



Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

# Key species and indicators revealed by an uncertainty analysis of the marine ecosystem model OSMOSE

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**ABSTRACT:** Systematic analyses that examine uncertainty in models are essential for assessing their credibility. In this study, we implemented an uncertainty analysis that quantifies the effect of parameter uncertainty on a set of ecological indicators in outputs of the marine ecosystem OSMOSE model applied to the northern Peru Current ecosystem (NPCE OSMOSE). We worked under simple uncertainty assumptions corresponding to ranges of 10, 20, and 30% variability around the reference values of the parameters describing the dynamics of the species modelled in NPCE OSMOSE. The results based on nearly 1.5 million simulations help to identify the main sources of uncertainty that could be of use to focus future research and point to the most reliable indicators in the face of uncertainty. First, uncertainty in the parameters of some species, in particular a key zooplankton species and Humboldt squid, have far-reaching impacts on the modelled biomass of other key species. Second, a set of ecological indicators appear to be relatively insensitive to input uncertainty and may therefore be useful in supporting ecosystem-based management. Furthermore, our findings underline the need for better species representation in terms of data quality but also bottom-up and top-down processes in trophic models. We highlight the difficulties of studying uncertainty in complex models while presenting an approach that can serve as a template for addressing uncertainty analysis in other ecosystem models. Finally, although this approach focuses on parameter uncertainty, it could also serve as a guide to address structural, initial conditions and model forcing uncertainties.

**KEY WORDS:** Uncertainty analysis · Parameter uncertainty · Ecosystem models · Northern Peru Current ecosystem · OSMOSE model

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## 1. INTRODUCTION

Substantial progress has been made in increasing the sustainability of fisheries worldwide over the past 2 decades (Lynch et al. 2017, Farmery et al. 2019, García-Lorenzo et al. 2021). This is important not only for the sustainable exploitation of target species, but

also because of the role of marine biodiversity in providing multiple ecosystem services (Barbier 2017, Shin et al. 2022). This shift in emphasis towards broader sustainability objectives for exploited marine ecosystems underlies the urgency of implementing the ecosystem approach to fisheries (EAF) (Jennings & Rice 2011, Serpetti et al. 2017). Ecosystem modelling

has emerged as a useful tool to support the practical implementation of the EAF (Plagányi 2007). An increasingly large scientific community has been improving the scope and performance of complex marine ecosystem models (e.g. Tittensor et al. 2018, Heymans et al. 2020, Steenbeek et al. 2021), but these types of models have come under criticism because their high degree of complexity can generate substantial uncertainty in ecosystem model predictions and therefore limit their use in decision-making (Fulton et al. 2003). This study shows that it is possible to characterise uncertainty in a widely used complex marine ecosystem model using a formal uncertainty analysis (UA) and that this provides important insights into how commonly used indicators of marine ecosystem structure and function respond to model uncertainty.

UA characterises the uncertainty in model predictions (Saltelli et al. 2019) by quantifying the variability in model outputs (Cariboni et al. 2007); for the purpose of this study, in response to uncertainty in model input parameters. Implementing UA of ecosystem models is a complicated task due to their high computational requirements (in terms of simulation time and memory space) and the multiple model evaluations that a UA requires (Fulton 2010). For these reasons, and despite the abundant literature explaining the importance of dealing with uncertainty in the use of ecosystem models (Link et al. 2012, Lehuta et al. 2016, Payne et al. 2016, Steenbeek et al. 2021), few practical applications have been published using UA for marine ecosystem models (e.g. McGregor et al. 2020, Heath et al. 2021). However, to improve the credibility of these models and increase their usefulness for the practical implementation of the EAF, we urgently need to strengthen our capacity to quantify the uncertainty in model outputs.

To address these issues, we have focused on quantifying the effect of parameter uncertainty in the Object-oriented Simulator of Marine ecOSystEms (OSMOSE) model applied to the northern Peru Current ecosystem (the NPCE OSMOSE model; Oliveros-Ramos et al. 2017). This model was built primarily as a tool to improve understanding of ecosystem functioning under global change and to support ecosystem-based management and decision-making (Oliveros-Ramos 2014). Therefore, the credibility of this tool is essential, but until now the uncertainties in this model have never been quantified using a formal approach. In this study, we have addressed this challenge by focusing on the uncertainty in modelling the NPCE (also known as the Humboldt Current ecosystem). In this paper, the NPCE is defined from 20° S to 6° N. The NPCE is one of the 4 eastern

boundary upwelling systems. It provides the highest fish production in the world, around 10% of global fish catches, and supports the fishery of the Peruvian anchovy (Bakun & Weeks 2008, Chavez et al. 2008), the most significant single-species fishery in the world (Chavez et al. 2003). This ecosystem is also characterised by high environmental variability at diverse temporal scales (i.e. at seasonal, interannual, and decadal scales; Gutiérrez et al. 2016). For the study of the NPCE, it is necessary to use holistic frameworks that integrate the effects of fisheries and climate, among which ecosystem end-to-end models are key tools (Tittensor et al. 2018).

Several ecosystem models have already been developed for the NPCE. Some examples are the Ecopath with Ecosim (EwE) platform (Walters et al. 1997, Christensen et al. 2005), used by Tam et al. (2008) and Taylor et al. (2008), and the OSMOSE modelling platform (Shin & Cury 2001, 2004) used in Marzloff et al. (2009) and more recently in Oliveros-Ramos et al. (2017). However, none of these applications have studied uncertainty in model outcomes. From our perspective, this is mainly due to the lack of practical guidance on how to implement a UA in a complex model. This includes a list of technical decisions to be made; for example, the selection of model inputs as well as of model outputs through which the uncertainty will be quantified, and the methodological approach to reduce the computational costs of uncertainty simulations. In addition, it is also important to show the practical benefits of uncertainty analyses from an ecological perspective. UA can help to shed light on the credibility of ecosystem models and can also provide insight into the dynamics of complex trophic relationships, the performance of ecological indicators in the face of uncertainty, and many other aspects of complex marine ecosystems that are difficult to study *in situ*. These are the key points that we develop in the present work.

We chose the NPCE OSMOSE model for this study because of its ability to consider the complexity and high stochasticity of the NPCE. This model explicitly takes into account the life history and spatio-temporal dynamics of 9 interacting species (one macro-zooplankton group, one crustacean, one cephalopod and 6 fish species). In addition, this model provides a variety of ecological indicators as model outputs (e.g. size-based, species-based, trophic-level based; Shin et al. 2018, Fu et al. 2019), which allows us to analyse and compare the responses of a set of ecological indicators to different levels of uncertainty. In this study, we hypothesised that (1) the uncertainty coming from one species' parameters could propagate

through the food web, (2) the response of ecological indicators to uncertainty is not homogeneous, and (3) depending on the indicators chosen in output of the model, these could amplify or dampen the level of uncertainty compared to uncertainty in inputs.

## 2. MATERIALS AND METHODS

To run the UA of the NPCE OSMOSE model, we (1) selected the model input parameters to be used in this study, (2) sampled the parameter values using a range of variability to then (3) run multiple model simulations using the sampled parameter values, and finally (4) characterise the uncertainty in the model outputs.

### 2.1. The NPCE OSMOSE model and selection of model parameters

We performed an UA on the NPCE OSMOSE model (Oliveros-Ramos et al. 2017). OSMOSE is a size-based trophic model that represents the life story and spatio-temporal dynamics of fish and macro-invertebrate species (Shin & Cury 2001, 2004). It is an individual-based model which assumes size-based opportunistic predation based on the spatial co-occurrence of a predator and its prey. OSMOSE models major life cycle processes (i.e. growth, reproduction, predation, natural and starvation mortalities) and fisheries impacts. It is forced by physical and biogeochemical models, enabling it to simulate the impacts of climate change and variability. OSMOSE applications simulate the complexity and stochasticity of marine ecosystems, integrating physical, biogeochemical, and biological processes. This

model has been applied across diverse marine ecosystems (e.g. Travers et al. 2009, Fu et al. 2013, Oliveros-Ramos 2014, Travers-Trolet et al. 2014, Halouani et al. 2016, Moullec et al. 2019). Complementary information about OSMOSE can be found on its official website ([www.osmose-model.org](http://www.osmose-model.org)).

The NPCE OSMOSE model, developed with the aim of having an integrated and multidisciplinary model for the ecosystem-based management of the NPCE, includes explicit forcing of the physical environment, primary and secondary production, as well as the spatio-temporal dynamics of the most important exploited fish communities. The NPCE OSMOSE model covers an extension of the northern Peru Current and the Peruvian Upwelling Ecosystem between the ranges of 20° S to 6° N and 93° W to 70° W, with 1/6° spatial resolution. Fitted to time series data from the years 1992 and 2008, the NPCE OSMOSE model includes 13 species (Table 1): 9 are explicitly modelled in OSMOSE (also called focal species) and 4 plankton groups (also called biotic resources) are represented in the Pelagic Interaction Scheme for Carbon and Ecosystem Studies (PISCES) biogeochemical model coupled to the Regional Ocean Modeling System (ROMS) physical model as part of model forcing (Aumont & Bopp 2006, Echevin et al. 2008). Additional information about the NPCE OSMOSE model can be found in Oliveros-Ramos (2014) and Oliveros-Ramos et al. (2017).

For the selection of model parameters, we used a broad approach including as many input parameters as we could, prioritising the consideration of parameters in relation with each simulated process in OSMOSE (i.e. major life cycle processes and fisheries impacts). We did not take into account the initial conditions or the model forcings in the UA. In addition,

Table 1. Species or functional groups included in the NPCE OSMOSE model

Types of model species	Species abbreviation	Group	Species or functional group	Scientific name	Model
Biotic resources	$pg_1$	Phytoplankton	Nanophytoplankton	–	ROMS-PISCES
	$pg_2$	Phytoplankton	Diatoms	–	ROMS-PISCES
	$pg_3$	Zooplankton	Microzooplankton	–	ROMS-PISCES
	$pg_4$	Zooplankton	Mesozooplankton	–	ROMS-PISCES
Focal species	$sp_1$	Small pelagics	Anchovy	<i>Engraulis ringens</i>	OSMOSE
	$sp_2$	Demersal	Peruvian hake	<i>Merluccius gayi peruanus</i>	OSMOSE
	$sp_3$	Small pelagics	Sardine	<i>Sardinops sagax</i>	OSMOSE
	$sp_4$	Medium pelagics	Jack mackerel	<i>Trachurus murphyi</i>	OSMOSE
	$sp_5$	Medium pelagics	Chub mackerel	<i>Scomber japonicus</i>	OSMOSE
	$sp_6$	Other pelagics	Mesopelagics	<i>Vinciguerria</i> sp.	OSMOSE
	$sp_7$	Other pelagics	Munida	<i>Pleuroncodes monodon</i>	OSMOSE
	$sp_8$	Other pelagics	Humboldt squid	<i>Dosidicus gigas</i>	OSMOSE
	$sp_9$	Zooplankton	Euphausiids	<i>Euphausia mucronata</i>	OSMOSE

we did not include the parameters of species' life history that are well constrained by data (e.g. lifespan, the exponent of the length–weight relationship [allometric power], spawning period). Also, in order to focus on parameter uncertainty, we removed the stochasticity in the spatial reallocation of schools by fixing the random number seed for that process. Despite this, the model retains some stochastic elements due to the order in which schools act and interact and the ordering of mortality events within a time-step. From the many possible NPCE OSMOSE model inputs (related to the 9 focal species), we focused on predation, growth, reproduction parameters, and the starvation, natural, fishing, and larval mortality rates (Fig. 1). This encompassed 237 parameters used for the UA (and 18 parameter types; Table 2). See Table S1 in the Supplement at [www.int-res.com/articles/suppl/m14465\\_supp.pdf](http://www.int-res.com/articles/suppl/m14465_supp.pdf) for the complete list of parameter values used in the UA. To ensure the compliance of mathematical constraints of the parameters needed to carry out the UA (e.g. parameters standardised between 0 and 1), we performed a reparametrization of the NPCE model before implementing the analysis (see Text S1).

## 2.2. Simulation design

When information about the distribution of parameter values is available, it is used to specify the probability density functions (e.g. in Brown et al. 2015, Engström et al. 2016). In the absence of infor-

mation on parameter distribution, another alternative is to use ranges of variability, i.e. using a numeric value and increasing and decreasing it on either side of the parameter reference value. This method is used to create a range of parameter values where the sampling will occur. Because we lacked detailed information on the distributions of most parameter values, we worked with ranges of 10, 20, and 30% in this study, which are typical ranges found in uncertainty studies (e.g. Lehuta et al. 2010, Ciric et al. 2012, Morris et al. 2014, Dantec-Nédélec et al. 2017). Where data were available, we also checked that these ranges were consistent with the expected ranges of parameter uncertainty based on data. In most cases, uncertainty estimated from observations for key parameters fell within parameter uncertainty ranges of 10–20% that we explored in this modelling study. For example, for the anchovy, the most studied species of this marine ecosystem, we have reviewed the literature where we found a theoretical range (with lower and upper bound). Using these bounds we calculated an uncertainty range, defined as the absolute value of:  $[(\text{lower bound or upper bound} / \text{average bound}) - 1] \times 100$ . Following this, the constant of proportionality of the allometric length–weight relationship has a range of 7.7% uncertainty (Ochoa et al. 2020), the ratio of the size at maturity and the asymptotic size ( $L_{\infty}$ ) of 11.1% (Froese & Pauly 2009), the fraction of females ( $\text{Frac}_{\text{fem}}$ ) of 13.1% (Castillo 2012) and the growth coefficient ( $K$ ) of 14.3% (Oliveros-Ramos et al. 2010).

We used the Monte Carlo method for the UA, undertaking multiple model simulations using sampled

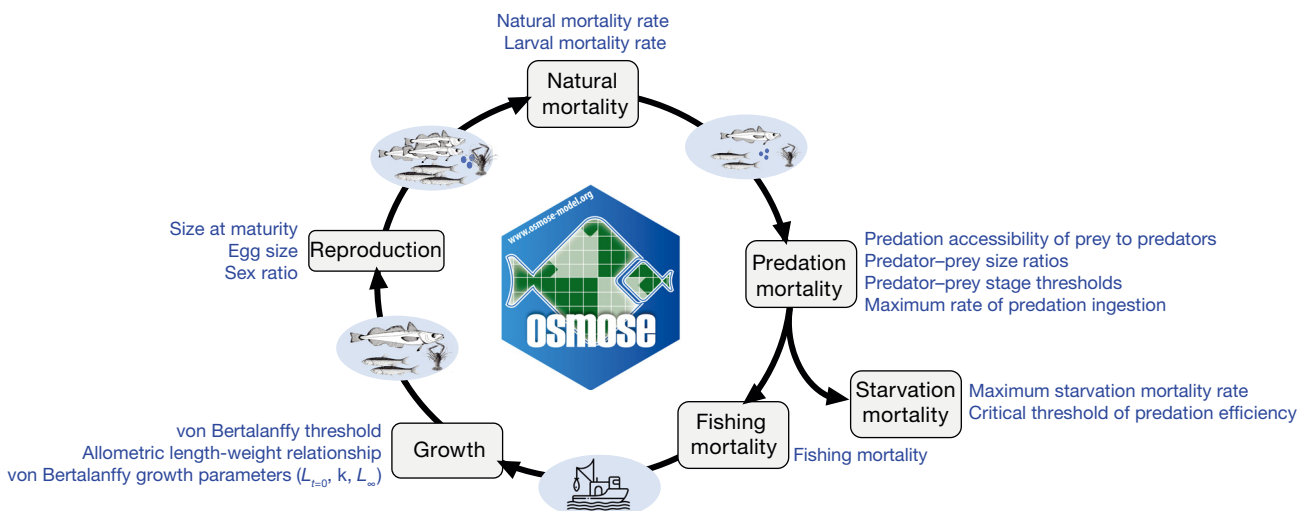


Fig. 1. Graphical representation of the OSMOSE model. The modelled processes are represented by the grey boxes: natural, predation, starvation and fishing mortality, growth and reproduction. The parameters related to each OSMOSE process that have been used for the uncertainty analysis of the NPCE OSMOSE model are in blue. See Table 2 and Table S1 for more details about the complete list of parameters used in this work

Table 2. NPCE OSMOSE parameters used in the uncertainty analysis (UA). The UA was implemented using baseline values which are outcomes of model re-parametrization. The  $f$  function describes the model re-parametrization. See Table S1 for additional information about baseline values of model parameters and Text S1 in the Supplement for details about model re-parametrization

No.	Parameter type	Species	Re-parametrization for the UA	Parameter and scale	No. of parameters
1	Predation accessibility of prey to predators $A(\text{predator}, \text{prey})$	For the 9 focal species	None	Logit	72
2	Minimum predator-prey size ratio for each species stage ( $\theta_{\text{stage}}$ )	For the 9 focal species	$R_{\min} = f_1(\theta_{\text{stage}})$	$\frac{\theta_{\text{stage}}}{(\pi/2)}$ Logit	17
3	Maximum predator-prey size ratio for each species stage ( $\alpha_{\text{stage}}$ )	For the 9 focal species	$R_{\max} = f_2(\theta_{\text{stage}}, \alpha_{\text{stage}})$	$\frac{\alpha_{\text{stage}}}{(\pi/2) - \theta_{\text{stage}}}$ Logit	17
4	Predator-prey stage threshold ( $s_{\text{thr}}$ in cm)	For 7 focal species ( $sp_1, sp_2, sp_3, sp_4, sp_5, sp_8, sp_9$ )	$f_3(s_{\text{thr}}, L_{\infty})$	$s_{\text{thr}}/L_{\infty}$ Logit	8
5	Maximum starvation mortality rate ( $M_{\text{emax}}$ in $\text{y}^{-1}$ )	For the 9 focal species	None	Logarithmic	9
6	von Bertalanffy threshold ( $a_{\text{thr}}$ in $\text{y}$ )	For the 9 focal species	$f_4(a_{\text{thr}}, a_{\text{max}})$	$\frac{a_{\text{thr}}}{a_{\text{max}}}$ Logit	9
7	Egg size (cm)	For the 9 focal species	None	Logarithmic	9
8	Critical threshold of predation efficiency ( $\epsilon_{\text{crit}}$ )	For the 9 focal species	None	Logit	9
9	Maximum rate of predation ingestion ( $I_{\text{max}}$ in $\text{g body g}^{-1} \text{y}^{-1}$ )	For the 9 focal species	None	Logarithmic	9
10	Natural mortality rate ( $M$ in $\text{y}^{-1}$ )	For the 9 focal species	None	Logarithmic	9
11	Larval mortality rate ( $M_0$ in $\text{month}^{-1}$ )	For the 9 focal species	None	Logarithmic	9
12	Fishing mortality multiplier ( $f_m$ )	For 6 focal species ( $sp_1, sp_2, sp_3, sp_4, sp_5, sp_8$ )	None	Logarithmic	6
13	Sex ratio ( $\text{Frac}_{\text{iem}}$ )	For the 9 focal species	None	Logit	9
14	$L_{t=0}$ (von Bertalanffy growth parameter in cm)	For the 9 focal species	$f_5(L_{t=0}, L_{\infty})$	$\frac{L_0}{L_{\infty}}$ Logit	9
15	$k$ (von Bertalanffy growth parameter in $\text{y}^{-1}$ )	For the 9 focal species	None	Logarithmic	9
16	$L_{\infty}$ (von Bertalanffy growth parameter in cm)	For the 9 focal species	None	Logarithmic	9
17	Size at maturity ( $s_{\text{mat}}$ in cm)	For the 9 focal species	$s_{\text{mat}} = f_6(L_0, s_x, L_{\infty}) = \frac{L_0 + s_x(L_{\infty} - L_0)}{L_0 + s_x(L_{\infty} - L_0)}$	$s_x = \frac{s_{\text{mat}} - L_0}{L_{\infty} - L_0}$ logit	9
18	Constant of proportionality of the allometric length-weight relationship ( $c$ in $\text{g cm}^{-3}$ )	For the 9 focal species	None	logarithmic	9

parameter values. This method performs numerous model evaluations using random samples. Then the results of model evaluations are used to determine the uncertainty in model outputs. However, a drawback of this method is the high number of simula-

tions required during the sampling process. We combined the Morris method (Morris 1991) with the Monte Carlo simulation approach to deal with this problem. Morris is a screening method composed of several randomized one-factor-at-a-time experi-

ments. This method is recommended for models with long run times and is typically used to perform global sensitivity analyses (e.g. Specka et al. 2015, Bracis et al. 2020). In this work, we applied the Morris method only to sample the parameter values during the sampling process and produce the design of experiments to be used in the Monte Carlo simulations.

Using the Morris method and considering a model with  $n$  parameters  $x_i$  (where  $i = 1, 2, \dots, n$ ), each  $x_i$  will be scaled to take on values in the interval  $[0, 1]$ . This creates a discrete parameter space  $\Omega$  (the  $n$ -dimensional unit hypercube) by dividing the parameter ranges into  $p$  discrete levels. Then the model is evaluated for  $r$  replicates within the parameter space, each of them building a trajectory inside  $\Omega$ . The starting point of a trajectory is selected randomly. Only a single parameter is changed for each trajectory, taking an element of the parameter space as a new value. In each trajectory, each parameter ( $x_i$ ) is only modified once, so it results in  $n + 1$  simulations. This procedure is repeated  $r$  times ( $r$  trajectories), resulting in a computation cost of  $r(n + 1)$  simulations. In this work, since each parameter was on a particular scale (Table 2), the sampling was done in the standardised interval  $[0, 1]$  after the corresponding transformation of scale.

### 2.3. UA experiments

Using the NPCE OSMOSE model, we executed 27 experiments for the UA (Fig. 2). The first 9 correspond to the uncertainty scenario of 10% for the parameters of each of the 9 species, the other 9 to 20% uncertainty scenario, and the last 9 to 30% uncertainty scenario. Within each uncertainty scenario, the experiments evaluated the effect of the uncertainty from each species separately (called species uncertainty). For example, in experiment  $sp_1$  at 10%, we addressed the uncertainty arising from the parameters related to species  $sp_1$  using the uncertainty scenario of 10%; experiment  $sp_1$  at 20% relates to  $sp_1$  parameters using the uncertainty scenario of 20%; experiment  $sp_1$  at 30% relates to  $sp_1$  parameters using the uncertainty scenario of 30%; and so on. We only perturbed the parameter values related to the species under study in each experiment, leaving the rest of the model configuration unchanged (i.e. their corresponding baseline values).

For each experiment, we performed  $r = 200$  trajectories (i.e. Morris replicates) by dividing the corresponding parameter range into 8 levels ( $p = 8$ ), including upper and lower bounds with values uniformly distributed between them, and using the grid jump ( $\Delta$ ) of  $4/7$  when  $p = 8$  ( $\Delta = p / [2(p - 1)]$ ) that is recom-

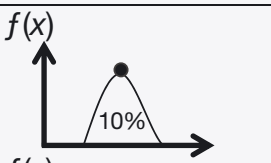







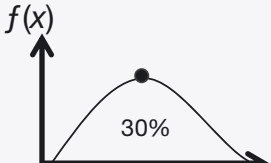



Scenario uncertainty	Species Uncertainty		
	$sp_1$ : anchovy  27 parameters	$sp_2$ : hake  27 parameters	$sp_3$ : sardine  27 parameters
	$sp_4$ : jack mackerel  27 parameters	$sp_5$ : chub mackerel  27 parameters	$sp_6$ : mesopelagics  23 parameters
	$sp_7$ : munida  23 parameters	$sp_8$ : humboldt squid  30 parameters	$sp_9$ : euphausiids  26 parameters

Fig. 2. In total, 27 experiments were run as part of the uncertainty analysis of the NPCE OSMOSE model (3 uncertainty scenarios for 9 species). Within each experiment for a given species, and for each Morris replicate, all the parameters of that species are varied (e.g. the 26 parameters of the euphausiids), while the parameters of other species are fixed. The 10, 20, and 30% uncertainty scenarios correspond to the experiments using a range of variability of 10, 20, and 30%, respectively, for the parameters of the 9 NPCE OSMOSE focal species. The complete list of parameter values related to each species is detailed in Table S1. The number of parameters related to each species is also indicated



Table 3. Ecological indicators used for the uncertainty characterisation using the NPCE OSMOSE model

Indicator	Calculation	Description	Suggested references
Biomass (by species) (t)	$B$	Biomass for each focal species	–
Mean length ( $ML$ ) of fish in the community	$ML = \frac{\sum_i L_i N_i}{\sum_i N_i}$	Where $L_i$ is the average length and $N_i$ is the mean abundance of species $i$	Shin et al. (2005)
Mean trophic level ( $MTL$ ) in the community	$MTL = \frac{\sum_i TL_i B_i}{\sum_i B_i}$	Where $TL_i$ is the trophic level and $B_i$ the biomass (t) of species $i$	Reed et al. (2017), Shin et al. (2018)
Mean lifespan ( $MLS$ ) of community (yr)	$MLS = \frac{\sum_i (A_i B_i)}{\sum_i B_i}$	Where $A_i$ is the lifespan (yr) and $B_i$ the biomass (t) of species $i$ . $A_i$ is defined for each species in the model input configuration	Shin et al. (2018), Fu et al. (2019)
Biomass over yield	$B/Y$	Where $B$ and $Y$ are the total biomass and catch of all modelled species	Shin et al. (2010)
Marine trophic index ( $MTI$ )	$MTI = \frac{\sum_{i(TL>3.25)} TL_i Y_i}{\sum_{i(TL>3.25)} Y_i}$	Where $TL_i$ is the trophic level and $Y_i$ the catch (t) for species $i$ with $TL > 3.25$	Pauly & Watson (2005), Shannon et al. (2014)
Slope of the size spectrum ( $SSP$ ) of community	$Ln(N_k) = \beta_0 + \beta_1 Ln\left(\frac{L_k + L_{k-1}}{2}\right)$ $SSP = \beta_1$	Where $N_k$ is the total fish numbers in the length interval $[L_{k-1}, L_k]$ and $k \in [1, \dots, k_{max}]$ is the index of length class	Rice & Gislason (1996), Shin & Cury (2004)
Large fish index ( $LFI_x$ ): $LFI_{20}, LFI_{30}, LFI_{40}$ of community	$LFI_x = \frac{\sum_i B_{i(L>x)}}{\sum_i B_i}$	Where $B_i$ is the biomass of species $i$ larger than $x$ cm ( $L > x$ ) and $B$ the total biomass of the community. This indicator is calculated for $x = \{20, 30, 40 \text{ cm}\}$	Greenstreet et al. (2011)

mended in Morris (1991). However, given the stochasticity of the OSMOSE model, 10 simulation replicates were executed (i.e. OSMOSE replicates) per Morris run. Thus, we performed a total of 1 476 000 simulations for this work, considering the parameters associated with the 9 species included in the model (Fig. 2), 3 uncertainty scenarios, 200 Morris trajectories, and 10 OSMOSE replicates. Finally, we characterised the uncertainty in model outputs for a set of selected indicators.

#### 2.4. Uncertainty characterization

The NPCE OSMOSE model provides a very large set of model outputs. For the uncertainty characterization, we decided to focus on a set of ecological indicators as model outputs that are frequently studied by the scientific community (Table 3). Most of them were chosen from the IndiSeas program ([www.indiseas.org/](http://www.indiseas.org/)). This program aimed to analyse a set of ecological indicators to assess the ecosystem effects of fishing in the context of environmental change and provide decision support for fisheries management. This set of indicators was tested against several per-

formance criteria, namely sensitivity, specificity and responsiveness (Shin et al. 2018, Fu et al. 2019), and have been already applied in studies using OSMOSE models (e.g. Halouani et al. 2019, Moullec 2019).

For each level of uncertainty (i.e. species ( $sp$ ) and scenario ( $sc$ ) uncertainty), we estimated the relative change ( $RC_{ind}$ ) in the indicator (Ind), which is calculated as:

$$RC_{ind} = \frac{Ind_{sp,sc} - Ind_{baseline}}{Ind_{baseline}} \quad (1)$$

The baseline represents the corresponding indicator estimated using the parameter reference values of the NPCE OSMOSE model with 10 OSMOSE replicates. Ten OSMOSE replicates were also run for each  $Ind_{sp,sc}$ . Additionally, we estimated the coefficient of variations (CV) of the indicators, where the standard deviation and mean were calculated over each Monte Carlo simulation by time step. All simulations and analyses were performed on the Datarmor supercomputer (a high-performance computing system hosted by IFREMER, <https://wwz.ifremer.fr/pcdm/Equipement>) using R 3.6.1 (R Core Team 2019).

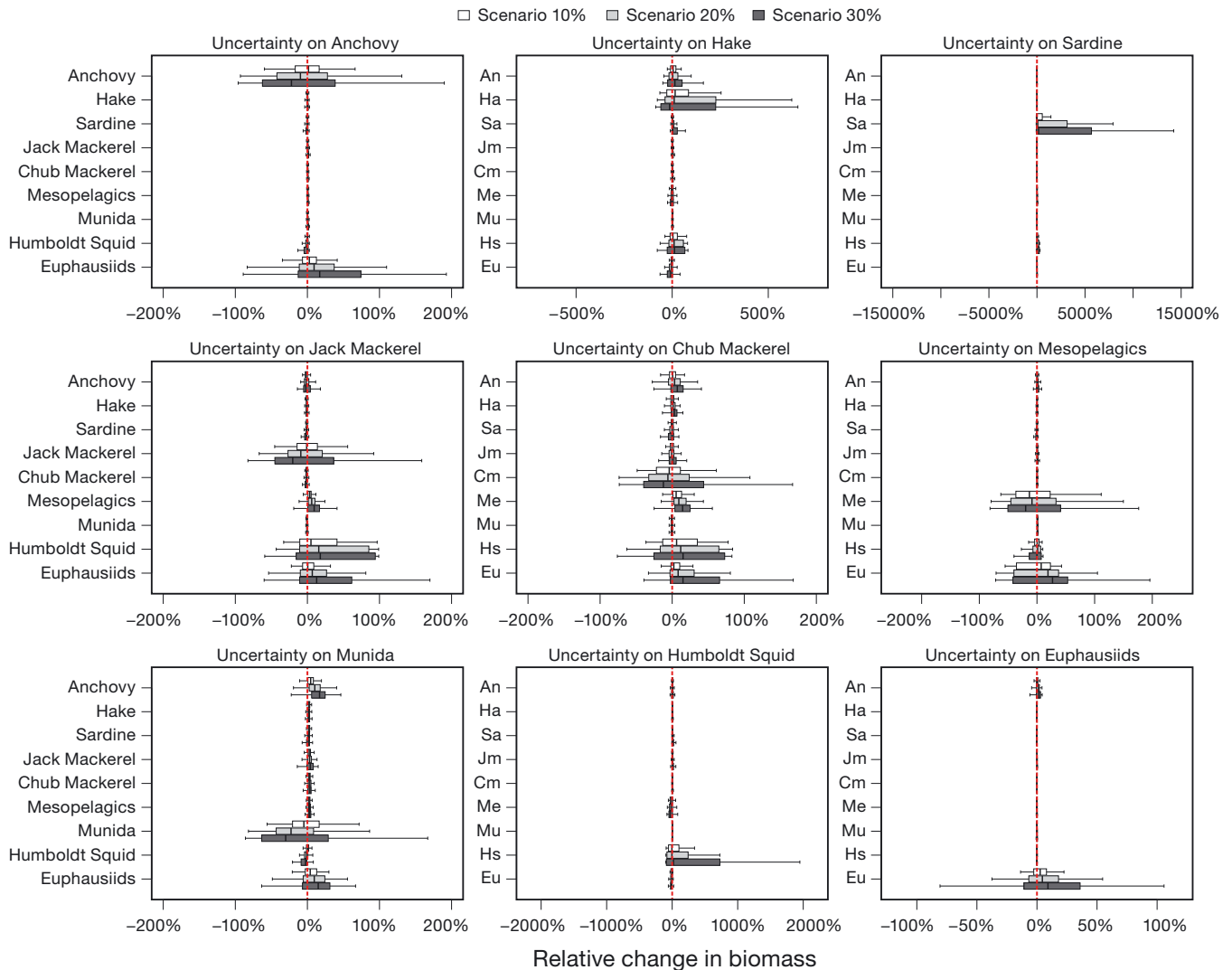


Fig. 3. Relative change (%) in biomass under uncertainty scenarios of 10%, 20%, and 30%. Each panel shows the resulting uncertainty in the biomass of one focal species of the NPCE OSMOSE model due to the uncertainty in the parameters of the 9 focal species. Changes were compared to a baseline simulation (dashed red line). Bar: median; box: 25th–75th percentile (IQR); whiskers: max./min.  $1.5 \times$  IQR above/below box

### 3. RESULTS

#### 3.1. The effects of species uncertainty on the modelled ecosystem

Under the 3 uncertainty scenarios (10, 20, and 30%), species uncertainty propagated through the modelled ecosystem (Fig. 3). For species like anchovy, hake, sardine, munida and Humboldt squid, the greatest uncertainty arose from their own biological parameters, although other focal species also caused uncertainty. For example, the uncertainty of anchovy biomass arises mainly from the uncertainty in its own parameters and those of euphausiids. In contrast to species like jack mackerel, chub mackerel and mesopelagics, the main source of uncertainty

comes from other modelled focal species. Only in the case of euphausiids and Humboldt squid did the uncertainty in their biomass come almost entirely directly from the uncertainty in its own parameters. In general, the uncertainty due to the parameters of Humboldt squid and especially euphausiids were particularly influential and affected the whole set of focal species.

#### 3.2. Ecological indicators behaviour under uncertainty

Uncertainty in ecological indicators across scenarios (Fig. 4) showed that in general, for all evaluated indicators, the 30% scenario produced a higher



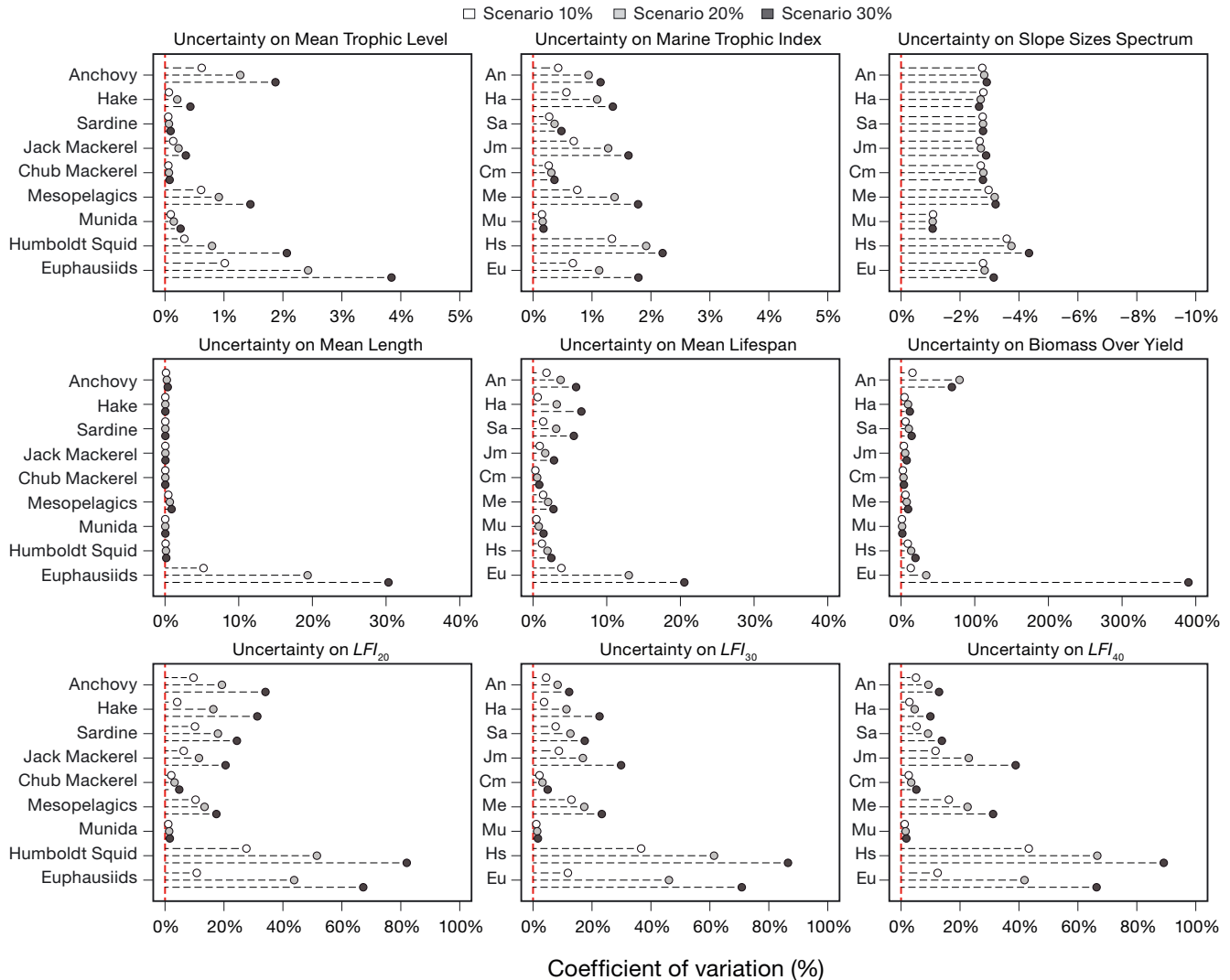


Fig. 4. Coefficient of variation of ecological indicators in the output of the NPCE OSMOSE model under uncertainty scenarios of 10 %, 20 %, and 30 %. Each panel shows the uncertainty of an indicator due to the uncertainty in the parameters of the 9 species

level of uncertainty than the 20% scenario, and the 20% scenario produced a higher level of uncertainty than the 10% scenario. Though only a limited range of uncertainty was explored, this suggests that the level of uncertainty in the model outputs depends on the level of uncertainty in the inputs. However, the level of uncertainty captured in model outputs was heterogeneous across the evaluated indicators. In addition, the uncertainty impact of individual species differed greatly depending on the indicators considered, except for the mean length and the slope of the size spectrum, which in general showed similar responses to individual species uncertainties (Fig. 4). Of all evaluated indicators, the mean trophic level and the marine trophic index had the lowest levels of uncertainty (with CVs less than 3% for the 10 and

20% uncertainty scenarios) and were substantially less than uncertainty in input parameters. These 2 indicators are followed in terms of uncertainty by the slope of the size spectrum (with CVs less than 5% in absolute value) and the mean lifespan (with CVs less than 10% on average for the 3 scenarios). Mean length uncertainty was very low ( $CV < 1\%$ ) in response to all species' uncertainties, except in response to euphausiid uncertainty (but still dampening the input uncertainty). Biomass over yield had a relatively high uncertainty (with a CV up to 70% in response to 20% and 30% anchovy uncertainty). This indicator had the highest value in response to 30% euphausiid uncertainty. Finally, the large fish indices  $LFI_{20}$ ,  $LFI_{30}$  and  $LFI_{40}$  were the 3 indicators that displayed the highest levels of un-

certainty, amplifying the uncertainty compared to uncertainty in input parameters (with CVs up to 90%).

Since the model produces time-varying outputs, we analysed the propagation of uncertainty through time and explored whether looking at mean uncertainty only could mask some important temporal features. For this analysis, we focused on the indicator with the highest uncertainty on average across all species: the  $LFI_{40}$  under the 30% scenario (Fig. 5). We find that the uncertainty in  $LFI_{40}$  is reduced during the El Niño event (the light grey area in Fig. 5, between the years 1997 and 1998), whereas it sharply increases after the El Niño event. This pattern is particularly marked for simulations that implement parameter uncertainty in low trophic level species such as mesopelagics, anchovy and euphausiids, but also other higher trophic level species such

as hake, sardine, jack and chub mackerel and Humboldt squid. The case of munida is particular because this species experienced a significant bloom in the NPCE after 1996 and was introduced in the model after the 1997–1998 El Niño.

We also compared the relative change of species biomass under the 30% uncertainty scenario before and after the El Niño event (Fig. 6). The results show that the uncertainty in species biomass is larger after El Niño than before; this was observed for almost all species except for euphausiids (and obviously munida, which was included in the model after El Niño 1997–1998). In addition, we analysed the behaviour of some output ecological indicators before and after El Niño (Fig. 7). The temporal changes of these indicators in response to species' parameter uncertainty are heterogeneous, but overall with more uncertainty after El Niño.

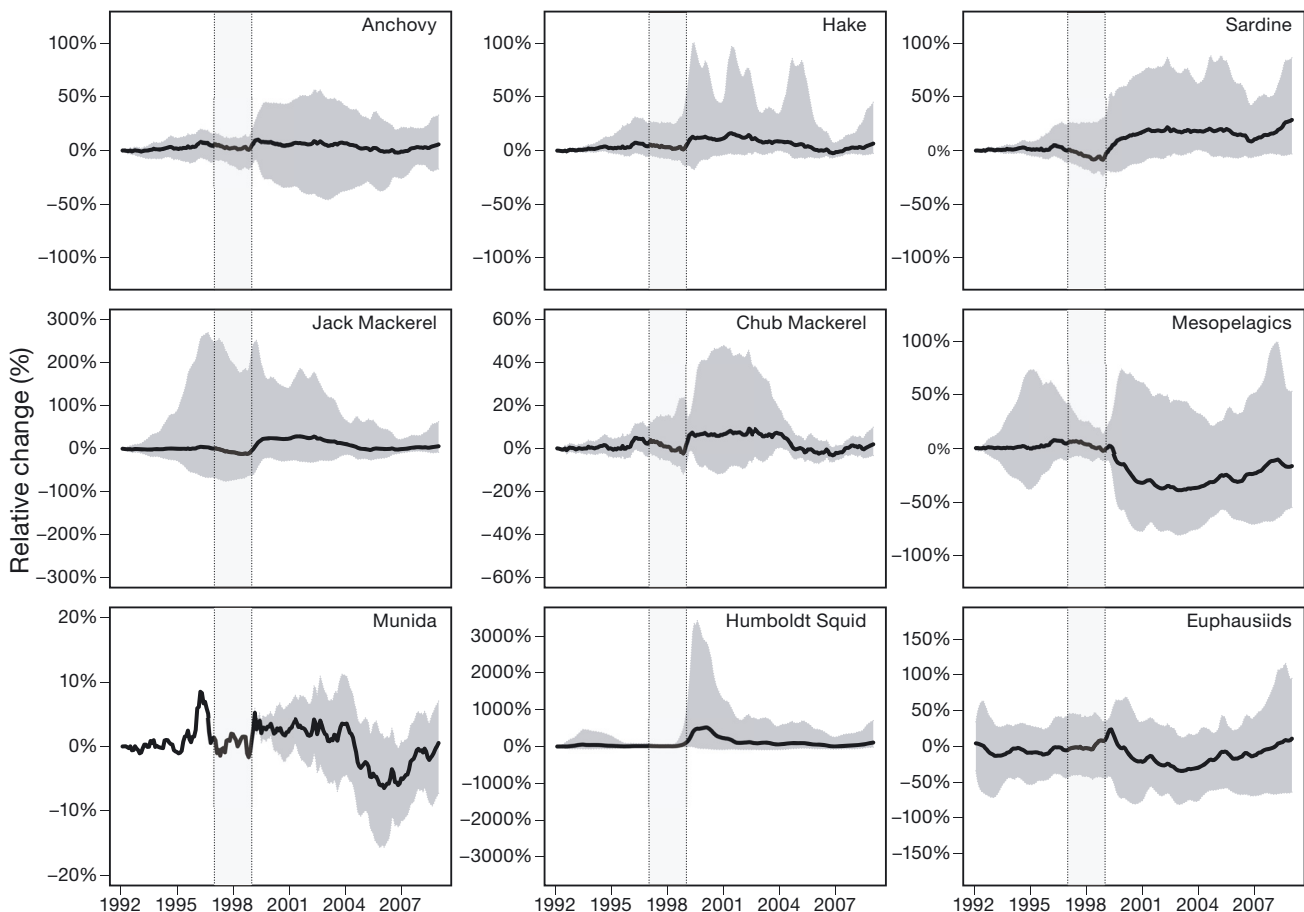


Fig. 5. Projected uncertainty in the large fish index ( $LFI_{40}$ ; see Table 3) indicator under the scenario of 30% uncertainty in species' parameters. Dark grey area: uncertainty between the lower quantile (2.5%) and upper quantile (97.5%); black line: median of the distribution; light grey vertical area: duration of the El Niño event in the northern Peru Current ecosystem (Dewitte et al. 2012)

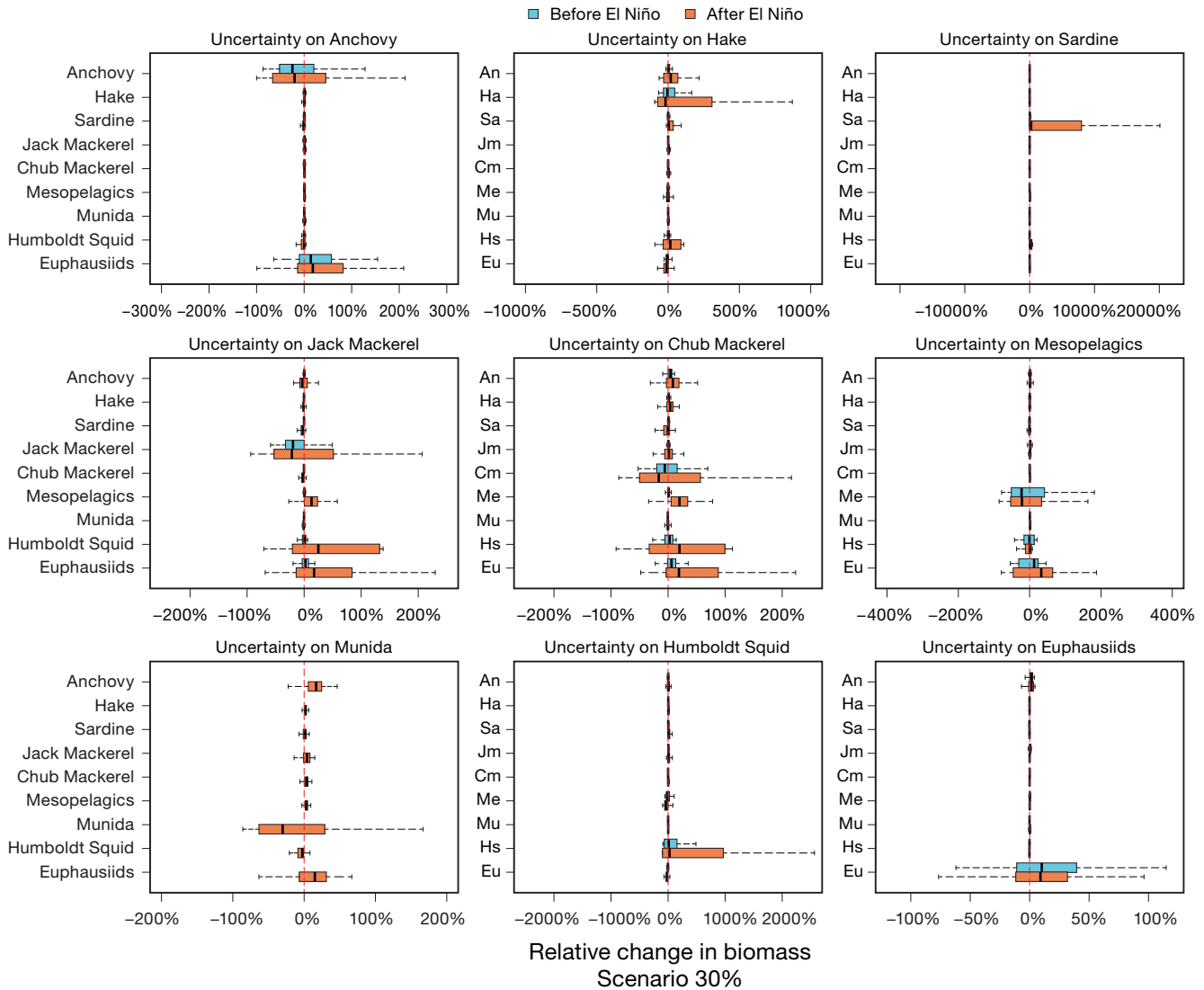


Fig. 6. Relative change in species biomass under the scenario of 30% uncertainty. Each panel shows the uncertainty in the 9 focal species' biomass of the NPCE OSMOSE model due to the uncertainty in the parameters of 1 species. The relative changes were compared to a baseline simulation (dashed red line). Boxplots show uncertainty before the El Niño event (from January 1992 up to December 1996) and uncertainty during and after El Niño (from January 1997 until December 2008). Bar: median; box: 25th–75th percentile (IQR); whiskers: max./min.  $1.5 \times$  IQR above/below box

#### 4. DISCUSSION

Despite the known importance of uncertainty quantification in ecosystem models, UA has generally been neglected due to the computational challenges it requires. In this work, even with the common limitations of implementing a UA in the NPCE OSMOSE model, the simulation experiments allowed us to evaluate uncertainty propagation from one species to the modelled ecosystem. The simulation results showed that as an outcome of the complex interactions in the NPCE OSMOSE model, the uncertainty from one species could impact the rest of

the modelled food web. In particular, uncertainty in the parameters of the euphausiids and Humboldt squid substantially affected the entire food web. Euphausiids are a key zooplankton species group that can exert bottom-up control on food webs by being the main prey of pelagic fishes such as chub mackerel and jack mackerel (Alegre et al. 2015), but also of anchovy (Espinoza & Bertrand 2008, 2014) and, to a lesser extent, of sardine (Espinoza et al. 2009) and Humboldt squid (Alegre et al. 2014). They also interact with hake, which feeds on both pelagic and benthic fish species as well as euphausiids (Ware 1992). On the other hand, Humboldt squid plays an

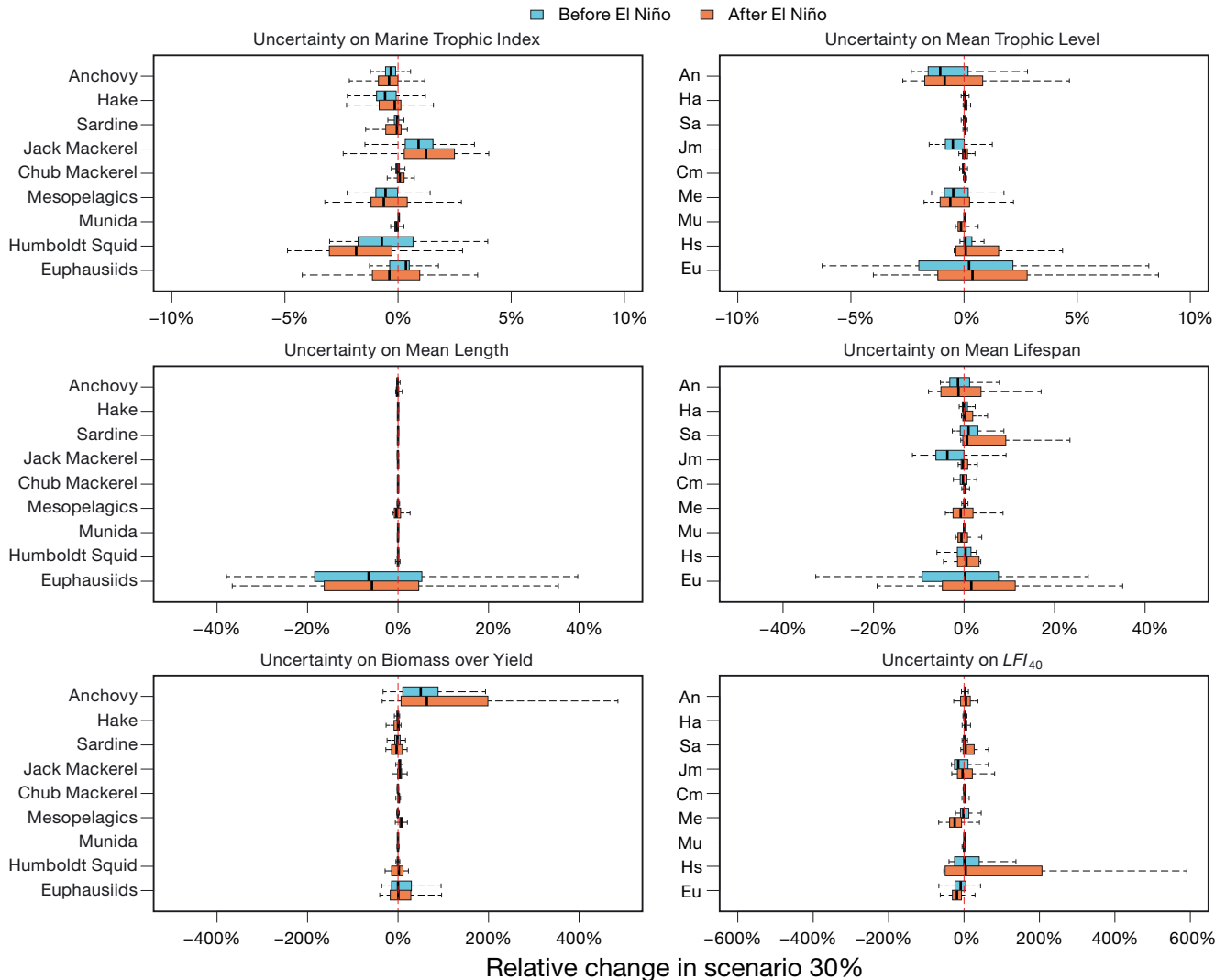


Fig. 7. Relative change in ecological indicators under the scenario of 30% uncertainty. Each panel shows the uncertainty of one of the indicators due to the uncertainty in species' parameters. The relative changes were compared to a baseline simulation (dashed red line). Boxplots show uncertainty before the El Niño event (from January 1992 up to December 1996) and uncertainty during and after El Niño (from January 1997 until December 2008). Bar: median; box: 25th–75th percentile (IQR); whiskers: max./min.  $1.5 \times$  IQR above/below box

important role in marine food webs as a predator (Budelmann 1995), exerting top-down control on euphausiids, mesopelagics, and sometimes on themselves (Alegre et al. 2014). However, there is not enough evidence that squids act as main predators of small pelagic fish such as chub mackerel and jack mackerel. This needs to be clarified and requires further trophic ecology studies.

Other instances in which zooplankton could produce a trophic cascade effect have also been reported by using the marine ecosystem models SthrE2E2 (Thorpe et al. 2022) and EwE (Whitehouse & Aydin 2020). These studies highlight the need to improve the understanding of bottom-up processes as well as their representation within simulation tools. For

Humboldt squid, but also for squids and cephalopods in general, despite their central role in marine pelagic food webs (Young et al. 2013), their ecology is still poorly understood, making it difficult to represent them in ecosystem models (de la Chesnais et al. 2019). Thus, both euphausiids and Humboldt squid need to be further studied to ensure a realistic representation of their dynamics in the modelled system. Also, the information used to parameterize these 2 species must rely on high data quality. The use of poor data quality and the resulting poor representation in the model could also explain the large contribution of some species to the uncertainty in the model output. Although we lacked the evidence to fully understand the main roles of euphausiids and

Humboldt squid in the NPCE, it should be noted that these 2 species lacked reliable time series of abundance indices (Oliveros-Ramos et al. 2017).

The relatively low contribution of the uncertainty in anchovy's input parameters to the biomass of other species was unexpected (Fig. 3) since the anchovy is considered a key species in the NPCE (Bertrand et al. 2008, Chavez et al. 2008, Gutiérrez et al. 2012). In addition, of the 9 focal species modelled, only 2 species (euphausiids and the anchovy itself) generated uncertainty in anchovy dynamics. A possible explanation is that in the NPCE OSMOSE model, anchovy predators have not been represented explicitly (e.g. birds and other predators; Bertrand et al. 2012) but only as mortality parameters. We thus highly recommend improving the representation of anchovy in the NPCE, and one way to do so would be to represent the dynamics and the life cycle of their main predators explicitly. Likewise, the dynamics of hake, a demersal species, could be improved in the model by better representing the dynamics of their main prey (such as euphausiids and *munida*) (Orrego & Mendo 2012, Castillo 2019). *Munida* was modelled through a biomass immigration flux in the NPCE OSMOSE model, which probably oversimplifies the complex life history dynamics of this species for which small individuals have a pelagic behaviour and adults have a demersal one (Gutiérrez 2002). In addition, the explicit representation of sharks as top predators of squid, but also with predation rates on small pelagic fishes (such as anchovy and sardine) and hake could also improve the model (Gonzalez-Pestana et al. 2017, Córdova-Zavaleta et al. 2018).

To increase the realism of UA analyses like those in this study, it would be preferable to use data to construct probability distributions for each model input parameter, designing the UA based on these distributions (e.g. in Yegnan et al. 2002, Brown et al. 2015, Engström et al. 2016). Unfortunately, as was the case in this study, observations, experiments and available data are typically insufficient to construct probability distributions for each model parameter in complex models of natural ecosystems. The use of fixed ranges of variability for input parameters is an option that is often used in such cases of relatively poor data situations. However, a minimum level of information is needed to select appropriate parameter ranges and avoid using arbitrary ones that could underestimate or overestimate the level of uncertainty in model inputs (Saltelli et al. 2004, C. Lujan et al. unpubl. data). These practices can also lead to erroneous results and potentially misleading conclusions about the uncertainty in model outputs. In addi-

tion, there is a strong need for the development of protocols and guidelines to address the uncertainty quantification in complex models with a large number of parameters. Here, we used arbitrary ranges as a first step in the UA of the NPCE OSMOSE model, with range values commonly adopted in other uncertainty studies (Lehuta et al. 2010, Ciric et al. 2012, Zheng et al. 2012, Dantec-Nédélec et al. 2017); but in addition, we verified that the uncertainty ranges based on the available information were within the arbitrary uncertainty ranges used.

Despite the mentioned limitations, by using 3 different ranges of parameter variability (i.e. uncertainty scenarios of 10, 20 and 30%) which required nearly 1.5 million simulations, we were able to confirm that increasing levels of uncertainty in the NPCE OSMOSE model inputs resulted in increased levels of uncertainty in the model outputs. However, this relationship is not linear. Increasing uncertainty from 10 to 20 and 30% in species parameters did not double and triple the uncertainty in model outputs. This finding can be explained by the non-linear and complex relationships found in ecosystem models. Nevertheless, the behaviour of this pattern remains to be tested with wider uncertainty ranges. However, for now, it is too expensive given both the characteristics of the NPCE OSMOSE model and the computational requirements of UA, unless the number of model input parameters, and hence the purpose of the study, is limited. Furthermore, for future implementations of OSMOSE in the NPCE, it would be interesting to follow standardised approaches that allow reliability and realism to be tested. Approaches like TRACE (Grimm et al. 2014) have emerged in the literature, allowing the evaluation of uncertainty in model input parameters but also encouraging the implementation of uncertainty and sensibility analysis (Ayllón et al. 2021, Planque et al. 2022).

The use of ecological indicators allows monitoring the state of ecosystems under fisheries impact and climate change, supporting decision-making for an EAF (Fulton et al. 2005). In this regard, several studies using the OSMOSE modelling platform have conducted indicator analyses to test their performance and usefulness (Shin et al. 2018, Fu et al. 2019, Halouani et al. 2019) but have never considered the effect of parametric uncertainty. We found that some indicators were relatively insensitive to the uncertainty associated with species' parameters, with 3 indicators especially emerging as having interesting properties: the slope of the size spectrum, the marine trophic index, and the mean trophic level. The CV of the slope of the size spectrum was homogeneous

across the 3 uncertainty scenarios; on average less than 4 % (absolute value). In support of this behaviour, this indicator has also been reported as having the best signal-to-noise ratio in the output of a multi-species size-structured model (Thorpe et al. 2015). The responses of the marine trophic index and the mean trophic level were more heterogeneous, depending on which species' uncertainty was considered, but their CVs were always very low, less than 2.5 and 4 %, respectively. However, further studies using more uncertainty scenarios are needed to explain these results and test their robustness. On the other hand, the large fish indices ( $LFI_{20}$ ,  $LFI_{30}$ ,  $LFI_{40}$ ) had relatively high levels of uncertainties in output of the NPCE OSMOSE model. Also, UA undertaken on a multispecies size-spectrum model indicated that the  $LFI$  is a highly uncertain indicator (Zhang et al. 2015). This result should be taken into account when using the  $LFI$  in model projections, especially as previous studies have shown that the  $LFI$  performed well in detecting changes in ecosystem structure (Halouani et al. 2019, Moullec 2019). In addition, Spence et al. (2016) showed that the increase of complex interactions within a model can change the response of the indicators and thus their behaviour in the face of uncertainty. Further studies of UA in complex marine ecosystem models would be needed to better evaluate the response and the performance of indicators.

An additional challenge in analysing uncertainty in complex ecosystem models is that uncertainty can potentially propagate over time. This temporal dynamic of uncertainty should be considered more often than is currently the case when using models for hindcast and forecast simulations. In our uncertainty experiments, the level of uncertainty rose strongly for most species after El Niño (especially for anchovy, mesopelagics, and euphausiids). This event had a massive impact on the NPCE, disrupting the ecosystem's structure (Chavez et al. 2002, Ñiquen & Bouchon 2004, Gutiérrez et al. 2011) and adding significant variability to the system. This impact was also detected in our results, with significant changes in uncertainty in the model's output before and after El Niño. We thus emphasise that uncertainty studies using time-averaged model outputs could mask important features for characterising model uncertainty.

This work involved some technical challenges that we report here. One major impediment was the computational cost of running UA of complex models since these tools are characterised by many inputs (e.g. parameters, initial and forcing conditions) and outputs (multiple simulated variables). To deal with

this, we decided to focus on parameter uncertainty, excluding uncertainty due to initial and forcing conditions. Then, we decided to implement a UA on the parameters associated with focal species; however, even with these restrictions, we were already considering over 200 parameters. Furthermore, we limited the study to the analysis of only 18 ecological indicators among the long list of model outputs. UAs, especially of complex models, also have high computational requirements in terms of simulation time and storage space. For example, each species scenario required about 264 h (11 d approximately); thus, the 27 UA experiments (10, 20, and 30 % uncertainty scenarios for each of the 9 species) required a total of 297 d of simulation (about 9.9 mo). To shorten the simulation time, we could run the simulations in parallel on the Datar-mor supercomputer. All of these technical difficulties are common during uncertainty quantification in complex models, including but not limited to marine ecosystem models. In this sense, our work represents an interesting methodological contribution, showing how we deal with these challenges.

The use of the Morris method for the sampling process in combination with the Monte Carlo approach is presented in this work as a proposal to reduce the computational cost of a UA. In this sense, a convergence analysis should be implemented to test the effectiveness of this approach. In addition, complementary studies related to Morris parameters (e.g. number of trajectories and levels; see Morris et al. 2014 and Bracis et al. 2020) are needed. On the other hand, future studies could explore alternative methods (Marino et al. 2008). For example, we could use the quasi-random sequence method (Jansen 1999, Sobol' et al. 2007), a Monte Carlo resampling procedure implemented in the R 'sensitivity' package (Iooss et al. 2021), with a computational cost of  $n(k+2)$  simulations, where  $n$  is the sample size (i.e. the parameter distribution is divided into  $n$  intervals that are sampled) and  $k$  is the number of parameters included in the analysis. Another possible method is the Latin hypercube sampling (McKay et al. 1979), which is also considered low cost (computational cost of  $n(k+1)$  simulations).

In this paper, we studied the effect of parameter uncertainty on the outputs of the NPCE OSMOSE. Analysis of other sources of uncertainty, such as those due to model forcing and initial conditions, could also provide valuable insights (Cheung et al. 2016, Payne et al. 2016, Rounsevell et al. 2021). Uncertainty due to initial conditions is perhaps the least explored type of uncertainty in complex marine ecosystem models (Steenbeek et al. 2021). The study by McGregor et al. (2020) using an Atlantis model can be cited as one of



the few examples in which the initial conditions of uncertainty were quantified. Model forcing is another important source of uncertainty in marine ecosystem end-to-end models. In the case of the NPCE OSMOSE model, 2 groups of variables force the model: the spatial distribution of fish structured by species and age, and the biomass of 4 classes of plankton, both as spatial time series. Species distribution models (SDMs) were used to produce the spatial distribution of fish forcing the model. Uncertainty propagation from SDMs within ecosystem models needs to be quantified, but this is a technical challenge due to computational costs that has yet to be resolved and was indeed discussed at the last ICES-PICES Symposium on 'Small pelagic fish: new frontiers in science for sustainable management' convened in Lisbon, Portugal, in November 2022 (<https://meetings.pices.int/meetings/international/2022/pelagic/scope>). Structural uncertainty is derived from the equations used to construct a model and the assumptions they represent. In this respect, dealing with this type of uncertainty in complex models requires subjective choices in the processes to include, together with the multiplication of nested models that will test the various model structures. Alternatively, multi-model and ensemble approaches are emerging to explore structural uncertainty (Lehuta et al. 2016, Spence et al. 2018) with recent notable international initiatives such as Fish-MIP ([www.isimip.org/about/marine-ecosystems-fisheries/](http://www.isimip.org/about/marine-ecosystems-fisheries/)), which seeks to produce ensemble projections of global change impacts based on the major ecosystem models developed by the marine science community.

Finally, we call for an increase in interdisciplinary work that could synergize the efforts and experiences of other scientific fields in the study of uncertainty in complex models. For example, modelling of climate (Murphy et al. 2004, Chandler 2013), environment (Pianosi et al. 2016), land-use (Buisson et al. 2010, Alexander et al. 2017), terrestrial (Ahlström et al. 2012) and socio-ecological systems (Rounsevell et al. 2021) provide good insights into the progress of this research field.

**Data availability.** The code used for this work has been documented step by step in a public GitHub repository ([www.github.com/CriscelyLP/lujan\\_etal\\_2023\\_ua\\_osmose](https://github.com/CriscelyLP/lujan_etal_2023_ua_osmose)). This repository allows reproducibility and transparency of our approach.

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