels of knowledge on different parts of the ecosystem, rather than trying to model all taxa in the same way. Similarly, some temporal processes may only need updating once per year while others may need to be updated daily. Some processes or components may also require a flexible representation to enable trials to determine how sensitive key model outputs are to assumptions about the functional form of model relationships.

The first stage in developing an ecosystem model for evaluating management strategies will be to decide how different components will be represented, if at all, and the detail required for them. Table 1 summarises the different classes of elements that need to be considered in an Antarctic marine ecosystem model.

## Conceptual elements for an ecosystem model

Although each class of element may vary in its complexity, a common rationale/structure can be applied to all elements. This will ensure that each element can effectively interact with other elements. Figure 4 illustrates the components and functions of a single element in a food-web model. Here, an element is defined as the lowest, indivisible quantity in the model. An element has the following **attributes**:

Table 1: Summary characteristics of the classes of elements to be included in an Antarctic marine ecosystem model.

Element class	Examples	General attributes	Example references
Physical environment	Sea-ice, light, nutrients, temperature	Ecological functions include: (i) production, with the attendant physical conditions in space, depth and time; (ii) stratification of the physical environment into natural units, including oceanic zones, depth zones, bathymetric features and ice; (iii) transport between areas and depths; (iv) sources of mortality, such as unfavourable atmospheric conditions.	Hofmann et al. (1998) Murphy et al. (1998) Constable et al. (2003) Murphy et al. (2004)
Particulate production	Microbial loop, phytoplankton, particulate matter	See Figures 1 and 2 and the appendix.	Lancelot et al. (1997) Appendix
Pelagic herbivores and invertebrate carnivores	Salps, copepods, other euphausiids, amphipods (e.g. <i>Themisto gaudichaudii</i> ) other invertebrate predators (e.g. chaetognaths and jellyfish)	Biomass production model.	
Target species	<i>Euphausia superba</i> , <i>Champtocephalus gunnari</i>	Age-structured models, taking account of on-shelf/off-shelf processes and coastal transport.	Nicol and Kawaguchi (2004) Williams (2004a)
Mesopelagic species with poorly understood dynamics	(i) epi- and mesopelagic fish, primarily small and large myctophids (ii) squid, primarily onychoteuthid, ommastrephid and 'medium nektonic' squid	Simple life stage biomass models, e.g. juveniles, adults.	Phillips (2004) Williams (2004b)
Central-place foraging marine mammals and birds	Penguins, land-based seals	Life-stage models taking into account an annual cycle of dependence on land; Figure 3.	Emmerson et al. (2004)
Non-central place foraging marine mammals and birds	Flying birds, whales, pack-ice seals	Life-stage models; Figure 3.	Gales and Southwell (2004)
Fisheries	<i>Euphausia superba</i> , <i>Champtocephalus gunnari</i>		Mangel (1988) Butterworth (1988) Constable (2000) Kawaguchi et al. (2004)

- (i) taxon – the group to which the element belongs, which could be an individual, population, species, guild, ecological group, sex or some other category;
- (ii) stage – the life stage of the element, whether it be age, life stage or some other subdivision of the taxon needed to allow ecological characteristics (below) to be distinguished from other stages;
- (iii) units – the type of units used to measure/monitor the quantity of the element, such as number, biomass, area or some other measure;
- (iv) location – if needed, the spatial compartment or cell in which the element resides;
- (v) depth – if needed, the depth stratum in which the element resides.

The **state** of an element is largely governed by its magnitude (abundance). The ‘stage’ of the element may be important, particularly if there are age/stage-specific interactions with other elements. Similarly, an age structure of the element may need to be known if the proportion of a life stage advancing to another life stage is not constant and governed by the present age structure.

The remainder of this section details the different components of an element, notably its **condition** and the **inputs** to and **outputs** from an element during a time step. The terms illustrated in Figure 4 are indicated in the text in bold type. As this is a conceptual discussion, it has been necessary to omit detailed discussion of some facets of some components that are not applicable to all potential model elements. An important interaction between elements in a food web is the predator–prey interaction, i.e. **consumption**. In this framework, the relationship between consumption and reproduction/recruitment is modelled explicitly such that consumption affects condition, which, in turn, affects reproduction. Obviously, consumption is also a primary cause of ‘output’ of prey elements. Due to its central role in model structure, consumption is considered first.

### Consumption

Models of consumption may be summarised as population-level functional feeding relationships (Holling, 1959), or some other derivative functions, or through more complex foraging models at the scale of individuals (e.g. Alonzo et al., 2003a, 2003b). While the former is less time-intensive in

simulations, the latter approach provides a greater opportunity for capturing the properties of a monitoring program (as proposed by Alonzo et al., 2003a, 2003b) as well as explicitly considering the interactions between species and the consequences of these interactions. The latter approach is also more able to include the effects of the physical environment on the foraging success of predators.

The manner in which consumption is translated into a change in populations will vary amongst species but will be dependent on the processes for resource allocation in individuals and on the relative timing of the foraging activity with respect to the reproductive cycle. For example, some fish species will invest heavily in egg production when food is in abundance while others will put their energy into body growth. On the other hand, marine mammals will create energy reserves for use at a later time, thereby creating a lag in the system between consumption and reproductive performance. In addition to these processes, the manner in which competition for food is manifested at the individual and population levels will need to be considered.

Predator functions for determining per capita consumption are well described in the literature as functional feeding relationships. A number of factors need to be considered within the development of these functional relationships, including (i) competition amongst predators, (ii) the potential for switching amongst prey/target species given different abundances and/or patchy distributions of prey, (iii) the degree to which a species is removed as a function of the removal of other species (incidental capture by predators), (iv) the influence of the environment on these relationships, such as the prevalence of sea-ice or terrain, and (v) the degree to which consumption is affected by aspects of foraging ecology, including fine-scale interactions and behaviours.

Another point to consider that will not be discussed at length here is the degree to which each element of the ecosystem might consume the waste or carcasses of animals from elsewhere in the system. For example, for some species, it will be necessary to include mortality from sources other than predation in their dynamics, as discussed below. This material might then be available to scavengers or lower trophic levels as particulate matter.

A general form of the functional relationship,  $f_{p,\bar{s}}$ , for a single prey species,  $\bar{S}$ , following Holling (1959) can be developed as

$$f_{p,\bar{s}} = \frac{B_{\bar{s}}^{(q+1)}}{B_{0.5\bar{s}}^{(q+1)} + (B_{\bar{s}} + GP)^{(q+1)}}$$

with

$$GP = \sum_{p'} \gamma_{p,p'} P_{p'} \quad ; p' \neq p \quad (1)$$

where  $\gamma_{p,p'} P_{p'}$  is the amount of prey made inaccessible to the predator,  $p$ , by other predators,  $p'$ , and  $\gamma_{p,p'}$  is the per unit (capita) amount of prey made inaccessible. This form includes a refinement by Gurney and Nisbet (1998) to include the abundance of prey,  $B_{0.5\bar{s}}$  when  $f_{p,\bar{s}} = 0.5$ . It also includes the addition of the competitive effects of predator abundance, as described by Beddington (1975). The parameter,  $q$ , provides for the difference between Holling Type II ( $q = 0$ ) and Holling Type III relationships ( $q > 0$ ). The consumption rate may remain constant by setting  $B_{0.5\bar{s}}$  to 0 and  $q$  to 0 (Holling Type I).

A Holling Type III function is one method for modelling a species' inaccessibility to prey at low abundance. Other approaches may be more detailed, such as in Fulton et al. (2004), where availability and other parameters are given in detail. The inclusion of competition in foraging and consumption models is a complex task and could be incorporated by means other than that presented here.

As this function ranges from 0 to 1, it can be viewed, in part, as the availability of the prey for consumption by the predator. Typically, the total per capita food ingested,  $I$ , by a predator of a single prey species could be determined as

$$I_{p,\bar{s}}(a, g, t) = i_{p,\bar{s}}(a, g, t) f_{p,\bar{s}} \hat{I}_{p,\bar{s}} \quad (2)$$

where  $\hat{I}_{p,\bar{s}}$  is the maximum biomass of the target prey species that could be ingested over the time interval of interest if it were the only prey being eaten,  $i_{p,\bar{s}}$  is the probability of an age class being ingested if encountered in a given geographic location and at a given time, and  $f_{p,\bar{s}}$  is the functional feeding relationship for a given predator. The probability of ingestion could be implemented as a function that incorporates feeding preferences, behaviours related to the presence of other food items and other factors associated with foraging theory. These are not addressed here.

Of course, many predators feed on multiple types of prey, with the total per capita consumption of each prey species potentially being influenced by the range of food species available (Harwood,

pers. comm.), their relative abundances, and the foraging tactics employed by the predator (Mangel and Switzer, 1998; Alonzo et al., 2003a, 2003b).

In order to take account of multiple prey species/units, one needs to consider (i) the potential amount of each prey available for consumption given the presence of other prey, as well as (ii) the potential variation (between prey) in the quantity of each prey required to satiate the predator. Thus, consumption of an individual prey species could be represented as a modified form of Equation 2, such that the maximum ingestible quantity of a given prey species could be

$$\tilde{I}_{p,\bar{s}}(a, g, t) = i_{p,\bar{s}}(a, g, t) f_{p,\bar{s}} B_{\bar{s}} \quad (3)$$

where  $B_{\bar{s}}$  is the abundance of the prey species, and the consumption of a prey species by a predator could then be

$$C_{\bar{s},p}(a, g, t) =$$

$$\begin{cases} \tilde{I}_{p,\bar{s}}(a, g, t) & ; N_p Sa_p > \sum_{s'} \tilde{I}_{p,s'}(a, g, t) \zeta_{p,s'} \\ N_p Sa_p \frac{\tilde{I}_{p,\bar{s}}(a, g, t)}{\sum_{s'} \tilde{I}_{p,s'}(a, g, t) \zeta_{p,s'}} & ; otherwise \end{cases} \quad (4)$$

where  $N_p$  is the number of predator units consuming prey,  $Sa_p$  is the maximum ingestible quantity per predator unit,  $\zeta_{p,s'}$  represents the conversion of a unit of the prey species to arbitrarily common units of ingestion across all prey, say volume or mass, and the summation for all  $s'$  represents the sum of the available ingestible quantities for all prey taxa of the predator.

This approach tries to represent the issues required to build consumption models within an ecosystem framework while maintaining the life history attributes at the level of the individual. These functions could be expanded, made into dynamic submodels or replaced completely. They are intended to provide the conceptual linkages between consumption (mortality of prey) and density-dependent recruitment models (population growth in predators) in order to ensure that critical processes are not necessarily lost in the process of formulating summary functions.

#### Element condition

The condition of the element refers to the condition of individuals, particularly as it relates to the usual life history traits in resource allocation, such as growth, fecundity and maintenance. In this

model framework, the conditions relative to these traits are ‘body size’, ‘reproductive condition’ and ‘health’ respectively.

The **body size** of individuals reflects their investment in growth. For some animals, such as mackerel icefish (*Champscephalus gunnari*), body size will be dependent on food availability (Everson et al., 1999). For others, body size may be considered as a fixed attribute with age, modelled as, say, a von Bertalanffy growth function. Choices will need to be made as to whether body mass is subject to variations in consumption, such as the reserve weight in the model of Fulton et al. (2004).

**Reproductive condition** is the per capita readiness to invest in reproduction. This will be based on a maturity function. In addition, it would need to be combined with the relative investment in reproduction given the per capita rate of food consumption relative to the maximum consumption rate. For many taxa, reproduction in a given year would be the result of the accumulated reproductive condition in that year. For some taxa, reproductive condition may need to be accumulated over more than one season. More typically, reproductive condition may need to be accumulated over many locations and/or time steps. The functions used to accumulate reproductive condition will have to be consistent with the functions that ultimately provide for reproduction and recruitment (see below). They may also need to include the effects of environmental factors.

The term ‘**health**’ is used in place of maintenance to indicate the propensity for an individual in that element to die as a result of insufficient resources or poor environmental conditions (e.g. pollution, freezing, disease).

Some consideration will also need to be given as to whether **waste** products, including faeces, urine and the like, need to be included as outputs of consumption. Models of nutrient dynamics may require the inclusion of waste.

Lastly, the metabolic costs of different processes, including, say, foraging activity, overwintering activity and migration may need to be included in some form depending on the degree to which the condition of the element will be impacted by these processes, and on the extent of any consequent effects on reproduction or mortality (e.g. Alonzo et al., 2003a, 2003b).

Consideration of how consumption translates to the three conditions is important for determining whether it translates readily to the growth of

a population/element, noting that growth in the biomass of individuals may be an immediate consequence of feeding but growth in the abundance of individuals through reproduction is a delayed response. It is conceivable that, following consumption, some elements may not contribute any further addition of biomass through growth but will contribute future biomass through reproduction. Thus, long-term changes in the biomass of a population/element is an accumulated function of consumption, perhaps over many years.

According to typical energy (resource) allocation models (see discussion in Constable, 2001), consumption will result in a per capita quantum of energy which could be divided among principle life-history functions – reproduction, growth and maintenance, noting that maintenance will include investment in health as well as in foraging and other factors. This per capita quantum of energy will be dependent on the proportion of food assimilated,  $A$ , combined with the value of that food,  $Fv$ , to the predator. In this context, the food value would be the conversion from food units to equivalent energetic units across all food items.

$$E_p = \frac{\sum_{s=1}^{nS} C_{s,p}(a, g, t) A_{s,p} Fv_{s,p}}{N_p} \quad (5)$$

In the absence of models which work specifically in units of energy, food value may become relative to a maximum food value of 1.0. Further, if the functions concerning the three elemental conditions will be governed by relative density-dependent responses, i.e. relative to a maximum energy intake, then Equation 5 could be modified to account for the relative quantity of prey consumed relative to that required for full satiation in Equation 4 by including  $\zeta_{p,s}$ , which relates the consumption of prey to a relative ingested quantity, and to ensure that the assimilation efficiency for each type of prey is relative to a maximum assimilation efficiency,  $A_{max,p}$ , recognising that it is unlikely that 100% of any prey species will be assimilated. Thus, the total energetic condition,  $Ec$ , arising from consumption could be

$$Ec_p = \frac{\sum_{s=1}^{nS} C_{s,p}(a, g, t) \zeta_{s,p} A_{s,p} Fv_{s,p}}{N_p} \frac{1}{A_{max,p}} \quad (6)$$

This equation will give results similar to density-dependent responses such as those found in

density-dependent functions relating population size, carrying capacity and reproduction (e.g. the predator model of Constable, 2001).

This estimate of energetic condition,  $Ec$ , can then be used to establish each of the three conditions: size, reproduction and health. Typically,  $Ec$  could be applied directly to the per capita reproductive output. It could be used to alter the mean body mass of fish at length (as for *C. gunnari*); the difference between skeletal growth (von Bertalanffy growth) and body reserves in fish modelled by Fulton et al. (2004). Lastly, health would naturally be an accumulated function of  $Ec$ , thereby assisting in specifying a function of mortality based on poor health.

These conditions interact in typical energy allocation models (see Constable, 2001 for description). Therefore, the tradeoffs in allocation between these three functions could be based on functions of  $Ec$  but those functions could include more detail than is indicated here.

Another aspect to consider is the degree to which reproduction will diminish the health of animals so that they become more susceptible to predation or other forms of mortality. Similarly, the effects of intraspecific interference competition, such as changes in investment in foraging resulting from an increase in the size of the population, have not been addressed here. It may be necessary to allow for this in the functions developed for each condition.

#### Element inputs

If not considering space, inputs to an element will include:

- (i) individuals advanced (moving) from another life stage (ontogenetic movement);
- (ii) production of new individuals.

Movement from another life stage is most easily envisaged for animals moving from one age class to the next, as in an age-structured model. Some populations may be more easily modelled as having individuals moving from egg to fledging to juvenile to adult. In these cases, all surviving individuals will advance to the next stage. Other populations might have mature individuals moving from breeding to non-breeding parts of the population, which may need to be modelled separately due to different sources of mortality. This movement may only involve a portion of the individuals from one or more other elements.

Production of new individuals will be a function of the reproductive condition of the mature individuals discussed above, how that condition translates to per capita number of offspring and, perhaps, some functions of the physical environment and the other elements present at the time of reproduction that might modify reproductive output. In its simplest form, the number of new individuals in the first recruitment stage, represented as age 0, is given by the sum of reproductive outputs for all elements in which mature individuals reside multiplied by the per capita reproductive rate,  $r_{el_T}$ , such that

$$N_T(0, g, t) = r_{el_T} \sum_e N_{T,e} R[m_{e,T}, f(Ec_{e,T}, RA_{e,T}), Env(e, T)] \quad (7)$$

where  $N_{T,e}$  is the number of individuals in an element and the per capita reproductive condition is a function,  $R$ , of (i) maturity of that element,  $m$ , (ii) the overall condition of that element,  $f(Ec, RA)$ , as a function of per capita condition,  $Ec$ , and the adjustment of the condition according to resource allocation amongst the key conditions,  $RA$ , and (iii) the effect of the environment on reproductive success,  $Env$ .

For the lowest species in the food web, reproduction may be governed by forcing functions from the environment rather than being directly related to consumption *per se*.

When spatially structured models are considered, individuals may move from other locations into the cell/compartment in which the element resides. Functions will be needed to provide for that movement, whether it is by proportional movement, some density-dependent function of the abundance of the animals present in a cell, a result of environmental factors, such as ocean movement, or some other signal, such as time of year.

Lastly, Figure 4 shows how provision is made for the introduction of new species into a model cell/compartment. While this may not be used often, the movement of vagrant taxa into an area is nevertheless one consideration that must be taken into account when modelling open systems and will be important if the element is an individual-based model.

#### Element outputs

The primary outputs of an element will be three potential forms of mortality (consumption by predators, other forms of natural death and exploitation). In addition, in spatial models, some

individuals may move out of a cell/compartiment as a result of environmental conditions, the abundance of animals in that cell or some other signal, such as time of year. As described above, ontogenetic movement out of an element to another life stage can also occur.

For lower trophic levels in the food web, consumption by model predators will be dictated by the functional relationships described above. For the predators at the top of their respective food chains in the model, mortality by predation (i.e. mortality due to predators outside the modelled chains) may be simply modelled as a rate function, as usually provided in simple population models in fisheries. These mortality rates may be modified by environmental or other factors.

Most natural mortality in marine ecosystems is considered to be predation. However, some taxa die from other causes. For example, squid die after their final reproduction and their body mass is largely consumed at the surface rather than where they were living at depth (Phillips, 2004). Other elements may suffer mortality from disease, cold or starvation, as in the case of penguin chicks waiting for their rations from parents (Emmerson et al., 2004). Thus, death from causes other than predation will need to be considered for some elements of the model, particularly if the dynamics of populations might be influenced by environmental parameters as well as food-web dynamics. Again, this highlights that the role of scavenging in the consumption of bodies may need to be addressed in some way in the overall model.

Lastly, exploitation of taxa will need to be modelled in some way, although it is possible to generate complex fishing behaviour with relatively simple models. In the long term, this may require detailed models of fleet dynamics. In the short term, exploitation could be modelled as a fishery mortality rate,  $F$ , as a function of fleet size and catch-per-unit-effort, or simply as a removal of biomass (catch). These formulations are well described in text books (e.g. Quinn and Deriso, 1999) but will need to include vulnerability functions (gear selectivity and availability of exploited populations to the fishery). Consideration will also need to be given to issues such as catchability,  $q$ , among other factors, such as ice, that might influence fishing operations.

#### Important model characteristics

Operating models are not intended to capture all of the dynamics of the physical and biological systems but should capture the important

properties of the system as they relate to the direct and indirect effects of fishing (Yodzis, 2000; Constable, 2001) and the field monitoring programs (ecology, physical environment, fishery) that can be employed (see Constable, 2002 for review). With respect to the latter, the simulation models need to be able to accommodate an observation model to replicate field programs that could assist with management or with refining hypotheses about the important dynamics and linkages in the ecosystem of interest.

Scale is a very important issue. Biological detail (biological scale – taxonomic grouping and population subdivision into life stages) may not need to be the same for each taxonomic group. Detail is only required in order to promulgate the important interactions between species which may only interact for part of their life history, as well as providing sufficient biological detail needed in a monitoring program.

The spatial scales of interactions will vary between taxa but may also vary between locations and/or regions (biogeographic differences). Spatial units may not need to be uniform geographic units but could be represented as compartments accommodating different spatial areas and extents, particularly if there is a need for some complex foraging models at smaller scales, such as those developed by Mangel and Switzer (1998) and Alonzo et al. (2003a, 2003b).

In a similar way, the temporal scales of interactions may vary between biota and locations. It may be possible to vary the duration of time steps so as to represent different lengths of time required to complete different processes, such as reproduction or other life-stage characteristics.

It is necessary to establish a model framework that provides a flexible structure which can incorporate complexity in life history and foraging behaviours when needed, and simplify the model structure if knowledge is inadequate. The degree to which cause and effect interactions are approximated or explicitly modelled will also be dependent on the types of measurements needing to be observed in the field monitoring program. Similarly, peripheral processes may only need sufficient detail in order to make the key model outcomes realistic (Yodzis, 2000).

Most simulations will not be dealing with closed systems. The manner in which the boundaries of the model system are simulated could impact on the function of that system. Figure 5 illustrates some of the processes that could be included in an

open system. The key features of boundary conditions include (i) the amount of material that may be exported, perhaps as detritus, (ii) the relationship between primary production and environmental 'drivers', and (iii) the rates of mortality of taxa at the end of the food chains. For Antarctic marine food webs, many species, such as whales and sea-birds, migrate each year to spend part of their life outside the area of interest. In these cases, the taxa may reproduce and/or change condition (feed or starve) or some individuals may die outside the model arena. These external processes may need to be approximated in some way in the model.

### Concluding remarks

The framework presented here is intended to assist the exploration and design of structures for ecosystem models for evaluating krill management procedures. It provides the opportunity to assess explicitly and decide (i) how to overcome the paucity of data in many areas, and (ii) how best to address uncertainties in model structure during the evaluation process.

Care is needed in developing conceptual models for the different element types so that the spatially structured models make sense. It might be best, in the first instance, to develop a non-spatial ecosystem model that develops all the features of the taxa of interest to provide a sensible foundation for the relationships between the elements. The next step would be to introduce the spatial features, but in an abstract series of compartments. The geographically oriented model, perhaps with depth strata, would then be the last step. This approach would help provide safeguards against the masking of inappropriate model behaviours as a result of too much complexity too soon, particularly in relation to the potential confounding of space-time interactions. It should be noted that some steps in the process, such as in the non-spatial models, may yield apparently unrealistic behaviour. Rather than dwell too much on these behaviours during the development of the overall model, it is important to distinguish poor model construction, particularly inconsistencies between elements, from plausible system behaviours.

This developmental process need not delay the evaluation of management procedures. For example, it may be possible to use non-spatial models to evaluate the characteristics of taxa that could be monitored to detect the effects of fishing under some plausible environmental scenarios. Spatial structure can then be used to choose the

spatial arrangements of the monitoring activity as well as for assessing the utility of some local-scale measures.

A great challenge in this exercise is to describe the foraging relationships among species or guilds. There are very few studies that provide a suitable foundation for these descriptions. However, an important component of the evaluation of candidate management procedures will be to explore the sensitivity of model outcomes to these very important structural uncertainties.

### Acknowledgements

A longer version of this paper was submitted to the Workshop on Plausible Models of the Antarctic Marine Ecosystem for Evaluating Krill Management Procedures (WG-EMM-04/24), held by the CCAMLR Working Group on Ecosystem Monitoring and Management in 2004. The application of principles and the development of conceptual models for the primary elements discussed in this paper are summarised in the workshop report submitted to WG-EMM as paper WG-EMM-04/73.

A number of people have contributed to the development of this work. In general, the author extends his thanks for discussions and contributions to this work to Barry Baker, Ian Ball, Judy Clarke, Campbell Davies, Louise Emerson, Di Erceg, Nick Gales, So Kawaguchi, Steve Nicol, Katrina Phillips, Sarah Robinson, Graham Robertson, Colin Southwell and Dick Williams. Many thanks to Katrina Phillips for the seabird figure, Graham Hosie for information on zooplankton, Simon Wright, Andrew Davidson and Harvey Marchant for information on plankton/bacteria and many others in the Australian Antarctic Division for discussions along the way. The author is indebted to Campbell Davies, Steve Nicol, Beth Fulton and an anonymous reviewer for thoroughly commenting on the manuscript and to Ian Ball, Simon Wright, So Kawaguchi and Di Erceg for suggested reforms to different parts of the manuscript.

### References

- Alonzo, S.H., P.V. Switzer and M. Mangel. 2003a. Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology*, 84 (6): 1598–1607.
- Alonzo, S.H., P.V. Switzer and M. Mangel. 2003b. An ecosystem-based approach to management:

- using individual behaviour to predict the indirect effects Antarctic krill fisheries on penguin foraging. *J. Appl. Ecol.*, 40 (4): 692–702.
- Andrewartha, H.G. and L.C. Birch. 1984. *The Ecological Web: More on the Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Beddington, J.R. 1975. Mutual interferences between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.*, 44: 331–340.
- Butterworth, D.S. 1988. A simulation study of krill fishing by an individual Japanese trawler. In: *Selected Scientific Papers, 1988 (SC-CAMLR-SSP/5)*, Part I. CCAMLR, Hobart, Australia: 1–108.
- CCAMLR. 1991. *Report of the Tenth Meeting of the Commission (CCAMLR-X)*. CCAMLR, Hobart, Australia: 101 pp.
- CCAMLR. 2001. *Report of the Twentieth Meeting of the Commission (CCAMLR-XX)*. CCAMLR, Hobart, Australia: 186 pp.
- CCAMLR. 2002. *Report of the Twenty-first Meeting of the Commission (CCAMLR-XXI)*. CCAMLR, Hobart, Australia: 205 pp.
- Constable, A.J. 2000. An example of an examination of trends in krill catches in Area 48 using non-metric multidimensional scaling (nMDS). In: *Report of the Nineteenth Meeting of the Scientific Committee (SC-CAMLR-XIX)*, Annex 4, Appendix D. CCAMLR, Hobart, Australia: 203–205.
- Constable, A.J. 2001. The ecosystem approach to managing fisheries: achieving conservation objectives for predators of fished species. *CCAMLR Science*, 8: 37–64.
- Constable, A.J. 2002. CCAMLR Ecosystem monitoring and management: future work. *CCAMLR Science*, 9: 233–253.
- Constable, A.J., W.K. de la Mare, D.J. Agnew, I. Everson and D. Miller. 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.*, 57 (3): 778–791.
- Constable, A.J., S. Nicol and P.G. Strutton. 2003. Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. *J. Geophys. Res. – Oceans*, 108 (C4), 8079: 21 pp.
- Cooke, J.G. 1999. Improvement of fishery-management advice through simulation testing of harvest algorithms. *ICES J. Mar. Sci.*, 56: 797–810.
- de la Mare, W.K. 1998. Tidier fisheries management requires a new MOP (management-oriented paradigm). *Rev. Fish Biol. Fish.*, 8: 349–356.
- Emmerson, L.M., J. Clarke, M. Tierney and L. Irvine. 2004. Developing conceptual models of elements of the Antarctic marine ecosystem: Adélie penguins. Document WG-EMM-04/53. CCAMLR, Hobart, Australia.
- Everson, I., G. Parkes, K.-H. Kock and I.L. Boyd. 1999. Variation in standing stock of the mackerel icefish *Champsocephalus gunnari* at South Georgia. *J. Appl. Ecol.*, 36 (4): 591–603.
- Fulton, E.A., A.D.M. Smith and C.R. Johnson. 2003. Effect of complexity on marine ecosystem models. *Mar. Ecol. Prog. Ser.*, 253: 1–16.
- Fulton, E.A., J.S. Parslow, A.D.M. Smith and C.R. Johnson. 2004. Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. *Ecol. Model.*, 173: 371–406.
- Gales, N. and C. Southwell. 2004. Developing conceptual models of elements of the Antarctic marine ecosystem: marine mammals. Document WG-EMM-04/65. CCAMLR, Hobart, Australia.
- Gurney, W.S.C. and R.M. Nisbet. 1998. *Ecological Dynamics*. Oxford University Press, New York.
- Hofmann, E.E., J.M. Klinck, R.A. Locarnini, B. Fach and E. Murphy. 1998. Krill transport in the Scotia Sea and environs. *Ant. Sci.*, 10 (4): 406–415.
- Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entomol.*, 91: 293–320.
- Kawaguchi, S., S. Nicol, K. Taki and M. Naganobu. 2004. A conceptual model of the krill fishery. Document WG-EMM-04/51. CCAMLR, Hobart, Australia.
- Kock, K.-H. (Ed.). 2000. *Understanding CCAMLR's Approach to Management*. CCAMLR: [www.ccamlr.org/pu/e/e\\_pubs/am/toc.htm](http://www.ccamlr.org/pu/e/e_pubs/am/toc.htm).

- Lancelot, C., S. Becquevort, P. Menon, S. Mathot and J.-M. Dandois. 1997. Ecological modelling of the planktonic microbial food-web. In: Caschetto, S. (Ed.). *Belgian Research Programme on the Antarctic, Scientific Results of Phase III (1992–1996)*, 1: 78 pp.
- Mangel, M. 1988. Analysis and modelling of the Soviet Southern Ocean krill fleet. In: *Selected Scientific Papers, 1988 (SC-CAMLR-SSP/5)*, Part I. CCAMLR, Hobart, Australia: 127–235.
- Mangel, M. and P.V. Switzer. 1998. A model at the level of the foraging trip for the indirect effects of krill (*Euphausia superba*) fisheries on krill predators. *Ecol. Model.*, 105 (2–3): 235–256.
- Murphy, E.J., J.L. Watkins, K. Reid, P.N. Trathan, I. Everson, J.P. Croxall, J. Priddle, M.A. Brandon, A.S. Brierley and E. Hofmann. 1998. Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. *Fish. Oceanogr.*, 7: 381–390.
- Murphy, E.J., J.L. Watkins, M.P. Meredith, P. Ward, P.N. Trathan and S.E. Thorpe. 2004. Southern Antarctic Circumpolar Current Front to the northeast of South Georgia: horizontal advection of krill and its role in the ecosystem. *J. Geophys. Res. – Oceans*, 109, C01029.
- Nicol, S. and S. Kawaguchi. 2004. Developing conceptual models of elements of the Antarctic marine ecosystem: Antarctic krill (*Euphausia superba*). Document WG-EMM-04/50. CCAMLR, Hobart, Australia.
- Phillips, K. 2004. Developing conceptual models of the Antarctic marine ecosystem: squid. Document WG-EMM-04/26. CCAMLR, Hobart, Australia.
- Quinn, T.J. II and R.B. Deriso. 1999. *Quantitative Fish Dynamics*. Oxford University Press, Oxford: 542 pp.
- SC-CAMLR. 2002. Report of the Working Group on Ecosystem Monitoring and Management. In: *Report of the Twenty-first Meeting of the Scientific Committee (SC-CAMLR-XXI)*, Annex 4. CCAMLR, Hobart, Australia: 121–308.
- SC-CAMLR. 2003. Report of the Working Group on Ecosystem Monitoring and Management. In: *Report of the Twenty-second Meeting of the Scientific Committee (SC-CAMLR-XXII)*, Annex 4. CCAMLR, Hobart, Australia: 137–286.
- Smith, A.D.M. 1993. Risks of over- and under-fishing new resources. In: Smith, S.J., J.J. Hunt and D. Rivard (Eds). *Risk Evaluation and Biological Reference Points for Fisheries Management*. National Research Council for Canada, Ottawa: 261–267.
- Smith, A.D.M., K.J. Sainsbury and R.A. Stevens. 1999. Implementing effective fisheries-management systems – management strategy evaluation and the Australian partnership approach. *ICES J. Mar. Sci.*, 56: 967–979.
- Williams, R. 2004a. Conceptual model of icefish (*Chamsocephalus gunnari*). Document WG-EMM-04/59. CCAMLR, Hobart, Australia.
- Williams, R. 2004b. Conceptual model of Antarctic epi- and mesopelagic fish. Document WG-EMM-04/58. CCAMLR, Hobart, Australia.
- Yodzis, P. 2000. Diffuse effects in food webs. *Ecology*, 81 (1): 261–266.

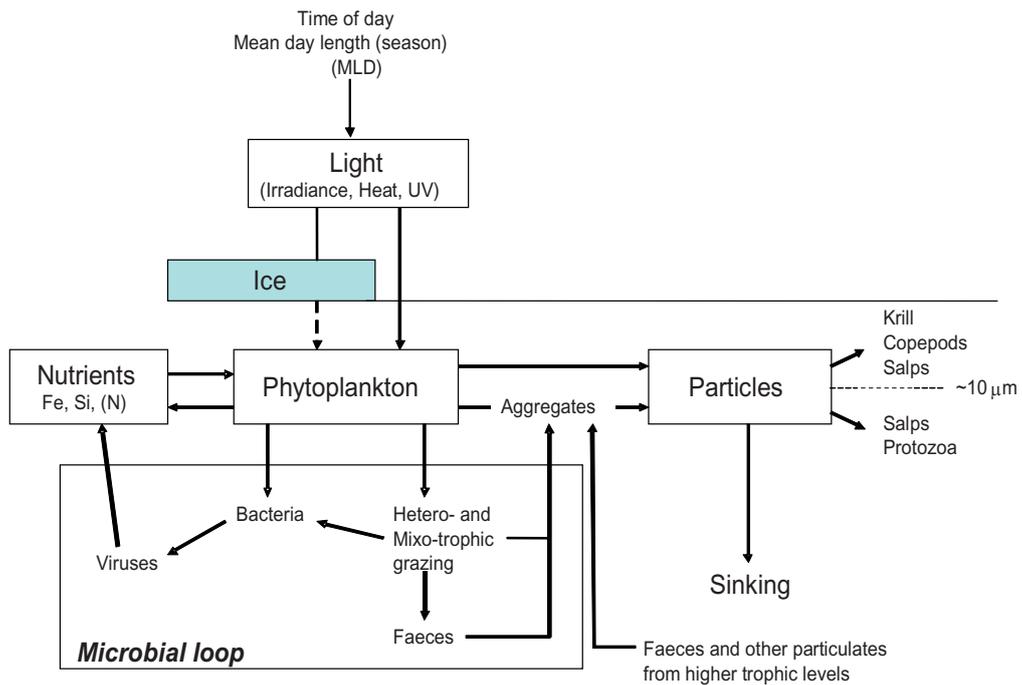


Figure 1: Conceptual model of the important linkages influencing production of particulates used as food by zooplankton. MLD = mixed layer depth. Note that dissolved organic matter (DOM) is a waste product from all organisms and DOM and particulate organic matter is an important source of carbon in winter (A. Davidson, S. Wright, H. Marchant and G. Hosie, Australian Antarctic Division, unpublished).

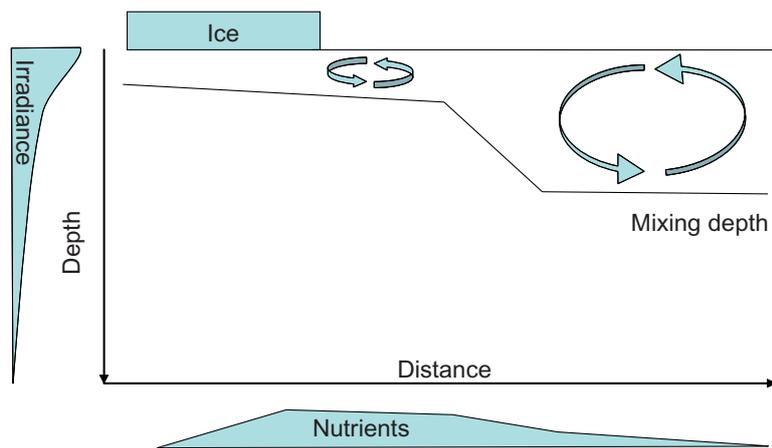


Figure 2: Diagrammatic representation of how the spatial characteristics of the environment influence primary production in the ice-edge region. Arrows indicate mixing. The width of the shapes surrounding nutrients and irradiance indicates the quantities available to phytoplankton given their proximity to ice and the depth of the mixing layer (S. Wright, Australian Antarctic Division, unpublished).

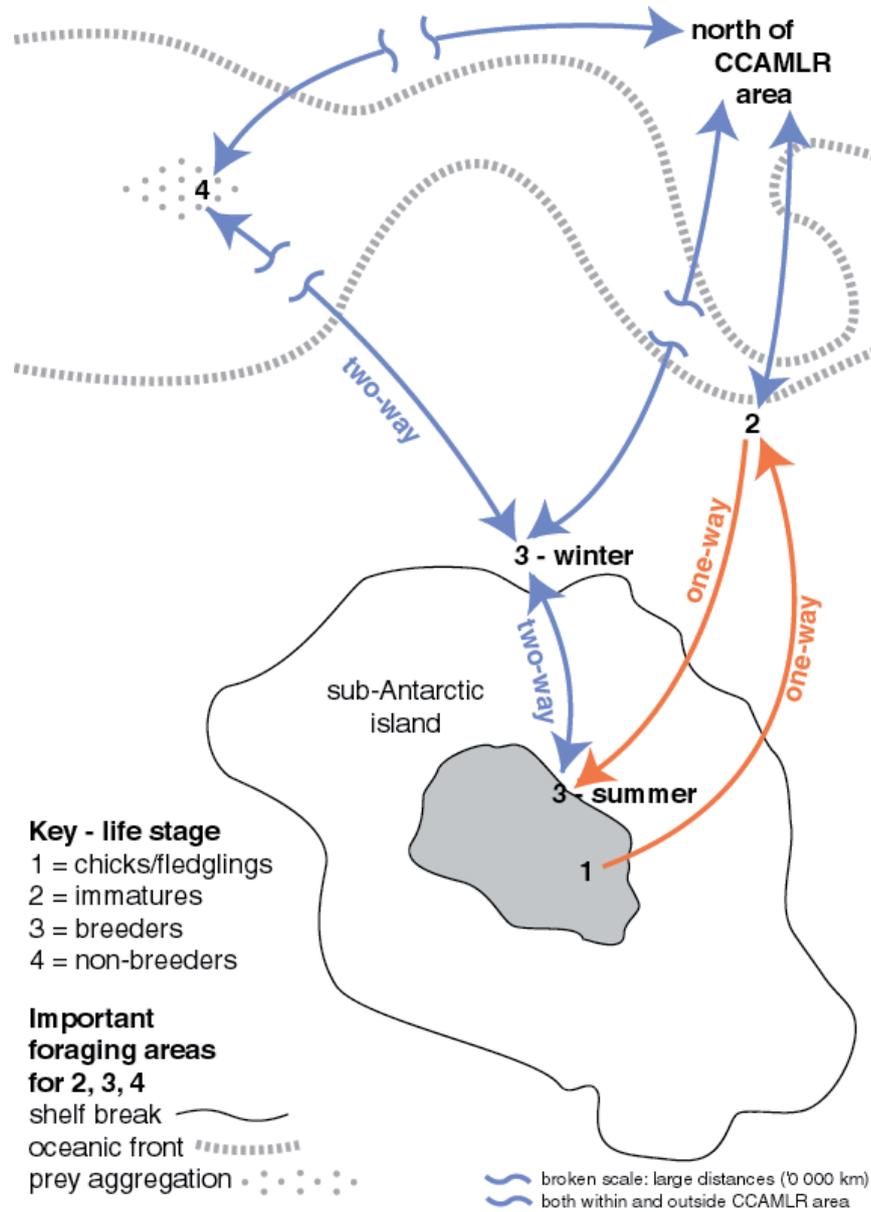


Figure 3: Schematic diagram of the spatial movement of sub-Antarctic oceanic flying birds throughout their life history. 1: chicks/fledglings; 2: immature birds; 3: mature breeding birds; 4: mature non-breeding birds. Chicks/fledglings make an irreversible (i.e. one-way) transition towards the immature life stage, while immature birds make a one-way transition towards the mature breeding/non-breeding life stage. Breeding birds may be located either at sea (foraging) or on a sub-Antarctic island (incubating/caring for a chick). Mature birds may intermittently exchange between the breeding and non-breeding life stages. Life stages 2, 3 and 4 are depicted in important foraging areas, although they are not restricted to these areas and may be dispersed anywhere within several thousand kilometres of the island including areas outside (north of) the CCAMLR Convention Area.

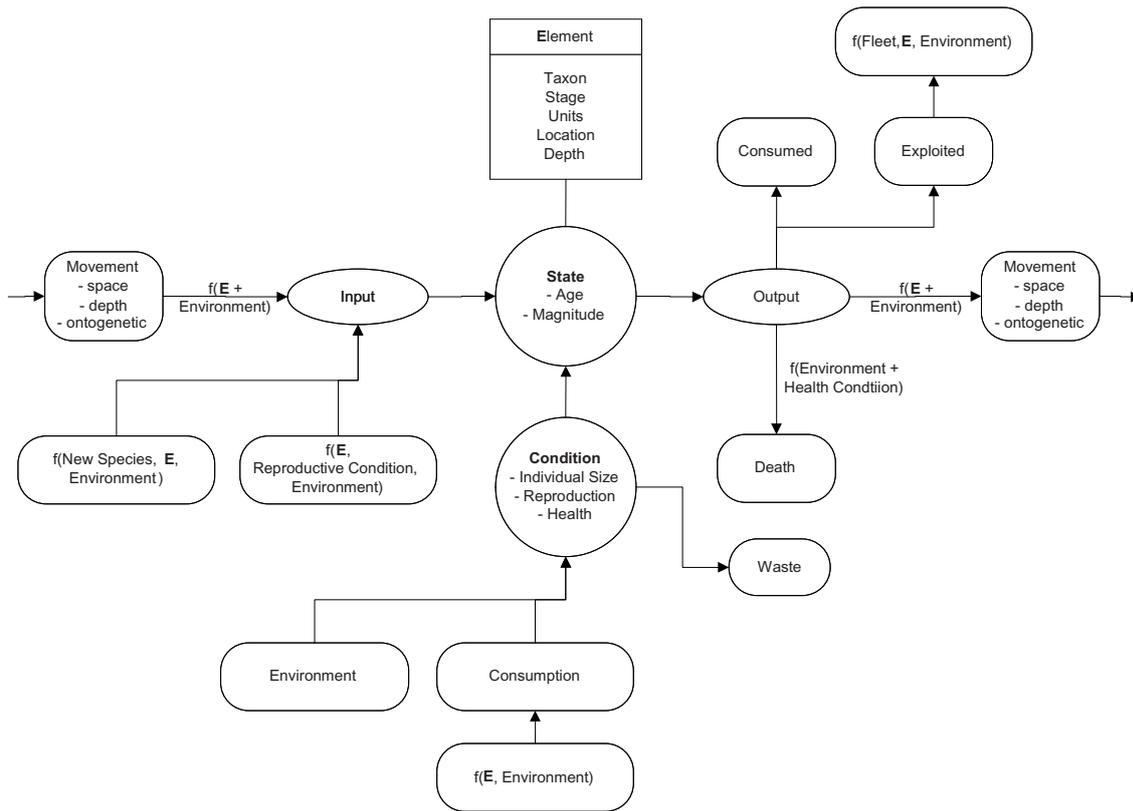


Figure 4: Conceptual element for a food-web model. In this case, an element has a state and a condition. The state alters from one time step to another, based on inputs and outputs during the time step. The processes that contribute to inputs, outputs and conditions are described in the text. *E* refers to the full set of elements in the model and their respective states.

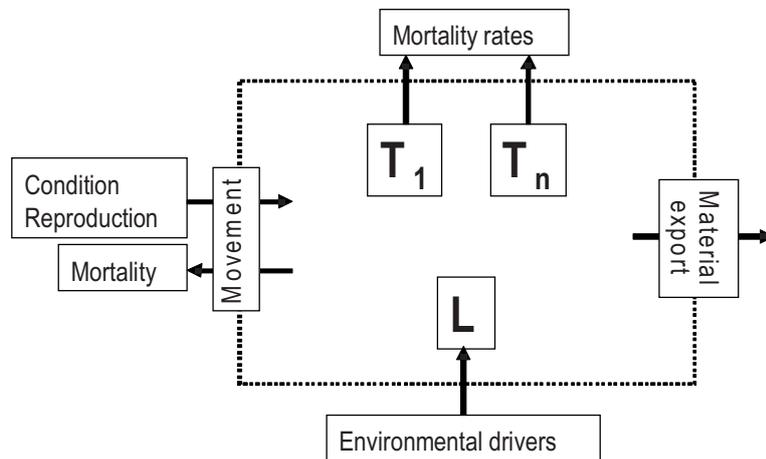


Figure 5: Schematic showing the processes at the periphery of the food web that may need to be captured in an ‘open’ ecosystem model – the model boundary is represented by the dotted rectangle, which encompasses many food-web interactions.  $T_1$  and  $T_n$  represent species at the end of their respective food chains represented in the model; it should be noted that their mortality will be modelled as rates rather than driven by interactions with other taxa or processes.  $L$  represents a lower trophic level, perhaps primary production, whose level of production is driven by environmental drivers. The environmental drivers (e.g. modelled as forcing functions) might also affect animals at higher trophic levels in the food web. The open nature of the system provides for movement of taxa into and out of the system (indicated on the left side). External dynamic processes, such as reproduction, feeding (change in condition) and mortality, may need to be modelled in some approximate way. Similarly, detrital material may be exported out of the system (indicated on the right side). Its return may be governed by environmental drivers.

## Liste des tableaux

- Tableau 1: Résumé des caractéristiques des classes d'éléments à inclure dans un modèle de l'écosystème marin de l'Antarctique.

## Liste des figures

- Figure 1: Modèle conceptuel des liens importants influençant la production de particules servant d'aliments au zooplancton. MLD = profondeurs de la couche mixte (ou : mixed layer depth, en anglais). Il convient de noter que les matières organiques dissoutes (DOM pour dissolved organic matter) sont des produits résiduels de tous les organismes et qu'avec les matières organiques particulaires, elles représentent une source importante de carbone en hiver (A. Davidson, S. Wright, H. Marchant et G. Hosie, Australian Antarctic Division, non publié).
- Figure 2: Représentation sous forme de diagramme de l'influence des caractéristiques spatiales de l'environnement sur la production primaire dans la région de la bordure de glace. Les flèches indiquent les mélanges. La largeur des formes entourant les nutriments et l'irradiation indique les quantités disponibles pour le phytoplancton vu leur proximité par rapport à la glace et la profondeur de la couche mixte (S. Wright, Australian Antarctic Division, non publié).
- Figure 3: Diagramme schématique du mouvement spatial des oiseaux volants océaniques tout au long de leur cycle vital. 1 : poussins/jeunes à la première mue; 2 : oiseaux immatures; 3 : oiseaux matures reproducteurs; 4 : oiseaux matures non reproducteurs. Les poussins/jeunes à la première mue vont connaître une transition irréversible (à savoir, à sens unique) vers le stade vital mature alors que les oiseaux immatures vont connaître une transition à sens unique vers le stade mature, avec ou sans reproduction. Les oiseaux reproducteurs peuvent se trouver soit en mer (pour s'alimenter) soit sur une île subantarctique (pour couvrir ou garder un poussin). Les oiseaux matures passent parfois du stade de reproduction au stade de non-reproduction, et vice versa. Les stades de vie 2, 3 et 4 sont décrits dans les secteurs d'alimentation importants, bien qu'ils ne soient pas limités à ces secteurs et qu'ils puissent être dispersés ailleurs, à plusieurs milliers de kilomètres de l'île, y compris dans des secteurs situés en dehors (au nord) de la zone de la Convention de la CCAMLR.
- Figure 4: Élément conceptuel d'un modèle de réseau trophique. Dans ce cas, un élément a un état et une condition. L'état varie d'une étape temporelle à l'autre, selon les entrées et les sorties, tout au long de l'étape temporelle. Les processus qui contribuent aux entrées et aux sorties, ainsi qu'à la condition sont décrits dans le texte. *E* fait référence au jeu complet d'éléments du modèle et à leurs états respectifs.
- Figure 5: Schéma illustrant les processus à la périphérie du réseau trophique qui pourraient devoir être représentés dans un modèle «ouvert» de l'écosystème – la limite du modèle est représentée par un rectangle en pointillés qui regroupe de nombreuses interactions dans les réseaux trophiques.  $T_1$  et  $T_n$  représentent les espèces à l'extrémité de leur chaîne alimentaire respective représentée dans le modèle; il convient de noter que leur mortalité sera modélisée en tant que taux plutôt que d'être gouvernée par des interactions avec d'autres taxons ou d'autres processus. *L* représente un niveau trophique inférieur, peut-être la production primaire, dont le niveau de production dépend de facteurs environnementaux. Ces facteurs (modélisés, par exemple, comme des fonctions de forçage) peuvent aussi affecter les individus de niveaux supérieurs du réseau trophique. La nature ouverte du système permet de tenir compte des déplacements des taxons hors du système (comme cela est indiqué sur le côté gauche). Les processus dynamiques externes, tels que la reproduction, l'alimentation (changement de condition) et la mortalité, peuvent devoir être modélisés de manière approximative. De même, les matériaux détritiques peuvent être exportés hors du système (comme cela est indiqué sur le côté droit). Leur retour peut dépendre de facteurs environnementaux.

## Список таблиц

- Табл. 1: Краткие характеристики классов элементов для включения в модель морской экосистемы Антарктики.

## Список рисунков

- Рис. 1: Концептуальная модель важных связей, влияющих на производство частиц, служащих кормом для зоопланктона. MLD = глубина слоя перемешивания. Заметьте, что растворенное органическое

вещество (DOM) является продуктом выделения всех организмов и что зимой DOM и частицы органического вещества представляют собой важный источник углерода (A. Davidson, S. Wright, H. Marchant y G. Hosie, Австралийский Антарктический отдел, неопубликовано).

Рис. 2: Схематическое изображение того, как пространственные характеристики окружающей среды влияют на первичную продукцию в районе кромки льда. Стрелками показано перемешивание. Ширина контуров вокруг питательных веществ и освещенности показывает их количество, доступное для фитопланктона, с учетом расстояния до льда и глубины слоя перемешивания (S. Wright, Австралийский Антарктический отдел, неопубликовано).

Рис. 3: Схематическая диаграмма пространственного перемещения суб-антарктических океанских летающих птиц в течение жизненного цикла. 1: птенцы/оперившиеся птенцы; 2: неполовозрелые птицы; 3: половозрелые размножающиеся птицы; 4: половозрелые неразмножающиеся птицы. Птенцы/оперившиеся птенцы совершают необратимый (т.е. односторонний) переход к неполовозрелой стадии жизни, а неполовозрелые птицы совершают односторонний переход к половозрелой стадии размножения/неразмножения. Размножающиеся птицы могут находиться или в море (в поисках корма), или на суб-антарктическом острове (высиживание/вскармливание птенца). Стадии размножения и неразмножения у половозрелых птиц могут чередоваться. Стадии жизни 2, 3 и 4 представлены в важных районах кормодобывания, хотя они не ограничены этими районами и могут находиться где угодно в радиусе нескольких тысяч километров от острова, включая районы вне (к северу от) зоны действия Конвенции АНТКОМ.

Рис. 4: Концептуальный элемент модели трофической сети. В данном случае элемент имеет состояние и условие. Состояние меняется от одного временного шага к другому, в зависимости от входных данных и результатов в течение временного шага. Процессы, влияющие на входные данные, результаты и условия, описываются в тексте. **E** относится к полному набору элементов модели и к соответствующим им состояниям.

Рис. 5: Схематический показ процессов на периферии трофической сети, которые, возможно, понадобится включить в «открытую» экосистемную модель (граница модели обозначена пунктирным прямоугольником), охватывающей множество взаимодействий трофической сети.  $T_1$  и  $T_n$  обозначают виды в конце соответствующих трофических цепей, представленных в модели; следует отметить, что их смертность будет моделироваться в виде коэффициентов, а не определяться взаимодействиями с другими таксонами или процессами. **L** представляет более низкий трофический уровень (возможно, первичную продукцию), где уровень продуктивности определяется движущими силами окружающей среды. Эти движущие силы (напр., моделируемые в виде вынуждающих функций) могут также воздействовать на животных на более высоких уровнях трофической сети. Открытый характер системы обеспечивает передвижение таксонов внутрь и за пределы системы (показано слева). Внешние динамические процессы, такие как воспроизводство, кормление (изменение условий) и смертность, вероятно, следует моделировать путем аппроксимации. Аналогично этому, детритный материал может выноситься из системы (показано справа). Его возвращение может определяться движущими силами окружающей среды.

#### Lista de las tablas

Tabla 1: Resumen de las características del tipo de elementos a ser incluidos en un modelo del ecosistema antártico.

#### Lista de las figuras

Figura 1: Modelo conceptual de los factores importantes de la producción de materia particulada que constituye el alimento del zooplankton. MLD = profundidad de la capa de mezcla. Nótese que la materia orgánica disuelta (DOM) es un producto de desecho de todos los organismos, y que tanto DOM como las partículas de materia orgánica son una fuente importante de carbono en invierno (A. Davidson, S. Wright, H. Marchant y G. Hosie, Australian Antarctic Division, inédito).

Figura 2: Diagrama del efecto de las características espaciales del medioambiente en la producción primaria en la zona del borde de hielo. Las flechas señalan que hay mezcla. El ancho de las figuras que abarcan a los nutrientes y la irradiación indica la cantidad disponible para el fitoplancton dadas su proximidad al hielo y la profundidad de la capa de mezcla (S. Wright, Australian Antarctic Division, inédito).

- Figura 3: Diagrama esquemático del desplazamiento aéreo de las aves marinas subantárticas durante su ciclo de vida. 1: polluelos/volantones; 2: aves inmaduras; 3: aves adultas reproductoras; 4: aves adultas no reproductoras. La transición del estadio de polluelo/volantón hasta el estadio de ave inmadura es irreversible (es decir, el vínculo es unidireccional), y también lo es la transición de ave inmadura al estadio de ave adulta reproductora o no reproductora. Las aves reproductoras pueden encontrarse en alta mar (buscando alimento) o en una isla subantártica (empollando/criando un polluelo). Las aves adultas pueden cambiar intermitentemente del estadio de ave reproductora al de ave no reproductora. Los estadios 2, 3 y 4 del ciclo vital se representan en áreas de alimentación importantes, si bien las aves no están circunscritas a dichas áreas sino que pueden encontrarse dispersas en un radio de varios miles de kilómetros de la isla, incluidas regiones fuera (hacia el norte) del Área de la Convención de la CCRVMA.
- Figura 4: Elemento conceptual de un modelo de la trama alimentaria. En este caso, un elemento tiene un estado y una condición. El estado cambia de un lapso de tiempo a otro, de conformidad con los parámetros de entrada y los resultados para ese lapso. Los procesos que constituyen parámetros de entrada, resultados y condiciones se describen en el texto. *E* se refiere al conjunto completo de elementos del modelo y sus respectivos estados.
- Figura 5: Esquema que muestra los procesos periféricos de la trama alimentaria que tendrían que ser representados en un modelo "abierto" de ecosistema – la línea punteada del rectángulo representa el límite del modelo, que contiene muchas interacciones de la trama alimentaria.  $T_1$  y  $T_n$  son especies en el extremo de sus respectivas tramas alimentarias representadas en el modelo; nótese que su mortalidad será representada por tasas y no por interacciones con otros taxones y procesos. *L* representa un nivel trófico más bajo, quizás la producción primaria, cuyo nivel está determinado por las condiciones ambientales. Los factores ambientales (representados como factores de forzado) también pueden afectar a los animales en un nivel trófico más alto de la trama alimentaria. La naturaleza abierta del sistema permite la entrada y salida de taxones (movimientos indicados en el lado izquierdo). Es posible que se deba representar de manera análoga los procesos dinámicos externos, como la reproducción, la alimentación (cambios de la condición) y la mortalidad. Asimismo, el detritus puede ser exportado fuera del sistema (como se indica en el lado derecho). Su retorno podría depender de factores ambientales.

**MODELLING PARTICULATE PRODUCTION (PHYTOPLANKTON AND MICROBIAL LOOP)  
TO LINK FOOD WEBS WITH THE PHYSICAL ENVIRONMENT**

A set of equations relating particulate production (primary production plus the microbial loop) to the physical environment of the Southern Ocean could be derived from Figures 3 and 4 and the following general sequence of functions:

$$\begin{aligned}
 P_g &= f(I, Nu, UV, gst_g) \\
 I &= f(\text{Daylength}, \text{Latitude}, \text{Ice}, \text{Depth}, d_g) \\
 UV &= f(\text{Daylength}, \text{Latitude}, \text{Ice}, \text{Depth}, d_g) \\
 Nu_i &= f(\text{IceP}, \text{IslP}, \text{Upwelling}, \text{Mixing}) \\
 \text{Mixing} &= f(\text{Stratification}, \text{Storms}) \\
 \text{Stratification} &= f(\text{Ice}, \text{Icemelt}, \text{Temp}, \text{Density}, I)
 \end{aligned} \tag{8}$$

where  $P$  = primary production (subscript  $g$  represents the group of taxa being modelled as a single component),  $I$  = irradiance,  $Nu$  = nutrients (subscript indicates individual nutrients),  $UV$  = ultraviolet radiation,  $gst$  = taxon group specific thresholds,  $d$  = phytoplankton density leading to density-dependent responses,  $\text{IceP}$  = proximity to ice, with higher nutrient levels being expected close to and under ice than further away, and  $\text{IslP}$  = proximity to islands with higher nutrient levels, particularly iron, nearer to islands.

Production,  $P$ , for a model phytoplankton group,  $g$ , will be dependent on the existing biomass of phytoplankton,  $B$ , and the maximum potential for production in an area,  $Pk_g(Nu)$ , given the concentration of nutrients, such that

$$P_g(B, Nu) = Pk_g(Nu) \left(1 - e^{-G_g(Nu)B}\right) \tag{9}$$

$G_g(Nu)$  is the rate of change of production with a changing biomass given the production to biomass ratio,  $Pb$ , where

$$G_g(Nu) = \frac{Pb_g}{Pk_g(Nu)} \tag{10}$$

and

$$Pk_g(Nu) = cb_g(Nu)Nu \tag{11}$$

with  $cb_g(Nu)$  being the conversion to biomass from a given nutrient concentration at the irradiance that gives maximum productivity. This is modelled according to the Michaelis-Menton kinetics law for production, which is the same as a Holling Type III functional relationship. This conversion is determined as

$$cb_b(Nu) = cbMax_g pP_g(t) \frac{Nu^{Nq_g}}{NuHalf_g^{Nq_g} + Nu^{Nq_g}} \tag{12}$$

where  $cbMax_g$  is the maximum productivity when nutrients are in excess abundance,  $NuHalf_g$  is the nutrient concentration when  $cb$  is half the maximum, and  $Nq_g$  is the same as  $q$  in the Holling Type III function.  $pP_g$  is the proportion of maximum productivity depending on the light regime which is influenced by:

- (i)  $pIMax_g$ , the net productivity, as a proportion of maximum net productivity, for the given irradiance over the time step;
- (ii)  $D_g$ , the average net productivity of the biomass in the water over a time step, i.e. the net productivity integrated over the depth interval, as a proportion of net productivity if the biomass was all at the surface (assuming a uniform distribution of the biomass down to a critical depth, taking into account the effects of mixing/movement rates to other depths in each time step);
- (iii)  $C_g$ , the proportion of surface irradiance reaching the water through ice, which will be, among other factors, a function of ice thickness and density of pack-ice);
- (iv)  $C'_g$ , the proportion of net productivity remaining after the effects of shading by the resident biomass.

Thus,

$$pP_g = pIMax_g D_g C_g C'_g(B) \quad (13)$$

A function will then need to be developed to determine how much of the production will be available in the two different size classes (Figure 1), recognising that the smaller particulates will form as a result of consumption of the production by heterotrophs and mixotrophs.