Individual-based modelling of seabird and marine mammal populations

JAAP VAN DER MEER[12] AND GEERT AARTS[13]

[1]Wageningen Marine Research, P.O. Box 57, 1780 AB Den Helder, The Netherlands, jaap.vandermeer@wur.nl, +31 317 488105

[2]Vrije Universiteit Amsterdam, Department of Ecological Science, Amsterdam, The Netherlands

[3]Aquatic Ecology and Water Quality Management Group, Wageningen University & Research, Wageningen, The Netherlands

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Abstract

Coastal seas are experiencing increasing human pressure, related to among other things fishing, oil and gas exploration and the construction of wind farms. Concerns about the impact of these activities on marine top-predators, such as pinnipeds, cetaceans, and seabirds, has stimulated the development of individual-based population models that should be able to predict changes in the population dynamics of these charismatic species in response to the pressures. In this paper we review existing models, evaluate their predictive capacity and propose future research lines that could help improving the applicability of these kind of models.

1 Introduction

Marine mammals and seabirds are often considered 'charismatic megafauna' (Reynolds et al., 2009), and as top-predators they play an important role in marine ecosystems. Changes in the marine system, including lower trophic-level changes in primary productivity may ultimately propagate through the system and influence these top predators. Therefore, marine mammals and birds have also often been used as ecosystem sentinels (Moore, 2008). These species groups can highlight hotspots in productivity, reflect changes in food webs, and also accumulate contamination which can be used as proxy for environmental pollution. As top-predators they also may impose top-down pressure on marine ecosystems. Because both marine mammals and seabirds were severely hunted in the last two centuries, overall numbers were low. Therefore, during and just after the era of intensive hunting, their top-down effect on marine systems was relatively small, particularly when compared to overall fishing pressure (Engelhard et al., 2014). However, increases in marine mammals and seabirds may ultimately place them back at the prominent position in the marine food web (Baum and Worm, 2009; Aarts et al., 2019).

1.1 Anthropogenic changes in the North Sea and its relevance for marine mammals and sea birds

The North Sea has seen rapid changes in human activities in the last decades. While some human activities like fishing effort has decreased, other activities like shipping, beach nourishment, and the construction of renewable energy sources have increased (Halpern et al., 2015). Particularly the construction

of offshore windfarms will likely expand in the coming years. There is how-ever a debate whether the reduced climate change effects of such renewable energy sources, outweigh their environmental impacts (Gibson et al., 2017; Wright et al., 2020). For example, the construction and operation of off-shore windfarms produce sound that may deter marine organisms, and the structures and rotating blades cause mortality from collisions (Drewitt and Langston, 2006) and may deter (or attract) marine mammals, seabirds and bats (Masden et al., 2010). The structures can also change wave-action and stratification in the wake of these turbines (Carpenter et al., 2016), which can influence lower trophic levels and these effects may propagate through the system and ultimately influence the survival and food availability of the marine top-predators.

1.2 What drives marine mammal and seabird distribution and population size?

The distribution and abundance of all organisms are strongly influenced by environmental features which can roughly be classified into three groups: re-sources, conditions and risks (Begon et al., 1996). Resources are substances or objects in the environment required by an organism for normal growth, survival and reproduction. A key aspect of resources is that their availability can be changed by an organism, for example, by consumption (e.g. prey) or occupation (e.g. breeding and foraging sites). This can lead to density dependent effects, such as limits to population growth and size (i.e. carrying capacity) or avoidance of areas with high density of conspecifics, despite high

prey availability. Conditions are environmental variables surrounding the organism and influencing the functioning of living organisms (e.g. temperature or salinity). In marine mammals and seabirds, oceanographic characteristics and seafloor properties (e.g. depth or sediment type) are important conditions that strongly influence their ability to catch prey (Aarts et al., 2008; Embling et al., 2013; Scott et al., 2013). Finally, risks are environmental variables that directly lower survival or reproduction and differ from conditions in that they always have a negative relationship with fitness. Historically, the main risks were actual or perceived predation pressures (i.e. landscape of fears). However, in the last centuries human activities have often been the main threat. These threats could be direct, like hunting or fishery bycatch, or indirect, like noise emitting anthropogenic activities such as shipping, pile-driving or underwater explosions that disturb marine mammals. The effect of resources, conditions and risks on species distribution and abundance often interact. Only under a narrow set of environmental properties can a species persist. Therefore, most species occupy areas with a narrow range of environmental properties, which leads to association with specific habitats. This association with specific habitats is driven by two main processes: Population dynamics (i.e. survival, growth and reproduction) and behavioral selection. For sessile organisms, demographic processes are often the main driver. For those organisms it is important to have all the right environmental properties in one location for the organism to experience positive fitness. For example, most bivalve species have a wide-ranging larval stage, but once settled, they must cope with the local environmental circumstances. In contrast, the distribution of marine mammals and seabirds, is also strongly driven by

behavioral selection. For those mobile species, the necessary resources rarely occur at the same time at the same place, and they have to move around to access those disparate resources (e.g. feeding grounds and resting grounds). In other words, no single point within the North Sea leads to long-term positive fitness, but they can accumulate positive fitness by moving around. This also highlights their need to roam freely, a requirement which can become more challenging in environments with human structures, like (rotating) offshore wind parks. So human activities may influence the overall productivity of the system, but also influence the ability to find and reach those places. What makes this study system particularly challenging is that not only the organisms are highly mobile, and changes in the system may impact their mobility, but also the system itself is highly dynamic. Changes that occur in remote regions, may ultimately propagate to other regions.

2   How to asses and predict the effect of environmental change on distribution and population size?

To assess the cumulative human impacts on marine top-predators, one approach that has been extensively used is to calculate the overlap between marine top-predator distributions and species-specific weighted maps of multiple anthropogenic stressors (Maxwell et al., 2013). Although this can be a valuable tool to highlight regions where conflicts between human activities and marine top-predators are more likely to arise, the approach has some severe

limitations. The distribution of top-predators might already be influenced by human activities, the effects of anthropogenic stressors on the different species are often poorly known, and perhaps most importantly, the approach ignores indirect ecosystem effects. For example, marine top-predators rely on prey species that are often highly mobile as well. Therefore, changes in lower-level productivity well outside the predators foraging range might be carried over and influence top-predator population dynamics. Therefore, to predict population level responses to human activities, taking into account such multi-trophic spatial and temporal dynamics, a more sophisticated model framework is needed that. For this, three model types have been identified (Figure 1):

1. Demographic models 2. Species distribution models 3. Individual-based models

modelling approach	spatially explicit	vital rates	individual variation	physiology	behaviour	evolution	examples
demographic models							
matrix population models (MPMs)	N	Y	N	N	N	N	Crouse *et al.* [36]
mechanistic MPMs	N	Y	N	N	N	Y	De Vries & Caswell [37]
integrated population models (IPopMs)	N	Y	N	Y	N	Y	Schaub *et al.* [38]
mechanistic IPopMs	N	Y	Y	Y	N	Y	Plard *et al.* [35]
integral projection models (IProjMs)	N	Y	Y	Y	N	Y	Smallegange *et al.* [33,34], Ozgul *et al.* [18], Coulson *et al.* [39]
species distribution models (SDMs)							
classical SDMs	Y	N	N	N	N	N	Elith & Leathwick [40]
process-based SDMs	Y	Y	Y	Y	N	Y	Buckley [41], Kearney *et al.* [42], Fordham *et al.* [43]
dynamic range models	Y	Y	N	N	Y	N	Zurell *et al.* [44]
individual-based models (IBMs)							
classical IBMs	Y	Y	Y	N	Y	N	Liu *et al.* [45], Becher *et al.* [46]
mechanistic IBMs	Y	Y	Y	Y	Y	Y	Bocedi *et al.* [47], Galic *et al.* [48], Johnston *et al.* [49], Boyd *et al.* [50]

Figure 1: Characteristic of various model types. Taken from Johnston et al. (2019).

2.1   Demographic models

Demographic models (e.g. matrix population models) can be used to esti-
mate how changes in the vital rates (e.g. survival, age at maturity, fecundity)
influence population dynamics. These models can be extended by including
individual variation (e.g. using integral projection models) or evolutionary
processes. Most demographic models are empirical and fitted to population
count or mark-recapture data, and hence are limited in their ability to pre-
dict the effect of environmental change on population dynamics. Although
they can be extended by inclusion of mechanistic components (de Vries and
Caswell, 2019), they are generally not spatially explicit, and cannot easily
include complex behavioral interactions between individuals and their envi-
ronment.

2.2   Species distribution models

Species distribution models capture the statistical relationship between the
distribution of a species and environmental variables. Although these types
of models are most often used for spatial estimation and inferences (i.e. un-
raveling which environmental variables influence species distribution), they
can be used to predict in space and in time. However, this is often problem-
atic for two main reasons. Firstly, species distribution and environmental
variables may covary in novel ways. This is particularly likely to happen
when the model is used to predict for regions outside the environmental
space for which the original models were fitted. Secondly, the species dis-
tribution models assume a (pseudo-) equilibrium distribution, which means

that all suitable habitats are colonized, and that the species-environment relationship do not change. In real systems, this is almost never the case. Most often there is a delay in the occupation of suitable habitats. For example, grey whales used to live in the North Sea, but were extirpated in the Atlantic Ocean centuries ago. They are still present in the Pacific, and some individual's sightings have been made in the Atlantic in the last decade. It is not unlikely that the eastern Atlantic contains suitable habitats and someday a small number of Pacific grey whales may settle. These delays in occupation occur at all spatial and temporal scales, from global and centennial scales (in the case of grey whales but also grey seals in the Wadden Sea), but also at kilometer and hourly time scales (e.g. the inability of foragers to find and reach the temporal appearance of foraging hotspots). Such delays hamper the fitting of distribution models, but also their ability to predict.

2.3 Individual-based models

Individual (or agent-) based models are centered around the individual and how it interacts with its environment (which is also allowed to be highly dynamic). IBMs are bottom-up models, often centered around the mechanisms that drive behavior and physiology, and the population distribution and abundance is an emerging property. Most IBMs are designed to mimic species as precisely as possible (i.e. digital twins), and in theory any relevant characteristics of a species and how it interacts with its environment can be included. There are a number of important advantages and reasons for using IBMs:

1. Movement is a stochastic process. When movement is a passive (e.g. dispersal by currents), it may be possible to describe movement by a deterministic mathematical formulation (e.g. a diffusion kernel). However, for individuals that move actively, like all higher trophic organisms do, movement becomes highly stochastic and cannot by captured by simple deterministic functions.

2. Experience and learning is a stochastic process and will influence future decisions.

3. Resource distribution is stochastic. Even if we have a perfect model of food distribution, the distribution of individual fish remains a stochastic process. The result of this is that two individuals arriving at a single site, may have different prey encounters and this will likely influence their future decisions to return or move elsewhere.

4. Individuals can have positive or negative effects on each other. E.g. seals tend to breed where other seals breed. The accidental grouping of individuals may fuel the development of persistent breeding colonies. Negative effects are often indirectly, as individuals influence resource density for others.

3 Individual-based models: General structure

Several individual-based models have been developed for marine mammals and seabirds, like Northern Gannets (Warwick-Evans et al., 2018). Although

such models differ in complexity, the models underlying these applications have some key elements in common (Fig. 2). The three elements working on the individual animal are physiology, behavior and evolution. We consider evolution to beyond the scope of this study since most marine mammal and seabird species are long-lived (>10 years) species.
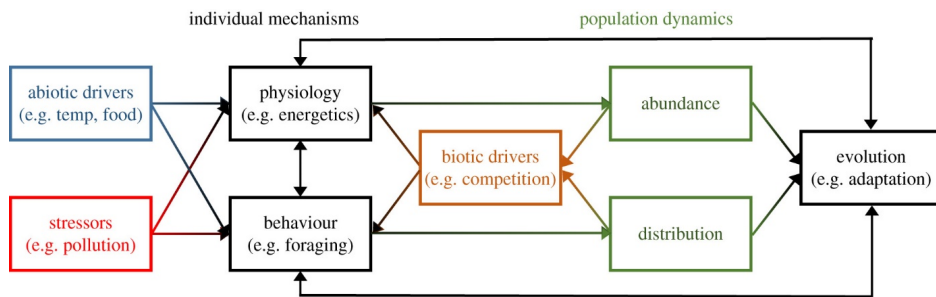

Figure 2: Conceptual standardized mechanistic approach for predicting animal population dynamics in response to spatially explicit abiotic drivers (blue) and multiple stressors (red). Individual mechanisms (black) interact to drive shifts in population abundance and distribution (green), and biotic drivers (orange) cause feedbacks between population dynamics and individual mechanisms. Taken from Johnston et al. (2019).

3.1 Physiology and behavior

1. Physiology can be described by Dynamic Energy Budget model (Kooijman, 2010; Brown et al., 2004; van der Meer, 2006) describing allocation of energy to maintenance, growth and reproduction.

2. Behavioral can be classified into distinct behavioral states and the state-switching probabilities of the decision tree (Patterson et al., 2008). These behavioral states include for example foraging, resting, digesting, breeding, etc. Once these behavioral states and properties (e.g. turning angle and movement speed) have been defined, they can be used to simu-

late the movement and behavior of individual animals (Michelot et al., 2017)

There is a tight link between physiology and behavior. For example, each behavioral state has different energetic costs (and gains). Conversely, the energetic state of the individual (e.g. size of energy reserves) strongly influences the behaviour, e.g. whether to forage or carry out other activities.

3.2 Abiotic drivers, stressors and biotic drivers

These individuals, defined by their physiology and behavior are strongly influenced by their environment (the blue, red and orange box in Figure 2). We prefer to make the classification into the resources, conditions and risks defined previously. For marine mammals and seabirds one important component is their prey. The spatial distribution of prey is a main driver of predator distribution, and the prey encounter rate and energetic content determine the energy gain of the predator. When marine mammals occur in high numbers, they may locally deplete resources, and therefore information on absolute prey availability is needed to account for such depletion. Also, data and models (e.g. DEB models) on prey growth (i.e. prey productivity) are needed. For example, if there are strong density dependent effects in prey communities, predators may alleviate such density-dependent competition and increase fish growth, and as a result those predators may have little impact on total prey biomass In addition to having data on spatio-temporal distribution of abiotic drivers (conditions), stressors (risk) and biotic drivers (resources), the relationship with the species (i.e. the arrows need to be defined). This is one of the most challenging part and requires information

on species habitat association. As noted previously, the distribution of a species is not only shaped by resources, but also by conditions and risk. For example, depth for marine mammals influences the costs to reach benthic prey, water clarity influences the probability to detect prey and internal water structure (e.g. stratification layer depth) can influence the accessibility of seabirds to reach those prey. Also, risk factors, like natural predators and anthropogenic activities may strongly influence their distribution. In summary, although there are obvious benefits for using IBMs, there is also a main disadvantage. All mechanisms included in the model need to be parameterized, and often there is insufficient data. This brings forward the dilemma of how much detail to include and how to deal with missing parameters.

4 Applications of IBMs for seabirds and marine mammals

A search within the Web of Science Core Selection was performed using the keywords 'individual-based model' AND ('marine mammal' OR 'seabird'). This resulted in 11 hits, from which 4 papers present a relevant model. Reference and citations list of these publications were further explored. Additional ad-hoc searches were performed with Google and in personal libraries. Finally, eighteen papers were selected, eleven of which focus on a marine mammal species (Table 1), the others on birds. Most papers were published in the last five years.

4.1   Model descriptions

The purpose of most models is to predict how human impact on food availability affects either the status (e.g. mass or condition) or fitness (reproductive capacity or survival) of individuals, or the size and dynamics of populations (Table 2). Food availability may be affected through the removal of part of the foraging habitat, for example as a result of the presence of wind farms that are avoided by the animals, or by lowering density of prey species. Lowering food availability will decrease food intake rates, affect the energy budgets of individuals, and consequently their state and fitness. It is therefore not surprising that the core of most models is the mass and energy balance of individual animals.

4.2   Energetics

The level of detail by which the energy budget is described varies enormously among the models (Table 3). Some models contain very detailed descriptions of energy intake, allocation and expenditures, including costs of diving, flying, thermoregulation, etc. (Beltran et al., 2017; Brinkman et al., 2003; van de Wolfshaar et al., 2018), using up to 55 parameters, including ones like the deposition efficiency of proteins or the energy density of hair (Beltran et al., 2017). Others describe the energy content of each individual with only a single state variable, which increases as a result of feeding and decreases at a constant rate (Nabe-Nielsen et al., 2014; van Kooten et al., 2019). Most studies presented models with an intermediate level of complexity, but only three studies used a model that was (partially) based on the well-established

280 Dynamic Energy Budget (DEB) theory (Kooijman, 2010).

4.3   Food

282 Only two studies used true data of food abundance (Brinkman et al., 2003;
283 van de Wolfshaar et al., 2018). Both studies concerned a diving duck (ei-
284 der and black scoter) feeding on bivalves, for which spatio-temporal data
285 are easier to obtain than for other prey types such as fish or zooplankton.
286 Two studies used an environmental proxy for food, that is an upwelling in-
287 dex (Pirotta et al., 2018) or water depth (Topping and Petersen, 2011). Most
288 studies generated a food landscape, usually on the basis of the observed spa-
289 tial distribution of the predator itself (Table 3). This generated food land-
290 scape could also consist of a landscape of potential intake rates, such that
291 the predation process is not included explicitly in the model.

292 Prey abundance or potential food intake is either static (Massardier-
293 Galata et al., 2017; van Kooten et al., 2019), gradually depleted (Brinkman
294 et al., 2003; van de Wolfshaar et al., 2018) or depleted and slowly replen-
295 ished (Testa et al., 2012; Nabe-Nielsen et al., 2014).

4.4   Movement

297 In slightly more than half of the models individuals move around in a 1D
298 (3 models) or 2D (6 models) food landscape (Table 3). The two diving
299 duck models do not consider movement explicitly, but calculate the potential
300 numbers of overwintering ducks that can feed upon the available food during
301 the cold season, in which the food is gradually depleted (Brinkman et al.,

2003; van de Wolfshaar et al., 2018). Movement in the 2D models usually follows a random walk or correlated random walk (which means that succeeding steps have a high probability of movement into the same direction), with (Massardier-Galata et al., 2017; Nabe-Nielsen et al., 2014; Zhang et al., 2017) or without (van Kooten et al., 2019) the possibility, for example when energy balance was not maintained, to move to better feeding areas, which are memorized from previous experiences (Massardier-Galata et al., 2017; Nabe-Nielsen et al., 2014; Zhang et al., 2017).

4.5   Status, fitness, and populations

Two studies restricted the output to the status of the individuals, in terms of the daily energetic balance of the seals (Steingass and Horning, 2017) or a description of the foraging movements (Zhang et al., 2017). Five studies described the consequences at the population level. Testa et al. (2012) simulated the predator-prey population dynamics of killer whales and one to three seal populations for a period up to 1000 years. Nabe-Nielsen et al. (2014) simulated the dynamics of a porpoise population in relation to regenerating food patches for a period of 40 years. As mentioned earlier, the two diving duck models calculate the potential numbers of overwintering ducks that can feed upon the available food during the cold season, in which the food is gradually depleted (Brinkman et al., 2003; van de Wolfshaar et al., 2018). They thus do not describe population dynamics but potential population size. Topping and Petersen (2011) also predicted potential population size only, in their case population size of the red-throated diver for various

wind farm scenarios. Output of all other studies contained one or more fitness measures, such as survival and/or reproduction rate. Massardier-Galata et al. (2017), for example, assumed a mass-dependent survival probability for adult Antarctic fur seals and their pups. Similarly, New et al. (2014) and Pirotta et al. (2018) related pup survival probability to wean mass by some statistical relationship. Beltran et al. (2017) assume that adult Weddell seals or their pups die when the fat content drops below 5%. Similar thresholds were applied in the other studies (Villegas-Amtmann et al., 2015; Langton et al., 2014; Warwick-Evans et al., 2018).

4.6 Data used

All studies used literature data to obtain the values for all energy budget parameters.

4.7 Predictions

None of the models has been used to predict population consequences for a very specific management scenario or scenarios. Almost all studies end with a somewhat vague conclusion about applicability and predictive potential, for example saying that 'our model can be used for assessing disturbance costs or other effects associated with climate change and/or anthropogenic activities' (Villegas-Amtmann et al., 2015). Only one paper is clearer, where Testa et al. (2012) write that 'We do not imply specific predictive ability to the model described here. Its value is primarily heuristic, and the lessons are general'.

5 Discussion and perspective for modelling the impact of North Sea wind farms on mammals and birds

Although considerable effort is put into developing the IBM part of the model, the functionality of each model strongly depends on an accurate description of the environment. For example, for the DEPONS model, the distribution of porpoises was used as proxy for prey fields. This philosophy is underpinned by the Ideal Free distribution, which assumes that animals will aggregate in various patches in proportion to the amount of resources available in each patch. Although appealing, it is the interaction between all relevant resources, risks or conditions that shape species distributions. Having a single proxy for all those factors is likely insufficient. Therefore, it is important to unravel which environmental variables influence species distribution. This could partly be achieved by species distribution models. Subsequently, mechanistic formulations of those dependencies can subsequently be included into the IBMs. For this to work, two key data ingredients are needed.

1. Detailed individual-level data on behavior (like movement) and physiology. Such data could best be collected using animal-borne data loggers (e.g. GPS-trackers, accelerometers and temperature sensors)

2. Accurate representation of their environment, and in particular the distribution and dynamics of their prey. Currently most fish surveys are carried out once (or twice) each year and provide a relative measure of abundance (since catchability is often unknown). Estimates of absolute abundance

370 are needed to calculate possible density dependent effects on the population

371 dynamics of the apex predators. Multiple surveys each year are needed to

372 quantify changes in distribution, abundance and energy content.

373 When the hurdle of an appropriate description of the (food and risk)

374 environment is taken, models should be more widely applied, e.g. for different

375 species, in different areas, and with different human impacts, to test their

376 predictive ability and to see whether they can provide more than general

377 lessons only.

Table 1: Individual-based models of seabird and marine mammal populations. Model approach is either forward simulation using fixed behavioural rules (S) or dynamic programming (DP) where behaviour is optimized in terms of fitness.

Number	Species	Approach	Reference
1	Atlantic fur seal	S	Massardier-Galata et al. (2017)
2	Elephant seal	S	New et al. (2014)
3	Southern elephant seal	S	Goedegebuure et al. (2018)
4	Harbour seal	S	Steingass and Horning (2017)
5	Gray seal	S	Silva et al. (2020)
6	Weddell seal	S	Beltran et al. (2017)
7	Killer whale	S	Testa et al. (2012)
8	Harbour porpoise	S	Nabe-Nielsen et al. (2014)
9	Long-finned pilot whale	S	Hin et al. (2019)
10	Gray whale	S	Villegas-Amtmann et al. (2015)
11	Blue whale	DP	Pirotta et al. (2018)
12	Common scoter	S	van de Wolfshaar et al. (2018)
13	Eider	S	Brinkman et al. (2003)
14	Common guillemot	S	Langton et al. (2014)
15	Red-throated diver	S	Topping and Petersen (2011)
16	Black petrel	S	Zhang et al. (2017)
17	Various seabirds	S	van Kooten et al. (2019)
18	Gannet	S	Warwick-Evans et al. (2018)

Table 2: Purpose of the various models

Number	Purpose is to assess the impact of:
1	Climate-related change in food density and distribution on reproductive success
2	Environment-induced change in foraging behaviour on pup survival
3	Changes in resource availability
4	Hypoxia increases on energy balance
5	Food limitation, endocrine disrupting chemicals and infectious diseases
6	Change in food density on growth, reproduction and survival
7	Prey species composition on population size
8	Noise and by-catch on population size
9	Yearly recurrent period of no resource feeding
10	Disturbance on reproduction
11	Anthropogenic perturbations on reproductive success
12	Food availability and disturbance on carrying capacity
13	Food availability on carrying capacity
14	Change in food density and distribution on reproductive success
15	Removal of feeding area by wind farms on population size
16	Food distribution on movement patterns
17	Removal of feeding area by wind farms on mortality rate
18	Removal of feeding area by wind farms on mortality rate

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Table 3: Structure of the various models. Description of energetics is classified as simple (S, less than 5 parameters), intermediate (I) or detailed (D, more than 30 parameters), depending upon the number of parameters used. Output is either at the level of individual status (S), fitness or demographic rates (F) or population size (P).

Number	Spatial	Food	Energetics	Output
1	2D	generated	I	F
2	n	intake generated	S	F
3	n	intake generated	I	F
4	1D	generated	I	S
5	n	intake generated	I	F
6	n	generated	D	F
7	n	simulated	I	P
8	2D	generated, dynamic	S	P
9	n	intake generated	I	F
10	n	intake generated	I	F
11	1D	upwelling index as proxy	S	F
12	2D	benthos survey	D	P
13	n	benthos survey	D	P
14	1D	generated	I	F
15	2D	water depth as proxy	S	P
16	2D	generated	S	S
17	2D	generated	S	F
18	2D	generated	I	F

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