ICES Journal of Marine Science, 2023, **80**, 1991–2007
DOI: 10.1093/icesjms/fsad129
Advance access publication date: 22 August 2023
Original Article

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

Integrating survey and observer data improves the predictions of New Zealand spatio-temporal models

A. Grüss [1,*], A. R. Charsley [1], J. T. Thorson [2], O. F. Anderson [1], R. L. O'Driscoll [1], B. Wood [1], O. N. Breivik [3], and C. A. O'Leary [4]

[1]National Institute of Water and Atmospheric Research, 301 Evans Bay Parade, Greta Point, Wellington 6021, New Zealand
[2]Resource Ecology and Fisheries Management, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way N.E., Seattle, WA 98115, USA
[3]Norwegian Computing Center, Gaustadalleen 23A, 0373 Oslo, Norway
[4]Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way N.E., Seattle, WA 98115, USA
[*]*Corresponding author: tel: +64 206 543 4270;* e-mail: Arnaud.Gruss@niwa.co.nz.

In many situations, species distribution models need to make use of multiple data sources to address their objectives. We developed a spatio-temporal modelling framework that integrates research survey data and data collected by observers onboard fishing vessels while accounting for physical barriers (islands, convoluted coastlines). We demonstrated our framework for two bycatch species in New Zealand deepwater fisheries: spiny dogfish (Squalus acanthias) and javelinfish (Lepidorhynchus denticulatus). Results indicated that employing observer-only data or integrated data is necessary to map fish biomass at the scale of the New Zealand exclusive economic zone, and to interpolate local biomass indices (e.g., for the east coast of the South Island) in years with no survey but available observer data. Results also showed that, if enough survey data are available, fisheries analysts should: (1) develop both an integrated model and a model relying on survey-only data; and (2) for a given geographic area, ultimately choose the index produced with integrated data or the index produced with survey-only data based on the reliability of the interannual variability of the index. We also conducted a simulation experiment, which indicated that the predictions of our spatio-temporal models are virtually insensitive to the consideration of physical barriers.

Keywords: data integration, New Zealand, observer data, research survey data, spatio-temporal models, VAST modelling platform.

Introduction

Species distribution models (SDMs) have become key tools in terrestrial and marine research, including in fisheries science. These statistical models rely on presence-only, encounter/non-encounter, count, or biomass-sampling data, and they relate encounter probability, abundance, or biomass to environmental variables and/or latent (unmeasured) spatial variation. One major use of SDMs consists of generating spatial predictions for broad geographic areas, including for the locations and years for which data are not available (Elith and Leathwick, 2009). The maps produced from SDMs constitute valuable inputs for the identification of essential fish habitats (geographic areas that are essential to fish life history) and marine spatial planning (Pennino *et al.*, 2016), as well as for investigations of the potential impacts of climate change (Guisan and Thuiller, 2005). Moreover, an area-weighted sum of the annual abundance densities (or biomass densities) predicted by SDMs can be performed to construct indices of relative abundance (or relative biomass) for fisheries stock assessments (Grüss and Thorson, 2019; Rufener *et al.*, 2021).

Fisheries scientists usually fit SDMs to data collected by research surveys (fisheries-independent monitoring data) or monitoring programmes that depend on fishing activities (fisheries-dependent monitoring data). The use of more opportunistic presence-only data, such as the data collected by citizen scientists, in SDMs is not common in fisheries science compared to terrestrial research. Surveys and fisheries-dependent monitoring programmes differ in their spatio-temporal extent, design, and protocols and, therefore, in terms of data quantity, data quality, costs, and potential sampling biases. Ultimately, each of these two data sources has its advantages and disadvantages. Using survey data in SDMs is, *a priori*, a preferable option, as survey data should arise from a well-defined sampling protocol that is either fixed or under experimental control following a probability sampling design (Cochran, 1977). Statistically designed surveys allow differences across space and time to be attributed to variation in the target variable rather than sampling methods or inclusion probabilities (Fletcher *et al.*, 2019; Miller *et al.*, 2019). However, surveys are costly, tend to be restricted geographically, are not conducted every year in many world's regions, and are typically confined to specific months of the year (Bourdaud *et al.*, 2017; Webster *et al.*, 2020; Rufener *et al.*, 2021). In many instances, individual surveys do not cover an important fraction of the distribution areas of fish stocks of interest, or of the environmental conditions driving the spatial distribution patterns of these fish stocks. In these situations, SDMs fitted to data coming from individual surveys result in incomplete insights into the spatial distribution patterns or spatial density patterns of the fish stocks of interest (Webster *et al.*, 2020; Thompson *et al.*, 2022), or in indices of relative abundance/biomass (henceforth simply "indices") that show conflicting patterns with the indices produced from other research surveys (Peterson *et al.*, 2017).

Received: 21 February 2023; **Revised:** 13 July 2023; **Accepted:** 31 July 2023

Observer programmes, i.e. fisheries-dependent programmes consisting of placing observers onboard fishing vessels, have some advantages over surveys. Specifically, observer programmes are more cost-effective in many world's regions, generally generate more observations than surveys, usually provide a long time series, tend to be carried out year-round, and often cover broad geographic areas (Bourdaud *et al.*, 2017; Grüss *et al.*, 2018; Rufener *et al.*, 2021). Thus, observer programmes can provide valuable information to understand how fish stocks of interest distribute over space and how environmental conditions drive the spatial distribution patterns of these fish stocks (Pennino *et al.*, 2016). On the other hand, sampling in observer programmes is reliant on fishing vessels, which target specific species and locations (i.e. non-random inclusion probabilities) and constantly adapt their fishing methods based on management and other constraints and technological developments (i.e. sampling attributes that are not fixed or under experimental control). Therefore, observer data constitute biased samples of fish stocks or "unstructured data" *sensu* Isaac *et al.* (2020) (as opposed to "structured" survey data), although usually much more so when the fish stocks of interest are targeted by fishing vessels rather than bycatch species (Pennino *et al.*, 2016). To correct for biases in observer data, fisheries scientists traditionally standardize the catch rate data reported by observers by including covariates in SDMs that filter out the variability in the data that is due to factors influencing catchability, referred to as "catchability covariates" (Maunder and Punt, 2004). However, catchability differences among fishing vessels result from myriad complex and often not well-understood interacting causes (Hilborn and Walters, 1992; Quinn and Deriso, 1999), making it hard to include all necessary catchability covariates in a model fitted to observer data. For this reason, many SDMs fitted to observer data have included a random vessel effect that represents multiple latent catchability variables that are not explicitly modelled (Thorson and Ward, 2014), often *in lieu* of any explicit catchability covariates (Xu *et al.*, 2019; Rufener *et al.*, 2021). The random vessel effect has been found to be a critical model component for explaining variation in observer data (Rufener *et al.*, 2021).

Given that individual surveys (fisheries-independent monitoring programmes) and fisheries-dependent monitoring programmes have their own strengths and weaknesses, there has been increased research into combining data collected by different monitoring programmes. Many recent studies have fitted SDMs to data collected by different surveys (e.g. Grüss and Thorson, 2019; Pirtle *et al.*, 2019; Maureaud *et al.*, 2021; Thompson *et al.*, 2022) or to a combination of survey and observer data (e.g. Grüss *et al.*, 2017, 2018; Ono *et al.*, 2018; Rufener *et al.*, 2021). The simplest way of combining datasets is "data pooling", where the observations coming from different datasets are employed in the same SDMs in the form of presence-only data without acknowledging data sources (Fletcher *et al.*, 2019; Isaac *et al.*, 2020). For example, Pirtle *et al.* (2019) used data from multiple surveys and other sources (a fish atlas and a tagging study) in the form of presence-only data in MaxEnt, to understand habitat suitability for groundfish in the Gulf of Alaska. By ignoring differences between data sources, data pooling offers a rapid way to get ecological insights with SDMs but also provides biased inference about target densities when inclusion probabilities vary across space and time (Warton and Shepherd, 2010). There exist several ways of combining datasets other than data pooling that are more insightful, including, *inter alia*, performing formal data integration that accounts for the observation process associated with each data source, a method referred to as "integrated modelling". [Note that the term "integrated modelling" in fisheries science is utilized beyond the field of SDMs, e.g. in the field of stock assessments (Maunder and Punt, 2013)].

Integrated SDMs have become popular in terrestrial research (Miller *et al.*, 2019; Zipkin *et al.*, 2019; Isaac *et al.*, 2020) and are increasingly being used in fisheries science (e.g. Dolder *et al.*, 2018; Grüss *et al.*, 2018; Rufener *et al.*, 2021; Thompson *et al.*, 2022). Their objective is to retain the strengths of several data sources (e.g. the high quality of structured survey data and the large spatio-temporal coverage of unstructured observer data) while correcting as much as possible for the weaknesses of the different data sources (e.g. the biases associated with unstructured observer data). Integrated SDMs consider (1) a latent (true but unknown) variable (also called "state variable"; e.g. the fish biomass density); and (2) an observation process that results, for each data source, in conditionally independent observations given the latent variable (e.g. biomass catch rates for both a survey and an observer program). The latent variable is related to environmental variables and/or latent spatial variation (as in any SDM), while the observation process accounts for differences in sampling that result in different catchabilities between data sources (Isaac *et al.*, 2020). Integrated SDMs can be implemented only if the individuals sampled to produce the different structured and unstructured datasets can be assumed to belong to the same population and if the likelihoods for the different structured and unstructured datasets have parameters in common (Maunder, 2004; Miller *et al.*, 2019). With different data sources sharing common parameters and, therefore, common likelihood components, a joint likelihood can be computed as the product of the likelihood components for each data source, enabling model estimation from a sharing of information across the different data sources (Fletcher *et al.*, 2019).

In fisheries science, many integrated SDM studies have combined data sources in the form of encounters/non-encounters (e.g. Grüss *et al.*, 2017, 2018; Pinto *et al.*, 2019; Thompson *et al.*, 2022), which is particularly useful when the incorporated data from different sources were collected using very different gears (e.g. longlines and bottom trawls in Thompson *et al.* 2022). In the integrated SDMs employing encounter/non-encounter data, differences in design and methods that result in different catchabilities are accounted for via a catchability factor with one level for each data source (but see Pinto *et al.*, 2019, where differences in catchability between data sources were ignored). Although the integrated SDMs using solely encounters/non-encounter data can produce useful spatial predictions of encounter probability for broad geographic areas, they cannot provide any insights into the abundance or biomass patterns of fish stocks, particularly the indices that are needed for most stock assessments. However, other integrated SDM studies have combined data sources in the form of count data (Rufener *et al.*, 2021) or biomass-sampling data (Dolder *et al.*, 2018; Ono *et al.*, 2018; Perretti and Thorson, 2019; Maureaud *et al.*, 2021). In all cases, the different data sources were acquired with the same gear (e.g. bottom trawl in the case of Perretti and Thorson, 2019), and the integrated SDMs included a catchability factor with one level for each data source. Grüss and Thorson (2019) provides a different case study, where the data coming from different sources were not only encounters/non-encounters yet were collected using different gears. Specifically, the integrated SDM in Grüss and Thorson (2019) relied on biomass-sampling data from a groundfish trawl survey, count data from a pelagic trawl survey, and encounters/non-encounters from a bottom longline survey, under the assumption that all data arise from a marked and thinned Poisson point process.

Numerous studies have demonstrated the benefits associated with integrated SDMs compared to SDMs that employ only one data source. First, integrated SDMs have frequently been found to allow for model estimation when SDMs relying on one single data source failed (Fletcher *et al.*, 2019; Isaac *et al.*, 2020). Second, by exploiting a larger number of observations, integrated SDMs usually improve the precision of estimations, particularly when a limited number of records are provided by the most reliable data source (e.g. Fletcher *et al.*, 2019; Grüss and Thorson, 2019; Rufener *et al.*, 2021; Thompson *et al.*, 2022). Thus, many studies have reported that integrated SDMs allowed for a better characterization of how the environment shapes spatial distributions (Fletcher *et al.*, 2019; Pinto *et al.*, 2019), a valuable understanding of fish spatial distribution patterns in geographic areas where some data sources provide very little or no observations (Grüss and Thorson, 2019; Rufener *et al.*, 2021; Thompson *et al.*, 2022), and the generation of indices for a longer time period that are also less uncertain (O'Leary *et al.*, 2020; Rufener *et al.*, 2021). Third, simulation experiments and cross-validation procedures revealed that integrated SDMs also improved the accuracy of estimations (Fithian *et al.*, 2015; Fletcher *et al.*, 2019; Grüss and Thorson, 2019; Thompson *et al.*, 2022). All this being said, integrated SDMs should not be seen as a panacea, and it is desirable, for particular applications, to evaluate their advantages and disadvantages relative to SDMs fitted to single data sources (Isaac *et al.*, 2020; Simmonds *et al.*, 2020).

Many of the above-mentioned SDMs are spatio-temporal models, i.e. models that account for spatial variation (long-term latent variation) and, possibly, spatio-temporal variation (latent variation that changes over time) at a very fine scale (at the scale of kilometres or tens of kilometres; e.g. Grüss *et al.*, 2018; Ono *et al.*, 2018; Rufener *et al.*, 2021; Thompson *et al.*, 2022). Modelling latent spatial/spatio-temporal variation in integrated SDMs is essential to borrow information across datasets when the different data sources involve different spatial scales, which is a frequent situation (Isaac *et al.*, 2020). Compared to models that ignore latent spatial/spatio-temporal variation, spatio-temporal models produce more precise estimations through their ability to predict quantities of interest (e.g. biomass density) at unobserved sites and times by sharing information across adjacent locations and time periods (Thorson *et al.*, 2015a; Rufener *et al.*, 2021; Thompson *et al.*, 2022). Recent simulation experiments also found that, compared to simpler models, spatio-temporal models generally result in more accurate estimations and/or a better characterization of uncertainty around these estimations (Grüss *et al.*, 2019; Brodie *et al.*, 2020; Hsu *et al.*, 2022).

Here, we present a spatio-temporal modelling framework integrating survey and observer data while accounting for physical barriers (islands, convoluted coastlines) in the estimation of spatial and spatio-temporal variation. By borrowing information across data sources, sites, and years, this integrated SDM framework intends to improve the precision and accuracy of estimations over SDMs that rely on a single data source. Our spatio-temporal modelling framework can integrate the biomass catch rate data collected by multiple monitoring programmes (surveys and/or observer programmes) using the same gear method (e.g. a bottom trawl) via the estimation of a fishing-power ratio for each monitoring program relative to a reference survey. When some observations come from an observer program, our spatio-temporal modelling framework also includes a random vessel effect to account for catchability differences among the fishing vessels onboard which the observers were placed. In the following, we describe the modelling framework and demonstrate it for two bycatch species in New Zealand (NZ) deepwater fisheries, spiny dogfish (*Squalus acanthias*) and javelinfish (*Lepidorhynchus denticulatus*), using data coming from 12 different bottom trawl surveys and a large observer program that places observers onboard commercial bottom trawlers in NZ waters. Then, we employ a simulation experiment to evaluate the accuracy, error, and confidence interval coverage of the indices predicted by our integrated SDMs vs. an SDM using survey-only data, when physical barriers are accounted for or not.

Materials and methods

As the data collected by monitoring programmes typically include many zeros, our spatio-temporal model is a two-stage (a.k.a. delta) model fitted to biomass catch rate data, $b(i)$, where i indexes samples. A delta model defines an encounter probability, $p(i)$, and an expected biomass catch rate given that the species of interest is encountered (positive catch rate), $r(i)$ (Lo *et al.*, 1992). The product of these two quantities gives biomass density, $d(i)$. More specifically, our spatio-temporal model is the Poisson-link delta model developed in Thorson (2018), which relates encounter probability and positive catch rate rather than assuming that these two quantities are independent. The Poisson-link delta model estimates two state variables, number density, $n(i)$, and biomass-per-number, $w(i)$, and the product of these two quantities is also equal to biomass density $d(i)$. Under the assumption that groups of fish are randomly distributed in the proximity of sampling, encounter probability $p(i)$ can be derived as a complementary log–log link from number density $n(i)$. It follows that, in the Poisson-link delta model, positive catch rate $r(i)$ is obtained as $^{n(i)w(i)}/_{p(i)}$ (Equation 5 of Thorson, 2018). Given the above, our model computes the probability of the biomass catch rate data $b(i)$ as (Thorson, 2018)

$$f\left(b\left(i\right)=B\right)=\begin{cases}1-p\left(i\right) & \text{if } B=0\\ p\left(i\right)\times Gamma\left(B|r\left(i\right);\sigma_r^2\right) & \text{if } B>0\end{cases}, \quad (1)$$

where $f(b(i)=B)$ is the data likelihood; $Gamma(B|r(i);\sigma_r^2)$ is the Gamma probability density function for an unexplained variation in positive catch rate $r(i)$; and σ_r^2 is the residual catch rate variation.

Our model estimates the two state variables $n(s,t)$ and $w(s,t)$ at each site s and in each year t via two linear predictors. When our model is fitted to data coming from a single survey, each linear predictor expresses the logarithm of the state variable as a function of year intercepts β, spatial variation (long-term latent variation) ω, spatio-temporal variation (latent variation that changes over time) ε, density covariates X, and catchability covariates Q, which are all estimated by the model:

$$\log\left(n\left(s_i,t_i\right)\right)=\beta_n\left(t_i\right)+\omega_n\left(s_i\right)+\varepsilon_n\left(s_i,t_i\right)+\sum_{p1=1}^{n_{p1}}\gamma_n\left(t_i,\ p1\right)X_n\left(i,\ t_i,\ p1\right)+\sum_{k1=1}^{n_{k1}}\lambda_n\left(k1\right)Q_n\left(i,\ k1\right),$$

$$\log\left(w\left(s_i,t_i\right)\right)=\beta_w\left(t_i\right)+\omega_w\left(s_i\right)+\varepsilon_w\left(s_i,t_i\right)+\sum_{p2=1}^{n_{p2}}\gamma_w\left(t_i,\ p2\right)X_w\left(i,\ t_i,\ p2\right)+\sum_{k2=1}^{n_{k2}}\lambda_w\left(k2\right)Q_w\left(i,\ k2\right), \quad (2)$$

where $p1$ indexes density covariates in the first linear predictor; n_{p1} is the number of density covariates in the first linear predictor; $\gamma_n(t_i,\ p1)$ is the average effect of density covariate $p1$ in the first linear predictor; $k1$ indexes catchability covariates in the first linear predictor; n_{k1} is the number of catchability covariates in the first linear predictor; $\lambda_n(k1)$ is the impact of catchability covariate $k1$ for the first linear predictor; and $p2$, n_{p2}, $\gamma_w(t_i,\ p2)$, $k2$, n_{k2}, and $\lambda_w(k2)$ have similar meanings for the second linear predictor. The X_n covariates and the X_w covariates affect, respectively, number density and biomass-per-number and, therefore, both affect biomass density; they are collectively referred to as "density covariates" for simplicity and are distinguished from the Q_n and Q_w covariates, which affect catchability in the first and linear predictors, respectively (Thorson *et al.*, 2023).

The density covariates X_n and X_w (Equation 2) approximate drivers of the latent variable. Coefficients γ_n and γ_w representing their estimated responses are treated as fixed effects, as is the case for the year intercepts β_n and β_w. By contrast with density covariates, the catchability covariates Q_n and Q_w are nuisance parameters, which are included in the model to filter out causes of variation in the data due to the characteristics of sampling (Grüss *et al.*, 2019; Hsu *et al.*, 2022). The variation in the state variables that is not explained by density covariates gets explained by the spatial variation term ω and the spatio-temporal variation term ε (Thorson *et al.*, 2015a; Thompson *et al.*, 2022). Both the spatial and spatio-temporal variation terms are treated as random effects that follow a multivariate normal distribution, and spatio-temporal variation can also be modelled as a first-order autocorrelation (AR1) process in situations where the spatial distribution of sampling has changed substantially over time (Charsley *et al.*, 2023; Grüss *et al.*, 2023a). Thus, in each linear predictor, spatial and spatio-temporal variations are modelled as

$$\omega \sim MVN\left(0, \sigma_\omega^2 \mathbf{R}\left(\kappa\right)\right)$$

$$\varepsilon\left(t\right) \sim \begin{cases} MVN\left(0, \sigma_\varepsilon^2 \mathbf{R}\left(\kappa\right)\right) & \text{if } t = t_{min} \\ MVN\left(\rho_\varepsilon \varepsilon\left(t-1\right), \sigma_\varepsilon^2 \mathbf{R}\left(\kappa\right)\right) & \text{if } t > t_{min} \end{cases}, \quad (3)$$

where ρ_ε is the temporal autocorrelation coefficient at lag 1, which can be turned off if modelling spatio-temporal variation as an AR1 process is not warranted; $\mathbf{R}(\kappa)$ is a matrix representing the Matérn covariance structure, which describes the correlation between locations as a function of the decorrelation distance κ (Lindgren *et al.*, 2011); σ_ω^2 is the estimated pointwise variance of spatial variation; σ_ε^2 is the estimated pointwise variance of spatio-temporal variation; t_{min} is the first year in the time series; and ρ_ε, κ, σ_ω^2, and σ_ε^2 are estimated separately for the first and second linear predictors. The spatio-temporal variation term is crucial to capture changes in spatial variation over time and obtain predictions at unobserved locations and times. The modelling of spatial and spatio-temporal variations is further detailed in the subsection "Estimation of covariance between locations".

When our model is fitted to data coming from an observer program rather than from a survey, catchability differences become very large between sampling events because of multiple complex and poorly understood interactions between fishers, the fishing gear, various fishing vessel characteristics, and the management and other constraints that occurred at the time of fishing (Hilborn and Walters, 1992; Quinn and Deriso, 1999). As a result, observer data tend to be overdispersed to the extent where catchability covariates Q_n and Q_w may not be sufficient to filter out the variation in the data due to the behavioural and technical characteristics of fishing and, therefore, to obtain indices whose variability is not substantially confounded with variability in catchability. Consequently, when our model is fitted to observer data, each linear predictor also includes a random vessel effect $\eta(v_i)$ following a normal distribution with a mean of zero and a standard deviation that is estimated (Thorson *et al.*, 2015a; Xu *et al.*, 2019; Rufener *et al.*, 2021). Note that there are case studies where vessel effects will not be normally distributed, e.g. if there are groups of vessels with similar catchability or significant trends in the catchability of vessels joining and leaving the fishery. This issue does not pertain to our NZ case study (detailed below), but future applications of our modelling framework that are concerned with this issue may want to add structure to the random vessel effect or define the vessel effect as a fixed factor effect (provided that the number of levels of the vessel factor is not too large to allow for model estimation).

When our model is fitted to data coming from several sources (different surveys and/or observer programmes), additional catchability differences arise between observations due to their source. To acknowledge the additional catchability differences between observations, the first linear predictor of the model then includes an additional catchability covariate M, which allows for the estimation of the fishing-power ratio for each monitoring programme relative to a reference survey (Grüss and Thorson, 2019):

$$\log\left(n\left(s_i,t_i\right)\right)=\beta_n\left(t_i\right)+\omega_n\left(s_i\right)+\varepsilon_n\left(s_i,t_i\right)+\ \eta\left(v_i\right)+\sum_{m=1}^{n_m}\delta\left(m\right)M\left(i,\ m\right)+\sum_{p1=1}^{n_{p1}}\gamma_n\left(t_i,\ p1\right)X_n\left(i,\ t_i,\ p1\right)+\sum_{k1=1}^{n_{k1}}\lambda_n\left(k1\right)Q_n\left(i,\ k1\right),$$

$$\log\left(w\left(s_i,t_i\right)\right)=\beta_w\left(t_i\right)+\omega_w\left(s_i\right)+\varepsilon_w\left(s_i,t_i\right)+\ \eta\left(v_i\right)+\sum_{p2=1}^{n_{p2}}\gamma_w\left(t_i,\ p2\right)X_w\left(i,\ t_i,\ p2\right)+\sum_{k2=1}^{n_{k2}}\lambda_w\left(k2\right)Q_w\left(i,\ k2\right), \quad (4)$$

where the random vessel effect $\eta(v_i)$ is fixed at 0 when sample i comes from a survey; m indexes monitoring programmes; n_m is the number of monitoring programmes considered in the model; and $\sum_{m=1}^{n_m} \delta(m)M(i,\ m)$ is the effect of monitoring program on expected number density; the design matrix $M(i,\ m)$ is 1 for the monitoring program that collected sample i and 0 otherwise; and the monitoring program effect $\delta(m)$ is set up so that $\delta(m) = 0$ for the reference data source, which is the survey with the largest sample size. The constraint imposed on $\delta(m)$ enables the identifiability of all β_n parameters (Grüss *et al.*, 2018). It also results in the estimation of a fishing-power ratio for each monitoring program relative to a reference survey, which gives more weight to the structured reference data source compared to the other data sources (that include the unstructured data). We elected to treat the monitoring program catchability factor as a fixed rather than a random effect so that we are not making any implicit assumption that included monitoring programmes are similar to one another (Grüss and Thorson, 2019). This contrasts with our treatment of fishing vessels as having fishing power as a random effect, where we assume that fishing vessels do on average have similar fishing power.

Our model is implemented with the Vector Autoregressive Spatio-Temporal (VAST) modelling platform, using the R package VAST release 3.10.0 (Thorson, 2019). VAST is a generalized linear mixed-effects modelling platform that incorporates the functionality of vector autoregression (Hamilton, 1994). Any mixed-effects modelling platform requires integration across all random effects during model fitting, or an approximation of the integral. This integration computes the likelihood of the parameters treated as fixed effects while integrating across all the possible values for the random effect, and simultaneously weighting each possible value given the probability of that value for the random effect (Equation 1 of Thorson *et al.*, 2015b). This integration is made computationally reasonable in VAST via the use of the Laplace approximation as implemented in Template Model Builder (TMB; Kristensen *et al.*, 2016). Specifically, TMB applies the Laplace approximation to the joint likelihood of fixed and random effects jointly with the model Hessian to compute marginal likelihood and, therefore, estimate the variance of random effects. VAST R codes and associated materials are available on a dedicated GitHub repository (https://github.com/James-Thorson-NOAA/VAST), along with a user manual (Thorson, 2022), other documentation, and examples. VAST also has a dynamic community of developers and users, as shown by its multiple applications worldwide and its use in >110 peer-reviewed publications as of July 2023. Further details about the estimation of our model, as well as details about its evaluation, which employs procedures that are standard for VAST models, can be found in Appendix 1.

Estimation of covariance between locations

With the VAST modelling platform, all the spatial and spatio-temporal variation terms are modelled as Gaussian Markov random fields $\boldsymbol{\varphi}$ following the multivariate distribution (Thorson *et al.*, 2015a):

$$\boldsymbol{\varphi} \sim MVN\left(\boldsymbol{\mu}, \boldsymbol{\Phi}\right), \tag{5}$$

where $\boldsymbol{\mu}$ is the expected value of the multivariate normal distribution for each location, which is typically set to zero unless an AR1 process is assumed Equation (3); and $\boldsymbol{\Phi}$ is a covariance matrix for random field $\boldsymbol{\varphi}$ at each location. Classically, in VAST (1) covariances between locations $\boldsymbol{\Phi}$ are assumed to be stationary and are estimated using the modified Matérn autocorrelation function developed in Thorson *et al.* (2015a), which accounts for geometric anisotropy (their Equation 4); (2) a predictive approach is adopted for computational efficiency where a triangulated mesh is defined around n_x "knots", and covariance is estimated between those knots (Shelton *et al.*, 2014); and (3) bilinear interpolation is then employed to obtain values between knot positions (Grüss *et al.*, 2020). This classical approach for estimating covariance between locations in VAST is referred to as the "stochastic partial differential equation (SPDE) model".

However, the SPDE model is not well suited for regions characterized by physical barriers (islands, convoluted coastlines) such as NZ waters. Using the SPDE model for such regions would lead to inappropriate smoothing over islands and/or convoluted coastlines. Thus, the "SPDE-Barrier model" presented in Bakka *et al.* (2019) was introduced in the VAST modelling platform. The SPDE model determines dependency between two locations based on all the paths that exist between them, including the paths that cross land. With the SPDE-Barrier model, dependencies along the paths that cross land are weakened to almost zero, so that they do not contribute to the estimation of the covariance between locations (Bakka *et al.*, 2019). Compared to the SPDE model, in the SPDE-Barrier model: (1) geometric anisotropy is ignored; and (2) only a fraction of spatial range (the distance at which two observations can be considered to be effectively independent) is applied in the presence of a barrier (i.e. over land), which is what weakens the dependencies along the paths that cross land to almost zero. In our implementation of the SPDE-Barrier model, spatial range over land was 0.2 of the in-water spatial range, following Bakka *et al.* (2019). As a result, the correlation between locations decayed five times more slowly with distance across water than with distance across land.

Demonstration

We demonstrated our spatio-temporal modelling framework by applying it to two bycatch species in the NZ deepwater fisheries, spiny dogfish and javelinfish. The demonstration relied on bottom trawl survey data collected in NZ waters over the period 1991–2021 and data collected by observers onboard commercial bottom trawlers over the same time period. Spiny dogfish was chosen because there is an interest in NZ in better understanding its biomass trends (Baird and Ballara, 2022). Javelinfish was chosen because it is one of the species contributing the most to bycatch in weight in NZ deepwater fisheries (Finucci *et al.*, 2019). None of the models developed for spiny dogfish and javelinfish included density covariates X_n or X_w or catchability covariates Q_n or Q_w, and we leave the inclusion of these covariates in our spatio-temporal modelling framework for future research (see the "Discussion" section).

The bottom trawl survey data were obtained from the Fisheries New Zealand (FNZ) database *trawl* (Mackay, 2020). One important detail about the *trawl* database is that it gathers data collected in different geographic areas using various designs and protocols, sometimes for very different purposes (e.g. targeted identification trawls complementing acoustic measurements for a specific species or random trawls for monitoring multiple species). In addition, not all the records included in the *trawl* database are valid for biomass estima-

Table 1. NZ bottom trawl research surveys considered in this study.

Survey short name	Survey long name
WCNI SNA	West Coast North Island inshore trawl survey
HAGU SNA	Northern inshore trawl survey series in the Hauraki Gulf
BPLE SNA	Northern inshore trawl survey series in the Bay of Plenty
ECNI	Northern inshore trawl survey series off the East Coast North Island
WCSI TBGB	Inshore trawl survey of the West Coast South Island and Tasman/Golden Bays
WGSI MD	West Coast South Island Tangaroa middle depth survey
SOUTH MD	Southland middle depth survey
SUBA AUT	Sub-Antarctic autumn middle depth trawl survey
SUBA SUM	Sub-Antarctic summer middle depth trawl survey
ECSI SUM	Summer inshore trawl survey of the East Coast South Island
ECSI WIN	Winter inshore trawl survey of the East Coast South Island
CHAT MD	Chatham Rise middle depth trawl survey

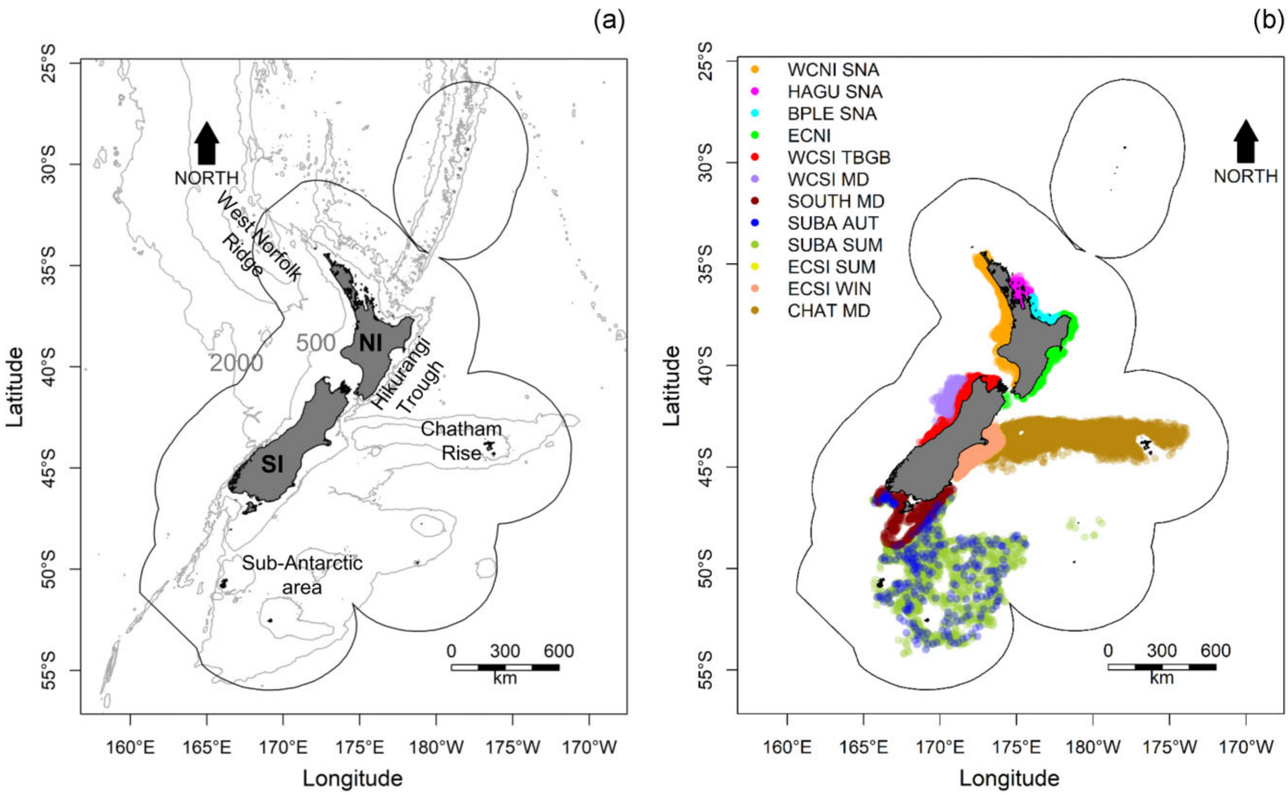

Figure 1. (a) Map of the NZ exclusive economic zone (delineated by a black line). Depth contours are labelled in 500- and 2000-m grey contours. Important features are also labelled and include NZ's North Island (NI), NZ's South Island (SI), the West Norfolk Ridge, the Hikurangi Trough, the Chatham Rise, and the Sub-Antarctic area. (b) Spatial distribution of the NZ survey data used in this study, which come from 12 different surveys (Table 1).

tion (e.g. due to poor gear performance). For these reasons, we enhanced the *trawl* database with additional tables that (1) identify the records that are valid for biomass estimation and can, therefore, be retained in our analyses; and (2) classify the valid records into individual surveys that were carried out in similar geographic areas, using similar designs and protocols, and that generally shared the same core stratification for the survey design, with consistent vessel and trawl gear throughout. Thus, we worked with a total of 12 NZ survey series in this study (Table 1 and Figure 1). The data collected in the 12 survey series were cleaned using procedures that are standard in NZ (Appendix 2). Over all 12 research survey series, our cleaned survey datasets for spiny dogfish and javelinfish included records for 10208 and 10833 hauls, respectively (Supplementary Figure S3). For both species, the Chatham Rise middle depth (CHAT MD) trawl survey was the survey with the largest sample size.

The observer data collected onboard commercial trawlers were extracted from the FNZ database *cod* (Sanders and Fisher, 2020). The *cod* database gathers the catch and effort (confidential) information for observed commercial fishing vessels that has been collected within the FNZ observer programme since 1986, as well as the age, length, and biological information collated by observers. Similar to the survey data, we cleaned the data collected onboard bottom trawlers over the period 1991–2021 employing procedures that are standard in NZ (Appendix 2). Our cleaned observer datasets for spiny dogfish and javelinfish included records for 127957 and 126768 hauls, respectively (Supplementary Figure S3). In addition to being much more numerous than the survey data,

Table 2. Areas of the NZ exclusive economic zone for which indices of relative biomass were produced in this study.

Area of the NZ exclusive economic zone for which indices of relative biomass were produced	Species for which indices were produced	Research survey encompassing the area
West Coast North Island (WCNI)	Spiny dogfish (*S. acanthias*)	West Coast North Island inshore trawl survey
West Coast South Island and Tasman/Golden Bays (WCSI TBGB)	Spiny dogfish	Inshore trawl survey of the West Coast South Island and Tasman/Golden Bays
West Coast South Island middle depth area (WCSI MD)	Spiny dogfish	West Coast South Island Tangaroa middle depth survey
Sub-Antarctic middle depth area (SUBA)	Spiny dogfish, javelinfish (*L. denticulatus*)	Sub-Antarctic summer middle depth trawl survey
East Coast South Island (ECSI)	Spiny dogfish	Winter inshore trawl survey of the East Coast South Island
Chatham Rise middle depth area (CHAT MD)	Spiny dogfish, javelinfish	Chatham Rise middle depth trawl survey

the observer data also covered a much larger fraction of the NZ exclusive economic zone (EEZ), e.g. deeper waters (>500-m depth) of the northern part of the EEZ.

Before fitting VAST models, we constructed prediction grids for the study species using the methodology of Grüss *et al.* (2018). First, we generated a 10 × 10 km spatial grid for the NZ EEZ. Second, using all the encounter data for spiny dogfish and javelinfish from the original *trawl* and *cod* databases (collected with a bottom trawl or other gears), we determined the longitudinal, latitudinal, and depth ranges of each species. The depth data employed in this step came from Mitchell *et al.* (2012). Third, based on the calculated longitudinal, latitudinal, and depth ranges of the study species, we subsetted the 10 × 10 km spatial grid for the NZ EEZ to obtain a 10 × 10 km prediction grid for spiny dogfish and another one for javelinfish. The prediction grids were used to define the spatial distribution of knots in VAST and produce density maps from the outputs of the models, and they were further subsetted to obtain indices for specific areas of the NZ EEZ (see below).

For both spiny dogfish and javelinfish, we developed three different VAST models and compared the predictions of the three models. The three different models were fitted to (1) the data collected by the 12 survey series (survey-only data); (2) observer-only data; or (3) both survey and observer data (integrated data). The data were biomass catch rate data in $\mathrm{kg\,km^{-2}}$ in all cases. In all models, spatio-temporal variation was modelled as an AR1 process [Equation (3)], because the spatial distribution of sampling has changed substantially over time for both the surveys and the observer program. In the models fitted to survey-only and integrated data, the monitoring program catchability factor included, respectively, 12 levels (for the 12 survey series) and 13 levels (for the 12 survey series plus the observer program) (Equation 4). The monitoring program effect $\delta(m)$ was set to zero for the CHAT MD survey in both models. In all models (as well as for the simulation experiment described below), $n_x = 200$ knots were distributed uniformly over the prediction grid of the species of interest (Supplementary Figure S4), and biomass densities were predicted across 2000 grid cells covering that prediction grid (Grüss *et al.*, 2020). We first mapped the spatial patterns of log density of the two study species and their associated standard errors (SEs). To obtain SEs, we (1) drew 1000 samples from the predictive distributions by sampling from the joint distribution of fixed and random effects (Goodman *et al.*, 2022); and (2) computed SEs for log-density estimates from the 1000 samples. In addition to generating log-density maps for the two study species, we processed the outputs of the VAST models to produce annual indices for specific areas of the NZ EEZ. These specific geographic areas correspond to the spatial footprint of some of the individual surveys (Table 2). These areas were chosen because they are relevant to the management of spiny dogfish and javelinfish. The SEs and, therefore, the 95% confidence intervals around all VAST indices for specific areas of the NZ EEZ were calculated using the generalized delta method implemented in TMB (Kass and Steffey, 1989). The VAST indices for the specific areas of the NZ EEZ were compared to the indices computed directly from survey-only data with the *SurvCalc* software (Francis, 2009).

Simulation experiment

In addition to the demonstration, we carried out a simulation experiment using the integrated spatio-temporal model for spiny dogfish fitted above (which employs the SPDE-Barrier model) as the operating model (OM), in order to further evaluate the performance of our modelling framework. Javelinfish was not considered in the simulation experiment primarily because the spatio-temporal model using survey-only data did not converge for this species (see the "Results" section). The simulation experiment consisted of (1) employing a simulator that generates new values of random effects conditional on the maximum likelihood estimates (MLEs) for fixed effects estimated by the OM and then produces simulated data conditional upon fixed and random effect values; (2) considering that the indices derived from simulated data represent "true indices"; (3) fitting alternative estimation models (EMs) to the simulated data, resulting in alternative estimated indices; and (4) comparing the estimated indices (obtained from the EMs) to the true indices (obtained from the simulated data) using performance metrics to evaluate the bias, error, and confidence interval coverage of the indices estimated by the alternative EMs. The alternative EMs were fitted to integrated simulated data vs. simulated survey-only data and considered physical barriers (i.e. used the SPDE-Barrier model) or not (i.e. used the SPDE model).

The simulation experiment was conducted with the "self-test simulator" included in the R package VAST (Thorson, 2019), which has already been employed in previous studies in a similar manner as in the present study to compare the performance of VAST models under alternative scenarios (e.g. Grüss and Thorson, 2019; Charsley *et al.*, 2023). In the present study, four scenarios were considered (integrated data + SPDE-Barrier model; survey-only data + SPDE-Barrier model; integrated data + SPDE model; and survey-only data + SPDE model), and 100 simulations were conducted with the self-test simulator for each of these four sce-

Table 3. In-water spatial range (the distance at which two observations can be considered to be effectively independent, in km) estimated by the first and second linear predictors of the VAST models fitted in this study.

Species	VAST model	In-water spatial range estimated by the first linear predictor (km)	In-water spatial range estimated by the second linear predictor (km)
Spiny dogfish (*S. acanthias*)	Fitted to survey-only data	222	218
	Fitted to observer data	176	135
	Fitted to integrated data	185	151
Javelinfish (*L. denticulatus*)	Fitted to observer data	156	120
	Fitted to integrated data	159	132

narios. The estimated indices (obtained from the EMs) were for the NZ areas listed in Table 2 and were compared to the true indices (obtained from the OM) for the same areas. Note that the EM under the first scenario (integrated data + SPDE-Barrier model) is the OM but re-estimated using the simulated data generated by the self-test simulator, with the goal to further understand the performance of our integrated spatiotemporal model employing the SPDE-Barrier model.

The following performance matrices (detailed in Appendix 5) were calculated to compare the performance of the four alternative EMs: (1) a bias metric indicating whether changes in the true index are accurately estimated (the closer to 1, the better; Thorson *et al*., 2015a); (2) root mean squared error (the lower, the better; Stow *et al*., 2009); and (3) coverage for a 50% confidence interval (henceforth usually "coverage"; the closer to 50%, the better; Bolker, 2008). Coverage is the percentage of years that the 50% confidence interval of an estimated index contains the "true" index. If coverage values are greater (smaller) than 50%, confidence intervals are too wide (too narrow; Bolker, 2008).

Results

For spiny dogfish, the three models (fitted to survey-only, observer-only, or integrated data) converged, most likely because there was no strong spatial imbalance in both the survey and the observer encounter data for the species (Supplementary Figure S3). The in-water spatial ranges estimated by the model fitted to integrated data were more similar to the in-water spatial ranges estimated by the model fitted to observer-only data than to those estimated by the model fitted to survey-only data (Table 3), likely because there were 12.5 times more observer records than survey records for spiny dogfish.

Compared to the other models, the model fitted to survey-only data provided incomplete insights into the spatial density patterns of spiny dogfish in the NZ EEZ (Figures 2 and 3). Specifically, the model fitted to survey-only data predicted that spiny dogfish high-density areas were located only on the CHAT and on the west and east coasts of the SI. By contrast, the models fitted to observer-only or integrated data predicted that spiny dogfish high-density areas are also found in the Sub-Antarctic area, the southern part of the west coast of the NI, and the West Norfolk Ridge (Figures 2 and 3).

Indices were generated for six specific NZ areas that are relevant to the management of spiny dogfish (Figure 4 and Supplementary Figure S6). For all NZ areas, the indices produced with the three models displayed the same signal. For all NZ areas, the indices resulting from survey-only data were more uncertain and, as expected, agreed more with the traditional stratified random (SurvCalc) indices, while the indices resulting from observer-only data tended to show larger interannual variability. Finally, for all NZ areas, integrating survey and observer data resulted in indices that (1) were less uncertain than when survey-only data were employed; and (2) displayed less interannual variability and agreed more with SurvCalc indices than when observer-only data were used (Figure 4 and Supplementary Figure S6). The index predicted for the CHAT MD area with observer-only data showed some very large interannual variability at the end of the time series that was highly uncertain and dubious. Integrating survey and observer data corrected a lot for this issue, yet the value predicted for 2019 remained potentially questionable (Figure 4).

For javelinfish, only the models fitted to observer-only or integrated data converged. The model fitted to survey data did not converge most likely because the survey encounter data for javelinfish were very spatially imbalanced; importantly, survey series did not provide any encounter data for javelinfish for a large fraction of the NZ EEZ located north and northwest of New Zealand's NI (Supplementary Figure S3). For both the first and the second linear predictors, the in-water spatial ranges estimated for javelinfish were smaller than those estimated for spiny dogfish (Table 3). Moreover, for javelinfish, the in-water spatial ranges estimated by the models fitted to observer-only and integrated data were similar (Table 3).

Both the models fitted to observer-only or integrated data predicted that javelinfish high-density areas are found in the Sub-Antarctic area, the Chatham Rise, and the Hikurangi Trough area (Figure 5). For javelinfish, indices were generated for two specific NZ areas that are relevant to the management of the species (Figure 6 and Supplementary Figure S7). For both NZ areas, the indices derived from integrated data displayed less interannual variability, were less uncertain, and tended to be in better agreement with the SurvCalc indices (Figure 6 and Supplementary Figure S7).

The simulation experiment conditioned on the MLEs for spiny dogfish confirmed that integrating survey and observer data resulted in more complete insights into fish spatial density patterns (Supplementary Figure S8) and more precise indices (Figure 7 and Supplementary Figure S9). The simulation experiment also revealed that bias and error in indices were reduced when using integrated data rather than survey-only data (Figure 8 and Supplementary Figure S10). Moreover, the indices resulting from integrated data had a smaller coverage than the indices resulting from survey-only data. Specifically (1) the uncertainty around the indices was underestimated when integrated data were employed, but overestimated when survey-only data were used; or (2) the uncertainty around the indices was underestimated both when integrated or survey-only data were employed, but uncertainty was better characterized when survey-only data were used (Figure 8 and Supplementary Figure S10). Finally, the simulation exper-

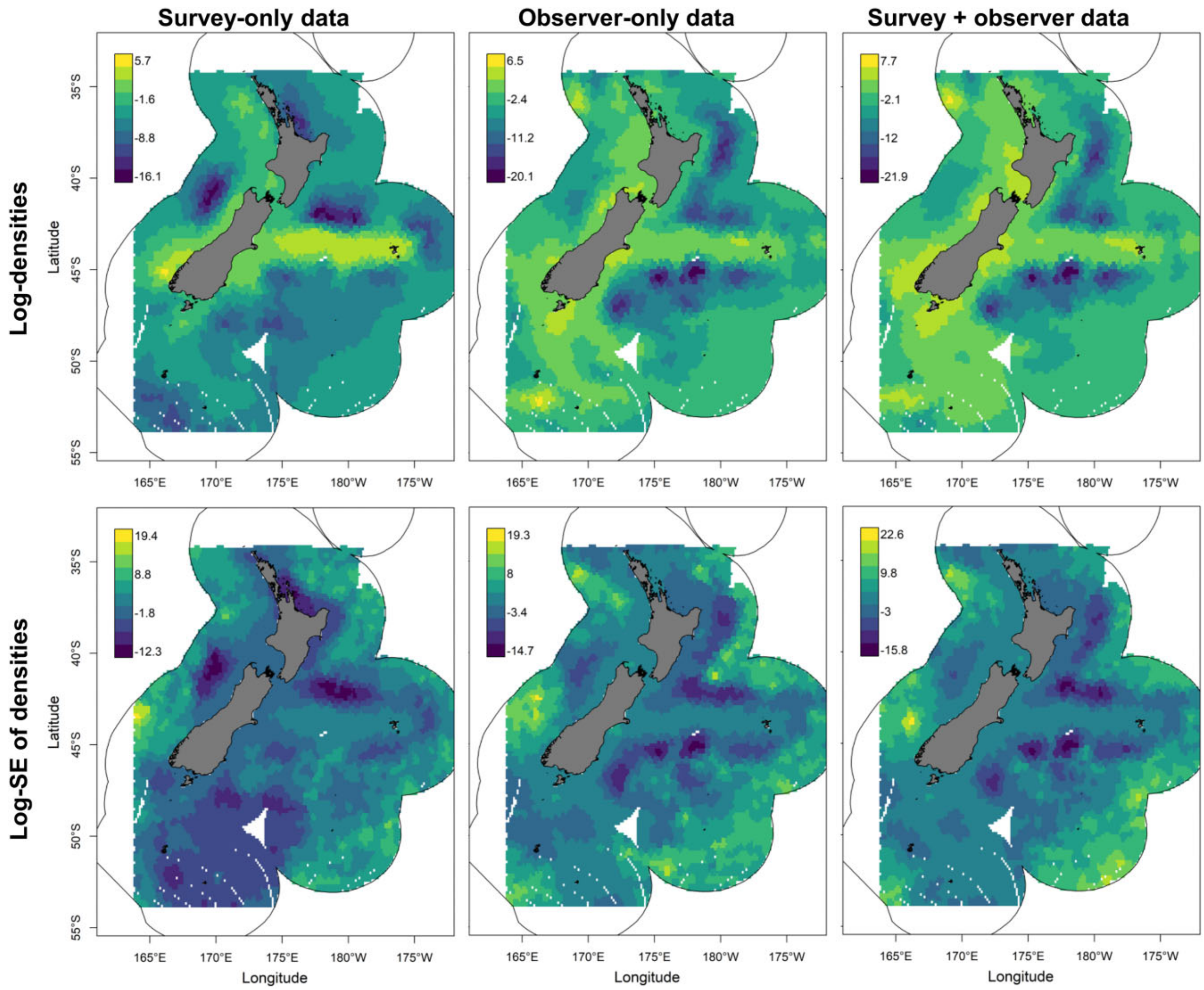

Figure 2. Mean spatial patterns of log-density over the period 1991–2021 (log-kg km^{-2}; top panels) and their associated SEs (bottom panels), predicted by the VAST models for spiny dogfish (*S. acanthias*) fitted to survey-only data (left panels); observer-only data (middle panels); or both survey and observer data (right panels).

iment revealed virtually no differences when physical barriers were accounted for or not in models (Figures 7–8 and Supplementary Figures S7–S10).

Discussion

Here, we presented and demonstrated an integrated spatio-temporal modelling framework that accounts for physical barriers in the estimation of spatial and spatio-temporal variation. The spiny dogfish and javelinfish applications highlighted the utility of our integrated modelling framework in providing density maps for a broad region (the NZ EEZ in this study) and reliable indices for specific geographic areas (specific NZ areas in this study). The javelinfish application also highlighted one large benefit of integrated SDMs, which is to allow for model convergence when SDMs fitted to one single data source fail. However, our applications and simulation experiment also confirmed that, while integrated SDMs constitute valuable tools by leveraging the strengths of different data sources, they are not necessarily preferable to SDMs fitted to one single data source in all situations (Isaac *et al.*, 2020; Simmonds *et al.*, 2020).

The spiny dogfish application corroborated previous studies (Grüss and Thorson, 2019; Rufener *et al.*, 2021) in that the benefits of integrated models in terms of better spatial density predictions are more straightforward than their ability to produce better indices. Using integrated data rather than survey-only data allowed for comprehensive insights into the spatial density patterns of spiny dogfish in the NZ EEZ, which concur with those reported in the literature (Hanchet, 1986; Bagley *et al.*, 2000) and knowledge of experts of the species (O. Anderson and R. O'Driscoll, pers. comm.). Regarding indices, those obtained with integrated data were less uncertain than those with survey-only data and showed less interannual variability than those with observer-only data. In addition, by sharing information across data sources, sites, and years, our integrated spatio-temporal model can provide indices for NZ areas for which survey data or SurvCalc indices are not available (e.g. areas off the northeast coast of the NI in the case of spiny dogfish). However, our results for spiny dogfish indicated that, for the Chatham Rise middle depth area,

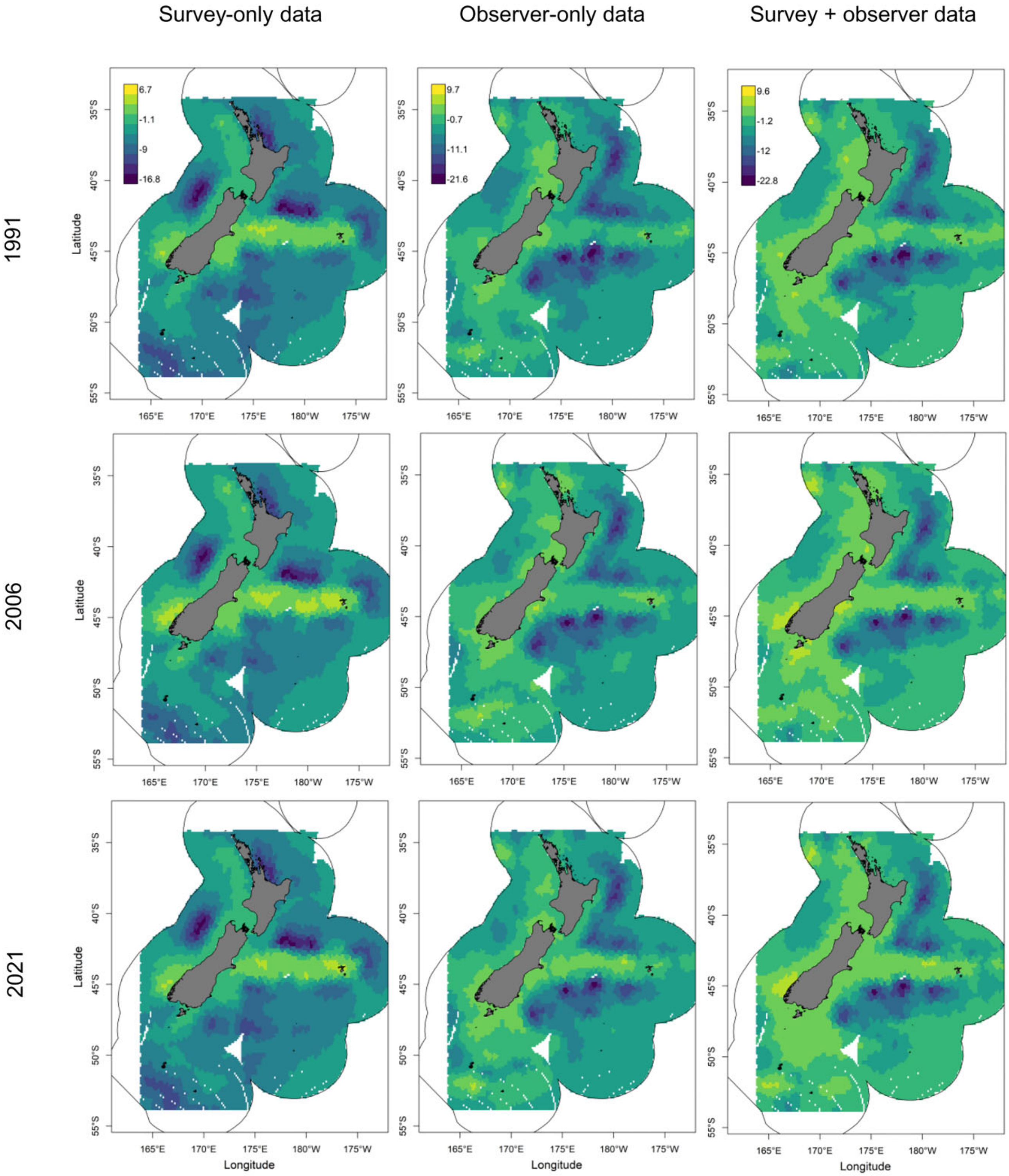

Figure 3. Spatial patterns of log-density (log-kg km^{-2}) in select years (1991, 2006, and 2021) predicted by the VAST models for spiny dogfish (*S. acanthias*) fitted to survey-only data (left panels); observer-only data (middle panels); or both survey and observer data (right panels).

one may have more confidence in the index generated with survey-only data than in the index generated with integrated data. The CHAT MD survey provides a very consistent time series, such that integrating the CHAT MD survey data with observer data is not warranted and results in an index in which the large interannual variability at the end of the time series may be questionable. Previous studies (Fletcher *et al.*, 2019; Thompson *et al.*, 2022) also reported the absence of benefits of data integration when one single survey dataset already provides ample information. We conclude that, if enough survey data are available, scientists should (1) fit models to both survey-only and integrated data; and (2) for a given geographic area, ultimately choose the index produced with integrated data or the index produced with survey-only data

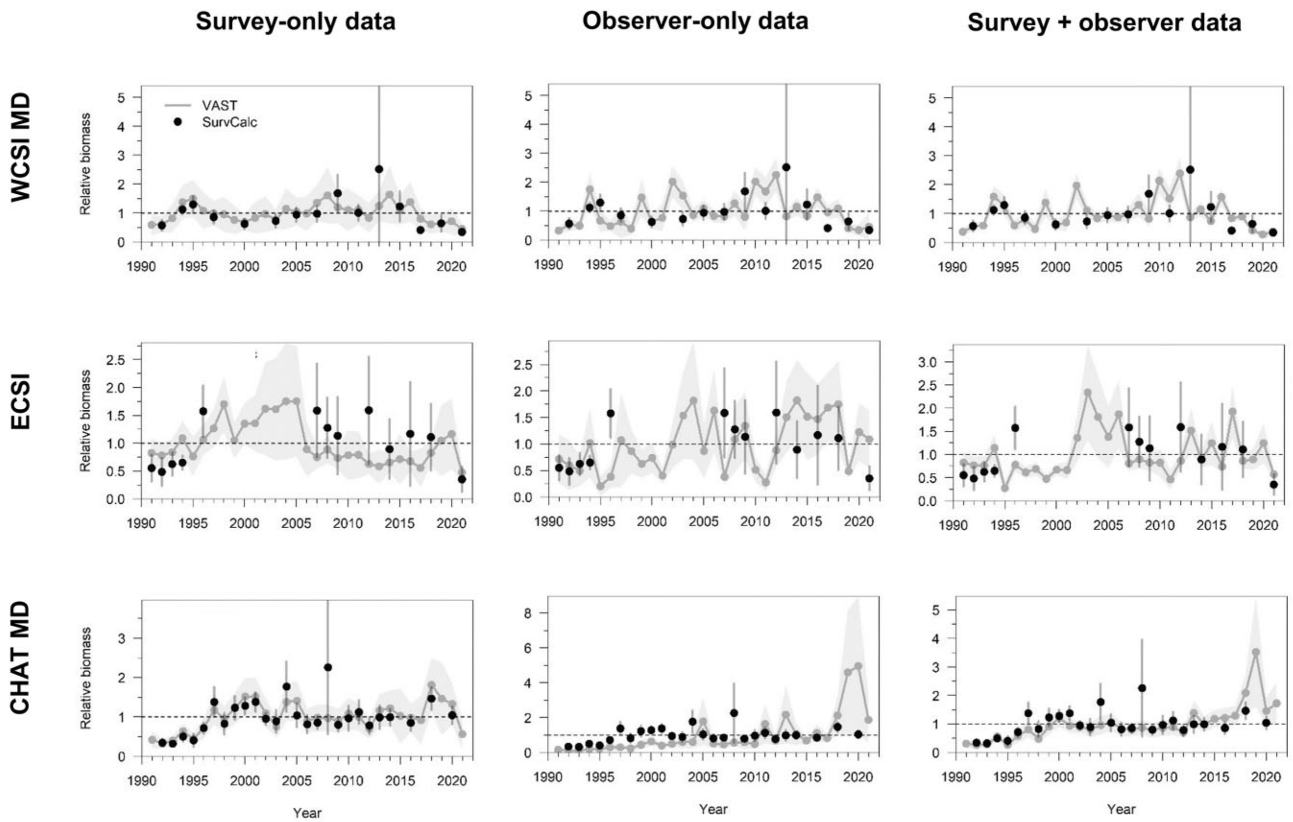

Figure 4. Indices of relative biomass for the West Coast South Island middle depth area (WCSI MD), the East Coast South Island (ECSI), and the Chatham Rise middle depth area, predicted by the VAST models for spiny dogfish (*S. acanthias*) fitted to survey-only data (left panels); observer-only data (middle panels); and both survey and observer data (right panels). Also shown are the traditional stratified random (SurvCalc) indices of relative biomass obtained from survey data (for years in which surveys were carried out). In all panels, the shaded areas represent 95% confidence intervals around VAST predictions, while vertical bars represent 95% confidence intervals around SurvCalc indices of relative biomass.

based on the reliability of the interannual variability of the index.

The simulation experiment confirmed that integrating survey and observer data resulted in more accurate spatial density predictions and more precise indices. The simulation experiment also indicated that integrating survey and observer data led to a reduction in bias and error in indices, consistent with the simulation experiment carried out in Grüss and Thorson (2019). On the other hand, the simulation experiment conducted in this study yielded a result that was unexpected *a priori*, which was that integrating survey and observer data did not improve confidence interval coverage, i.e. did not improve the characterization of uncertainty around the estimated indices. More specifically, the simulation experiment revealed that our integrated model was less conservative than the model using survey-only data in terms of uncertainty characterization and greatly underestimated uncertainty around the estimated indices. The consequence of this result is that, for a given geographic area, the ultimate choice between an index generated with integrated data and an index generated with survey data should be based more on the plausibility of the interannual variability of the index than on the uncertainty around that index. We recommend that future studies seeking to obtain indices explore ways to downweight the influence of the observer data in the integrated model, e.g. by defining survey data as reference data while estimating the spatially varying catchability of the observer program (Thorson *et al.*, 2023; Grüss *et al.*, 2023b).

Another unexpected result of the simulation experiment was that accounting for physical barriers in the estimation of spatial and spatio-temporal variation had virtually no impact on the accuracy, error, and confidence interval coverage of the indices estimated with our NZ spatio-temporal model. This result is not specific to the SPDE-Barrier model but rather to our NZ EEZ application, and is due to the large extent of our study region (Supplementary Figure S4) combined with the absence of geophysical considerations in our implementation of the SPDE-Barrier model. This result echoes some of the findings of the generalized additive mixed modelling study of Augustin *et al.* (2013), which employed a similar barrier model, namely the soap film smooths from Wood *et al.* (2008). While Augustin *et al.* (2013) reported a decrease in root mean squared prediction error (RMSPE) with the use of the soap film smooths instead of standard thin plate regression splines, that decrease in RMSPE was small. To gain more insights into the performance of the SPDE-Barrier model in VAST, we recommend that future studies evaluate the consequences of employing the SPDE-Barrier model vs. the classical SPDE model in VAST for regions where physical barriers (islands and/or convoluted coastlines) represent a much larger fraction of the system (e.g. the Baltic Sea, the inshore domain of the US Gulf of Mexico). Moreover, future research should attempt to integrate geophysical considerations into the SPDE-Barrier model.

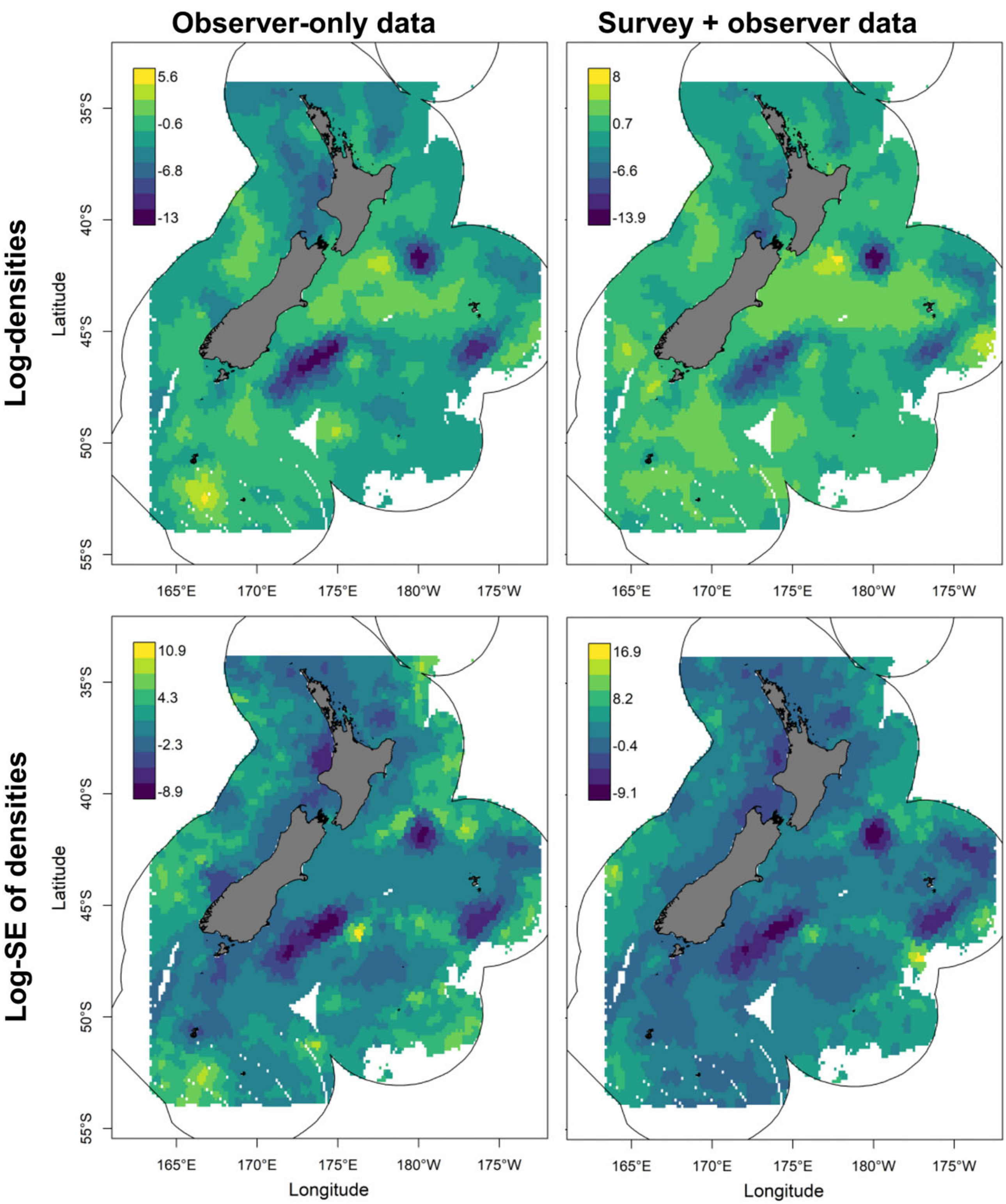

Figure 5. Mean spatial patterns of log-density over the period 1991–2021 (log-kg km^{-2}) and their associated standard errors (SEs), predicted by the VAST models for javelinfish (*L. denticulatus*) fitted to observer-only data (left panels); or both survey and observer data (right panels). Note that the VAST model fitted to survey-only data did not converge, most likely because the survey data for javelinfish were very spatially imbalanced.

For example, for island regions such as the Hawaiian Islands archipelago, future studies could develop an SPDE-Barrier model that has differential decorrelation strength for land-based barriers and deep channels between islands. In this implementation, the channel barrier decorrelation strength could be a function of maximum channel depth or average current speed through the channel (N. Ducharme-Barth, pers. comm.).

The demonstration in this study was for two bycatch species in NZ deepwater species and did not require the inclusion of density covariates X_n or X_w or catchability covari-

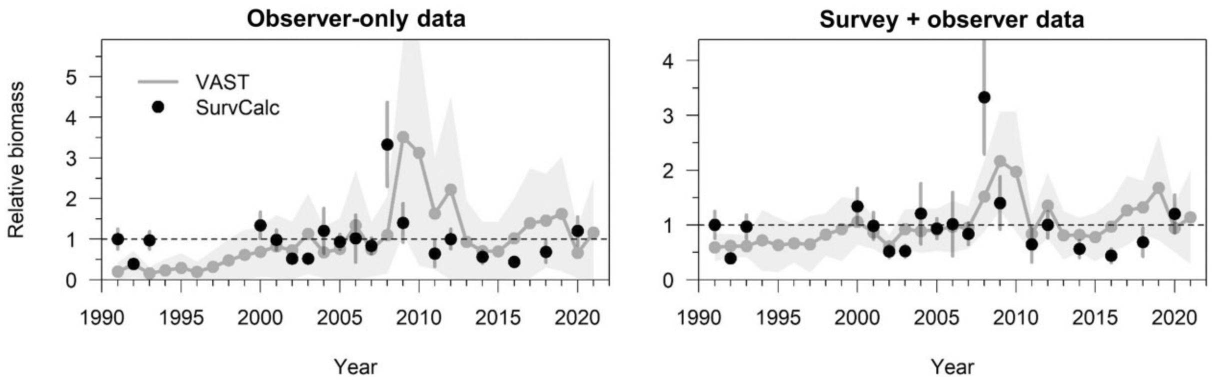

Figure 6. Indices of relative biomass for the Sub-Antarctic middle depth area (SUBA) predicted by the VAST models for javelinfish (*L. denticulatus*) fitted to observer-only data (left panel); and both survey and observer data (right panel). Also shown are the traditional stratified random (SurvCalc) indices of relative biomass obtained from survey data (for years in which surveys were carried out). In all panels, the shaded areas represent 95% confidence intervals around VAST predictions, while vertical bars represent 95% confidence intervals around SurvCalc indices of relative biomass. Note that the VAST model fitted to survey-only data did not converge, most likely because the survey data for javelinfish were very spatially imbalanced.

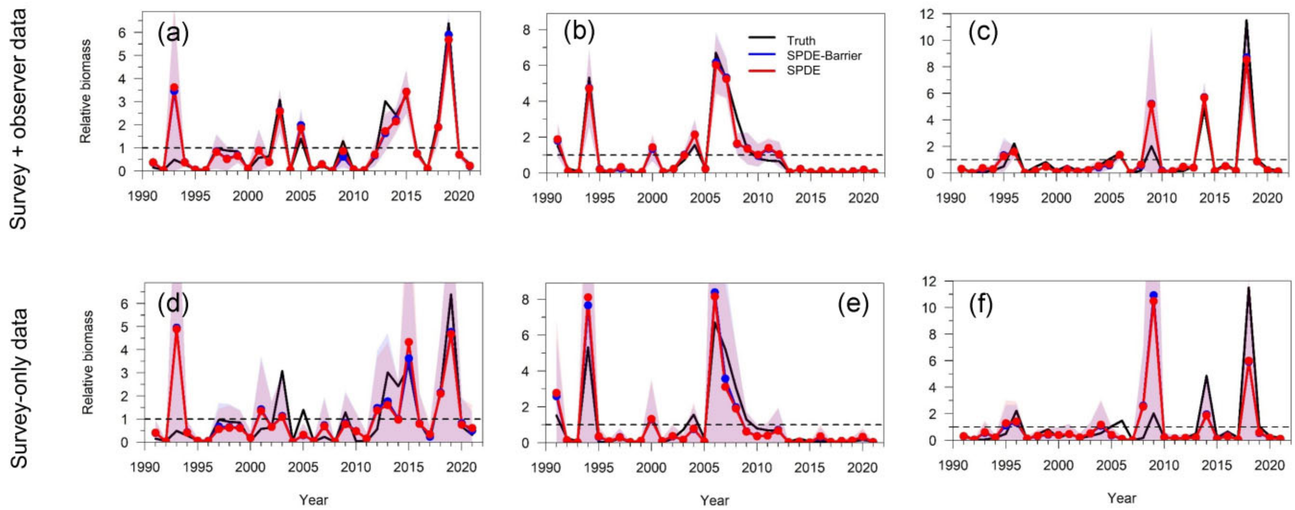

Figure 7. Indices of relative biomass for the West Coast North Island (WCNI) estimated in three replicates (columns) of the simulation experiment. The indices of relative biomass shown in top panels were estimated with VAST models fitted to both survey and observer data, while the indices of relative biomass shown in bottom panels were estimated with VAST models fitted to survey data only. In all panels, the shaded areas represent 95% confidence intervals.

ates Q_n or Q_w (i.e. catchability covariates beyond the catchability factor representing fishing-power ratios among monitoring programmes) in spatio-temporal models. The spatial and spatio-temporal variation terms in spatio-temporal models account, respectively, for latent static and latent dynamic variables that influence fish densities (Shelton *et al.*, 2014; Thorson *et al.*, 2015a; Ono *et al.*, 2018). Future studies could test the inclusion of alternative static environmental covariates (e.g. bottom depth, bottom type) and/or dynamic environmental covariates (e.g. sea temperature) in our integrated model, and determine whether this inclusion improves or degrades the spatial predictions of the integrated model (Pacifici *et al.*, 2017; Simmonds *et al.*, 2020; O'Leary *et al.*, 2022). Exploring the inclusion of dynamic environmental covariates in our model would be particularly useful given increased calls for investigations of climate change impacts on fish and fisheries, including in NZ (Pinkerton, 2017). Evaluating the impacts of including bottom depth in our model would also be a good idea, because this variable has been found to explain a fair percentage of the deviance in the data in many SDM studies as it encompasses many diverse environmental features (Elith and Leathwick, 2009; Grüss *et al.*, 2016).

Moreover, the models that we fitted to observer-only or integrated data in this study included a random vessel effect that substituted any explicit catchability covariates. Such a model structure is appropriate to account for catchability differences between vessels, particularly so when the fish stocks of interest are bycatch species rather than species targeted by fishing vessels (Pennino *et al.*, 2016; Xu *et al.*, 2019; Rufener *et al.*, 2021). That being said, it remains preferable to include explicit catchability covariates in addition to a random vessel effect in models that rely on fisheries-dependent data, as a vessel effect most likely encompasses a lot but not all the factors affecting the catchability of the stock of interest (Grüss *et al.*, 2023c). Recently, two modelling studies (Rufener *et al.*, 2021; Alglave *et al.*, 2022) integrated survey with fisheries-dependent data for species targeted by fishing (observer data in Rufener *et al.* 2021 and commercial data in Alglave *et al.* 2022). In addition to including a monitoring program catchability effect or a random vessel effect, the two integrated modelling studies

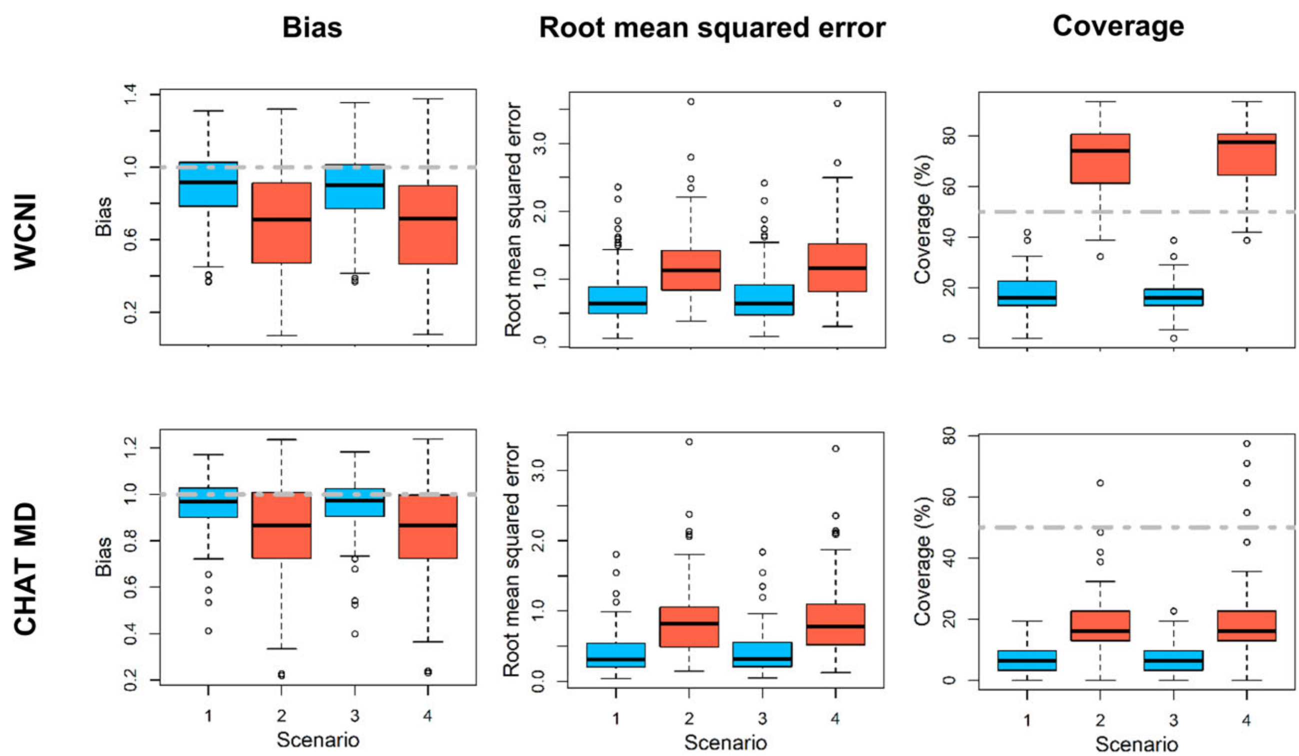

Figure 8. Bias (the closer to , the better), root mean squared error (the lower, the better), and coverage (in %; the closer to 50%, the better) of the indices of relative biomass estimated with VAST models for the West Coast North Island (WCNI; top panels) and the the Chatham Rise middle depth area (CHAT MD; bottom panels) within the simulation experiment. The VAST models in Scenarios 1 and 2 used an SPDE-Barrier model to estimate the spatial dependency between data points, while the VAST models in Scenarios 3 and 4 used an SPDE model. Moreover, the VAST models were fitted to both survey and observer data in Scenarios 1 and 3 (blue boxplots), while they were fitted to survey data only in Scenarios 2 and 4 (red boxplots).

also accounted for preferential sampling (the likely correlation between sampling locations and fish abundance) for the fisheries-dependent data, which was modelled as an inhomogeneous Poisson point process. However, Rufener *et al.* (2021) found that, when the fisheries-dependent data that are integrated with survey data are observer data, accounting for preferential sampling does not improve the integrated model and does not alter parameter estimates. We recommend further research regarding when to account for preferential sampling in either targeted or bycatch species.

We also envision several other avenues for future research. First, individual research surveys are typically restricted to a few months of the years (Pennino *et al.*, 2016; Bourdaud *et al.*, 2017; Webster *et al.*, 2020), which is the case in NZ. In this context, expanding our integrated modelling framework into a seasonal integrated spatio-temporal modelling framework (Thorson *et al.*, 2020) would allow for the borrowing of information across data sources, sites, and years but also across seasons, thereby likely further improving the performance of the integrated model. Second, we used only one data type in the present study (biomass-sampling data), while other data types, including counts and encounters/non-encounters, are provided by monitoring programmes (e.g. count data are collected by observers placed onboard commercial longliners in NZ). In addition, while the plentiful presence-only observations that are collected opportunistically (e.g. through a tagging study or by citizen scientists) are very often tapped into in terrestrial integrated modelling studies, they remain underused in fisheries science. Therefore, we encourage future studies to leverage more datasets by modifying our integrated modelling framework so that it can accommodate multiple data types (biomass sampling, counts, encounters/non-encounters, but also presence-only data), similar to what was achieved in Grüss and Thorson (2019). Third, the survey and observer data that were employed in this study were for the same time period (1991–2021), yet fisheries-dependent monitoring programmes usually provide a longer time series than individual research surveys (Lunn and Dearden, 2006; Pennino *et al.*, 2016). Therefore, future applications of our integrated modelling framework will likely rely on more years of data in the fisheries-dependent dataset than in the survey dataset, thereby demonstrating the ability of integrated models to also provide stock assessments with one single index rather than multiple indices for different time periods (e.g. several indices derived from different research surveys and an index derived from the catch rate data reported by fishing vessels). We encourage future studies to evaluate the impacts of using one single index produced from integrated data vs. multiple indices derived from individual survey and/or fisheries-dependent datasets in the stock assessment models of the species of interest (Peterson *et al.*, 2021). Fourth, future studies could investigate the consequences of varying the sample size of survey data relative to that of observer data, similar to what was done in Alglave *et al.* (2022). Finally, we recommend the development of a metric summarizing the effective degrees of freedom calculated using the Laplace approximation via TMB or similar tools. This would then allow scientists to compare the flexibility of spatio-temporal smoothers between alternative model structures.

Our modelling framework employs the Poisson-link Delta–Gamma distribution model to accommodate the large number of zeros typically found in fish catch rate datasets, as has been generally done in VAST papers since Thorson (2018). The Poisson-link Delta–Gamma distribution model makes the assumption that encounter probabilities and expected positive catches are correlated in a way that is approximated by a Poisson process (Thorson, 2018). This assumption is reasonable for species such as spiny dogfish and javelinfish, but may not be so for species whose individuals form tight aggregations (e.g. schools, shoals, clusters). For such species, the Tweedie distribution seems more appropriate (Peel *et al.*, 2013). A recent study (Thorson *et al.*, 2021) found that the Poisson-link Delta–Gamma distribution model and the Tweedie distribution model resulted in a similar scale for VAST-based indices as design-based indices for 20 fish stocks of Alaska, which included species that form aggregations. That being said, we encourage future research considering multiple stocks worldwide to better understand whether and when it is reasonable to use the Poisson-link Delta–Gamma distribution model rather than the Tweedie model for species whose individuals form tight aggregations.

In conclusion, this study confirmed the usefulness of integrated spatio-temporal models, which can provide distribution/density maps for broad geographic areas to assist habitat management (e.g. marine spatial planning, essential fish habitat designation when working with data for specific fish life stages) and indices of relative biomass/abundance for fish stocks and substocks to inform fisheries management. A key result of this study is that, for a given fish stock or substock for which enough survey data are available, fisheries scientists should (1) develop both integrated models and models relying on survey-only data; and (2) choose the index produced with integrated data or the index produced with survey-only data based on the reliability of the interannual variability of the index. Integrated SDMs are powerful tools and we hope to see their more widespread use in fisheries science to support resource management, as well as investigations of climate change impacts on fish and fisheries.

Acknowledgements

Foremost, we express our gratitude to the scientists and the scientific observers who collected the data employed in the present study and to Fisheries New Zealand (FNZ) for letting us use the data, as well as to Darren Parsons and Jennifer Devine (NIWA) and the Aquatic Environment Working Group (AEWG) for very helpful discussions and feedback on our research. We also wish to thank very much Jeremy Yeoman and Shaun Carswell (NIWA) for assistance with the survey and observer databases, Sira Ballara and Dan MacGibbon (NIWA) for providing us with SurvCalc indices for the present study, and Nicholas Ducharme-Barth (NOAA's PIFSC) for his personal communication. The RDM Team from FNZ is also thanked very much for their evaluation of our paper. Finally, we are very grateful to two internal reviewers (Dan Ovando and Brad Moore), the editor, and three anonymous journal reviewers whose comments have dramatically improved the quality of our manuscript. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the Department of Commerce.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of Interest

The authors have no conflict of interest to declare.

Author contributions

AG, ARC, JTT, RLO, ONB, and CAL contributed to the conceptualization and methodology of the study. AG, ARC, and JTT performed the analyses. AG and RLO conducted the validation of the results. AG, OFA, and BW prepared the data for analyses. AG, ARC, JTT, OFA, RLO, ONB, and CAL wrote the manuscript.

Funding

This work was supported by NIWA Strategic Science Investment Funding.

Data availability

The research survey data are the property of Fisheries New Zealand and can be obtained via an email to rdm.sharedrdm@mpi.govt.nz. The observer data are confidential and, therefore, cannot be shared.

References

Alglave, B., Rivot, E., Etienne, M.-P., Woillez, M., Thorson, J. T., and Vermard, Y. 2022. Combining scientific survey and commercial catch data to map fish distribution. ICES Journal of Marine Science, 79: 1133–1149.

Augustin, N. H., Trenkel, V. M., Wood, S. N., and Lorance, P. 2013. Space-time modelling of blue ling for fisheries stock management. Environmetrics, 24: 109–119.

Bagley, N. W., Anderson, O. F., Hurst, R. J., Francis, M. P., Taylor, P. R., Clark, M. R., and Paul, L. J. 2000. Atlas of New Zealand fish and squid distributions from midwater trawls, tuna longline sets, and aerial sightings. NIWA Technical Report 72: 171.

Baird, S. J., and Ballara, S. L. 2022. Fishery characterisation and standardised CPUE for spiny dogfish, *Squalus acanthias*. in SPD 3, SPD 4, and SPD 5, 1989–90 to 2010–11. New Zealand Fisheries Assessment Report 2021/21. 196 p.

Bakka, H., Vanhatalo, J., Illian, J. B., Simpson, D., and Rue, H. 2019. Non-stationary Gaussian models with physical barriers. Spatial Statistics, 29: 268–288.

Bolker, B. M. 2008. Ecological Models and Data in R. Princeton University Press, Princeton, NJ.

Bourdaud, P., Travers-Trolet, M., Vermard, Y., Cormon, X., and Marchal, P. 2017. Inferring the annual, seasonal, and spatial distributions of marine species from complementary research and commercial vessels' catch rates. ICES Journal of Marine Science, 74: 2415–2426.

Brodie, S. J., Thorson, J. T., Carroll, G., Hazen, E. L., Bograd, S., Haltuch, M. A., Holsman, K. K., *et al.* 2020. Trade-offs in covariate selection for species distribution models: a methodological comparison. Ecography, 43: 11–24.

Charsley, A. R., Grüss, A., Thorson, J. T., Rudd, M. B., Crow, S. K., David, B., Williams, E. K., *et al.* 2023. Catchment-scale stream network spatio-temporal models, applied to the freshwater stages of a diadromous fish species, longfin eel (*Anguilla dieffenbachii*). Fisheries Research, 259: 106583.

Cochran, W. G. 1977. Sampling Techniques. John Wiley and Sons, New York, NY.

Dolder, P. J., Thorson, J. T., and Minto, C. 2018. Spatial separation of catches in highly mixed fisheries. Scientific Reports, 8: 1–11.

Elith, J., and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics, 40: 677–697.

Finucci, B., Edwards, C. T. T., Anderson, O. F., and Ballara, S. L. 2019. Fish and Invertebrate Bycatch in New Zealand Deepwater Fisheries from 1990–91 until 2016–17. New Zealand Aquatic Environment and Biodiversity Report 210. 77 pp.

Fithian, W., Elith, J., Hastie, T., and Keith, D. A. 2015. Bias correction in species distribution models: pooling survey and collection data for multiple species. Methods in Ecology and Evolution, 6: 424–438.

Fletcher, R. J., Hefley, T. J., Robertson, E. P., Zuckerberg, B., McCleery, R. A., and Dorazio, R. M. 2019. A practical guide for combining data to model species distributions. Ecology, 100: e02710.

Francis, R. I. I. C. 2009. SurvCalc User Manual. NIWA, Wellington. 39pp.

Goodman, M. C., Carroll, G., Brodie, S., Grüss, A., Thorson, J. T., Kotwicki, S., Holsman, K., *et al.* 2022. Shifting fish distributions impact predation intensity in a sub-Arctic ecosystem. Ecography, 2022: e06084.

Grüss, A., Yemane, D., and Fairweather, T. P. 2016. Exploring the spatial distribution patterns of South African Cape hakes using generalised additive models. African Journal of Marine Science, 38: 395–409.

Grüss, A., Thorson, J. T., Sagarese, S. R., Babcock, E. A., Karnauskas, M., Walter , J. F. III, and Drexler, M. 2017. Ontogenetic spatial distributions of red grouper (*Epinephelus morio*) and gag grouper (*Mycteroperca microlepis*) in the US Gulf of Mexico. Fisheries Research, 193: 129–142.

Grüss, A., Perryman, H. A., Babcock, E. A., Sagarese, S. R., Thorson, J. T., Ainsworth, C. H., Anderson, E. J., *et al.* 2018. Monitoring programs of the US Gulf of Mexico: inventory, development and use of a large monitoring database to map fish and invertebrate spatial distributions. Reviews in Fish Biology and Fisheries, 28: 667–691.

Grüss, A., Walter III, J. F., Babcock, E. A., Forrestal, F. C., Thorson, J. T., Lauretta, M. V., and Schirripa, M. J. 2019. Evaluation of the impacts of different treatments of spatio-temporal variation in catch-per-unit-effort standardization models. Fisheries Research, 213: 75–93.

Grüss, A., and Thorson, J. T. 2019. Developing spatio-temporal models using multiple data types for evaluating population trends and habitat usage. ICES Journal of Marine Science, 76: 1748–1761.

Grüss, A., Gao, J., Thorson, J. T., Rooper, C. N., Thompson, G., Boldt, J. L., and Lauth, R. 2020. Estimating synchronous changes in condition and density in eastern Bering Sea fishes. Marine Ecology Progress Series, 635: 169–185.

Grüss, A., Moore, B. R., Pinkerton, M. H., and Devine, J. A. 2023a. Understanding the spatio-temporal abundance patterns of the major bycatch species groups in the Ross Sea region Antarctic toothfish (*Dissostichus mawsoni*) fishery. Fisheries Research, 262: 106647.

Grüss, A., Thorson, J. T., Anderson, O. F., O'Driscoll, R., Heller-Shipley, M., and Goodman, S. 2023b. Spatially varying catchability for integrating research survey data with other data sources: case studies involving observer samples, industry-cooperative surveys, and predators-as-samplers. Canadian Journal of Fisheries and Aquatic Sciences, 10.1139/cjfas-2023-0051.[CrossRef]

Grüss, A., McKenzie, J. R., Lindegren, M., Bian, R., Hoyle, S. D., and Devine, J. A. 2023. Supporting a stock assessment with spatio-temporal models fitted to fisheries-dependent data. Fisheries Research, 262: 106649.

Guisan, A., and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters, 8: 993–1009.

Hamilton, J. D. 1994. Time Series Analysis. Princeton University Press, Princeton, NJ.

Hanchet, S. M. 1986. The distribution and abundance, reproduction, growth and life history characteristics of the spiny dogfish (*Squalus acanthias Linnaeus*) in New Zealand. PhD thesis, University of Otago, New Zealand. 292 p.

Hilborn, R., and Walters, C. J. 1992. Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty. Chapman and Hall, London, UK. 570pp.

Hsu, J., Chang, Y.-J., and Ducharme-Barth, N. D. 2022. Evaluation of the influence of spatial treatments on catch-per-unit-effort standardization: a fishery application and simulation study of Pacific saury in the Northwestern Pacific Ocean. Fisheries Research, 255: 106440.

Isaac, N. J., Jarzyna, M. A., Keil, P., Dambly, L. I., Boersch-Supan, P. H., Browning, E., Freeman, S. N., *et al.* 2020. Data integration for large-scale models of species distributions. Trends in Ecology and Evolution, 35: 56–67.

Kass, R. E., and Steffey, D. 1989. Approximate Bayesian inference in conditionally independent hierarchical models (parametric empirical Bayes models). Journal of the American Statistical Association, 84: 717–726.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. 2016. TMB: automatic Differentiation and Laplace Approximation. Journal of Statistical Software, 70: 1–20.

Lindgren, F., Rue, H., and Lindström, J. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. Journal of the Royal Statistical Society Series B: Statistical Methodology, 73: 423–498.

Lo, N. C., Jacobson, L. D., and Squire, J. L. 1992. Indices of relative abundance from fish spotter data based on delta-lognornial models. Canadian Journal of Fisheries and Aquatic Sciences, 49: 2515–2526.

Lunn, K. E., and Dearden, P. 2006. Monitoring small-scale marine fisheries: an example from Thailand's Ko Chang archipelago. Fisheries Research, 77: 60–71.

Mackay, K. A. 2020. Database documentation for the Ministry for Primary Industries Fisheries research trawl survey database trawl. In NIWA Fisheries Data Management Database Documentation Series, 82pp.

Maunder, M. N. 2004. Population viability analysis based on combining Bayesian, integrated, and hierarchical analyses. Acta Oecologica, 26: 85–94.

Maunder, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research, 70: 141–159.

Maunder, M. N., and Punt, A. E. 2013. A review of integrated analysis in fisheries stock assessment. Fisheries Research, 142: 61–74.

Maureaud, A., Frelat, R., Pécuchet, L., Shackell, N., Mérigot, B., Pinsky, M. L., Amador, K., *et al.* 2021. Are we ready to track climate-driven shifts in marine species across international boundaries?—A global survey of scientific bottom trawl data. Global Change Biology, 27: 220–236.

Miller, D. A., Pacifici, K., Sanderlin, J. S., and Reich, B. J. 2019. The recent past and promising future for data integration methods to estimate species' distributions. Methods in Ecology and Evolution, 10: 22–37.

Mitchell, J. S., Mackay, K. A., Neil, H. L., Mackay, E. J., Pallentin, A., and Notman, P. 2012. Undersea New Zealand, 1:5,000,000. NIWA Chart, Miscellaneous Series No. 92.

O'Leary, C. A., Thorson, J. T., Ianelli, J. N., and Kotwicki, S. 2020. Adapting to climate-driven distribution shifts using model-based indices and age composition from multiple surveys in the walleye pollock (*Gadus chalcogrammus*) stock assessment. Fisheries Oceanography, 29: 541–557.

O'Leary, C. A., DeFilippo, L. B., Thorson, J. T., Kotwicki, S., Hoff, G. R., Kulik, V. V., Ianelli, J. N., *et al.* 2022. Understanding transboundary stocks' availability by combining multiple fisheries-independent surveys and oceanographic conditions in spatiotemporal models. ICES Journal of Marine Science, 79: 1063–1074.

Ono, K., Ianelli, J. N., McGilliard, C. R., and Punt, A. E. 2018. Integrating data from multiple surveys and accounting for spatio-temporal correlation to index the abundance of juvenile Pacific halibut in Alaska. ICES Journal of Marine Science, 75: 572–584.

Pacifici, K., Reich, B. J., Miller, D. A., Gardner, B., Stauffer, G., Singh, S., McKerrow, A., *et al.* 2017. Integrating multiple data sources in species distribution modeling: a framework for data fusion. Ecology, 98: 840–850.

Peel, D., Bravington, M. V., Kelly, N., Wood, S. N., and Knuckey, I. 2013. A model-based approach to designing a fishery-independent survey. Journal of Agricultural, Biological, and Environmental Statistics, 18: 1–21.

Pennino, M. G., Conesa, D., Lopez-Quilez, A., Munoz, F., Fernández, A., and Bellido, J. M. 2016. Fishery-dependent and-independent data lead to consistent estimations of essential habitats. ICES Journal of Marine Science, 73: 2302–2310.

Perretti, C. T., and Thorson, J. T. 2019. Spatio-temporal dynamics of summer flounder (*Paralichthys dentatus*) on the Northeast US shelf. Fisheries Research, 215: 62–68.

Peterson, C. D., Belcher, C. N., Bethea, D. M., Driggers III, W. B., Frazier, B. S., and Latour, R. J. 2017. Preliminary recovery of coastal sharks in the south-east United States. Fish and Fisheries, 18: 845–859.

Peterson, C. D., Courtney, D. L., Cortés, E., and Latour, R. J. 2021. Reconciling conflicting survey indices of abundance prior to stock assessment. ICES Journal of Marine Science, 78: 3101–3120.

Pinkerton, M. H. 2017. Impacts of climate change on New Zealand fisheries and aquaculture. In Climate Change Impacts on Fisheries and Aquaculture: a Global Analysis, pp. 91–119. Ed. by Phillips B.F.and and Perez-Ramirez M.. Wiley-Blackwell, Hoboken, NJ.

Pinto, C., Travers-Trolet, M., Macdonald, J. I., Rivot, E., and Vermard, Y. 2019. Combining multiple data sets to unravel the spatiotemporal dynamics of a data-limited fish stock. Canadian Journal of Fisheries and Aquatic Sciences, 76: 1338–1349.

Pirtle, J. L., Shotwell, S. K., Zimmermann, M., Reid, J. A., and Golden, N. 2019. Habitat suitability models for groundfish in the Gulf of Alaska. Deep Sea Research Part II: Topical Studies in Oceanography, 165: 303–321.

Quinn, T. J., and Deriso, R. B. 1999. Quantitative Fish Dynamics. Oxford University Press, New York, NY.

Rufener, M.-C., Kristensen, K., Nielsen, J. R., and Bastardie, F. 2021. Bridging the gap between commercial fisheries and survey data to model the spatiotemporal dynamics of marine species. Ecological Applications, 31: e02453.

Sanders, B., and Fisher, D. 2020. Database documentation for the Ministry for Primary Industries Centralised Observer Database: cod. In NIWA Fisheries Data Management Database Documentation Series. 628pp.

Shelton, A. O., Thorson, J. T., Ward, E. J., and Feist, B. E. 2014. Spatial semiparametric models improve estimates of species abundance and distribution. Canadian Journal of Fisheries and Aquatic Sciences, 71: 1655–1666.

Simmonds, E. G., Jarvis, S. G., Henrys, P. A., Isaac, N. J., and O'Hara, R. B. 2020. Is more data always better? A simulation study of benefits and limitations of integrated distribution models. Ecography, 43: 1413–1422.

Stow, C. A., Jolliff, J., Jr, McGillicuddy, D., J., Doney, S. C., Allen, J. I., Friedrichs, M. A., *et al.* 2009. Skill assessment for coupled biological/physical models of marine systems. Journal of Marine Systems, 76: 4–15.

Thompson, P. L., Anderson, S. C., Nephin, J., Robb, C. K., Proudfoot, B., Park, A. E., Haggarty, D. R., *et al.* 2023. Integrating trawl and longline surveys across British Columbia improves groundfish distribution predictions. Canadian Journal of Fisheries and Aquatic Sciences,80: 195–210,.

Thorson, J. T., and Ward, E. J. 2014. Accounting for vessel effects when standardizing catch rates from cooperative surveys. Fisheries Research, 155: 168–176.

Thorson, J. T., Shelton, A. O., Ward, E. J., and Skaug, H. J. 2015a. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES Journal of Marine Science, 72: 1297–1310.

Thorson, J. T., Hicks, A. C., and Methot, R. D. 2015b. Random effect estimation of time-varying factors in Stock Synthesis. ICES Journal of Marine Science, 72: 178–185.

Thorson, J. T. 2018. Three problems with the conventional delta-model for biomass sampling data, and a computationally efficient alternative. Canadian Journal of Fisheries and Aquatic Sciences, 75: 1369–1382.

Thorson, J. T. 2019. Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST) package in stock, ecosystem, habitat and climate assessments. Fisheries Research, 210: 143–161.

Thorson, J. T., Adams, C. F., Brooks, E. N., Eisner, L. B., Kimmel, D. G., Legault, C. M., Rogers, L. A., *et al.* 2020. Seasonal and interannual variation in spatio-temporal models for index standardization and phenology studies. ICES Journal of Marine Science, 77: 1879–1892.

Thorson, J. T., Cunningham, C. J., Jorgensen, E., Havron, A., Hulson, P.-J. F., Monnahan, C. C., and von Szalay, P. 2021. The surprising sensitivity of index scale to delta-model assumptions: recommendations for model-based index standardization. Fisheries Research, 233: 105745.

Thorson, J. T. 2022. VAST model structure and user interface. https://github.com/James-Thorson-NOAA/VAST (last accessed 1 December 2022).

Thorson, J. T., Barnes, C. L., Friedman, S. T., Morano, J. L., and Siple, M. C. 2023. Spatially varying coefficients can improve parsimony and descriptive power for species distribution models. Ecography, 2023: e06510.

Warton, D. I., and Shepherd, L. C. 2010. Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. The Annals of Applied Statistics, 4: 1383–1402.

Webster, R. A., Soderlund, E., Dykstra, C. L., and Stewart, I. J. 2020. Monitoring change in a dynamic environment: spatiotemporal modelling of calibrated data from different types of fisheries surveys of Pacific halibut. Canadian Journal of Fisheries and Aquatic Sciences, 77: 1421–1432.

Wood, S. N., Bravington, M. V., and Hedley, S. L. 2008. Soap film smoothing. Journal of the Royal Statistical Society Series B: Statistical Methodology, 70: 931–955.

Xu, H., Lennert-Cody, C. E., Maunder, M. N., and Minte-Vera, C. V. 2019. Spatiotemporal dynamics of the dolphin-associated purse-seine fishery for yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Fisheries Research, 213: 121–131.

Zipkin, E. F., Inouye, B. D., and Beissinger, S. R. 2019. Innovations in data integration for modeling populations. Ecology, 100: 1–3.

Handling editor: Sam Subbey

Received: 21 February 2023; **Revised:** 13 July 2023; **Accepted:** 31 July 2023