



# Fine-scale spatial variation of northern shrimp and Atlantic cod across three Norwegian fjord systems and implications for management

Fabian Zimmermann<sup>a,\*</sup>, Jessica Tengvall<sup>b</sup>, Hans Kristian Strand<sup>c</sup>, Kjell Nedreaas<sup>d</sup>, Trude H. Thangstad<sup>d</sup>, Berengere Husson<sup>d</sup>, Guldborg Søvik<sup>d</sup>

<sup>a</sup> Institute of Marine Research, Frantsenteret, Postboks 6606, Stakkevollan, 9296, Tromsø, Norway

<sup>b</sup> Department of Biological Science, University of Bergen, Postbox 7803, Bergen, Norway

<sup>c</sup> Institute of Marine Research, Holmfjord Field Station, Postboks 146, Lakselv, Norway

<sup>d</sup> Institute of Marine Research, Postboks 1870, Nordnes, 5817, Bergen, Norway

## ARTICLE INFO

### Keywords:

Fisheries management  
Ecosystem dynamics  
Marine resources  
Pandalid shrimp  
Atlantic cod

## ABSTRACT

The spatial complexity of coastal ecosystems represents a challenge for the management of inshore resources. Here we compared two large fjord systems in northern Norway that have been closed for all bottom trawling for 50 years to a fjord with continuous shrimp fishery with bottom trawls. No significant differences were found between fjords with and without commercial trawling in population density and stock composition of northern shrimp (*Pandalus borealis*) and their main predator, Atlantic cod (*Gadus morhua*). Shrimp density was instead linked with bottom depth, while shrimp size and stage composition as well as cod density were explained by seasonal effects and shrimp density. For shrimp, a large degree of the observed variation was captured by spatial correlation that could not be explained by other covariates. The results underline the complex ecology in heavily structured coastal habitats and indicate that coastal shrimp dynamics are shaped by an interplay of multiple ecological and environmental drivers, possibly in concert with local genetic adaptations. The substantial fine-scale spatial variation adds to the challenges of assessing and managing fisheries resources in these fjord ecosystems. Because shrimp are an important forage species, notably as prey for cod, there are potential management conflicts between rebuilding cod stocks and reopening closed shrimp trawling areas.

## 1. Introduction

Restricting fisheries access to areas is an important management tool, especially in inshore areas, often aimed at protecting key habitats such as spawning grounds or nursery areas to bolster the resilience and productivity of marine resources (Fogarty and Botsford, 2007). However, the track record of spatial regulation is mixed, partly because of often unclear or conflicting management objectives and varying levels of implementation and enforcement (McCook et al., 2010; Rassweiler et al., 2012). Furthermore, many different management tools have been summarized under the umbrella terms spatial regulation and marine protected areas (MPAs), ranging from restricting specific fishing gears to complete bans of resource extraction and other harmful activities. Selecting the right management tool for a specific management target is therefore crucial, i.e. the type, area and restrictiveness of spatial regulation depend ultimately on whether the objective is to benefit fisheries, conserve species or habitats, or boost tourism and recreational activities.

Given appropriate design and enforcement, closing areas for fishing has shown to increase biomass and reverse demographic truncation within the protected area (Edgar et al., 2014; Fenberg et al., 2012; Guidetti et al., 2014; Halpern, 2003). Benefits for conservation and restoration are therefore well established, especially for relatively localized populations (Knutsen et al., 2022) or demographic structure and life-history traits (Dimarchopoulou et al., 2018; Sørtdalen et al., 2022), whereas effects of MPAs diminish with higher mobility of species (Hilborn et al., 2004). Additionally, spillover effects from protected areas are often difficult to quantify (Di Lorenzo et al., 2016; Ovando et al., 2021). Because MPAs have often been designed around protecting specific species or habitats, they may have unforeseen consequences for other ecosystem components by altering species composition and food availability. Spatial closures and MPAs as tools for fisheries management have, thus, remained controversial (Abbott and Haynie, 2012; Hilborn et al., 2006; Kaiser, 2005; Kriegl et al., 2021; Ohayon et al., 2021). In contrast to strict forms of MPAs such as no-take zones, spatial

\* Corresponding author.

E-mail address: [fabian.zimmermann@hi.no](mailto:fabian.zimmermann@hi.no) (F. Zimmermann).

<https://doi.org/10.1016/j.ecss.2023.108435>

Received 26 March 2023; Received in revised form 31 May 2023; Accepted 13 July 2023

Available online 16 July 2023

0272-7714/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

restrictions for specific fleet segments or gear types have been used more commonly to regulate fisheries.

Spatial restrictions tend to be relatively low-cost policy measures that are intuitive for the public, can improve population status of some species quickly (Dimarchopoulou et al., 2018; Knutsen et al., 2022), and may protect ecosystem services such as biodiversity from fisheries impact (Sala et al., 2021). This applies to bottom trawling for fish and shellfish, which is together with dredging one of the most widespread causes for disturbance of benthic habitat worldwide (Eigaard et al., 2016; Hiddink et al., 2017) and climate impacts in global fisheries (Parker and Tyedmers, 2015). Despite being an intrusive way of fishing, bottom trawling has also been shown to lead to increased abundances and body sizes of some benthic organisms (Sköld et al., 2018) because trawling may increase availability of food sources (Duplisea et al., 2002; Hiddink et al., 2016). The impacts of bottom trawling may, thus, differ by species and ecosystem.

In most inshore areas in Norway, bottom trawling is restricted with few exceptions for shrimp trawling, and completely banned from two large fjord ecosystems in northern Norway, Porsanger and Tana fjords, since the early 1970s (Søvik et al., 2020). The permanent closures to bottom trawling were triggered by high by-catches of undersized demersal fish species of locally overfished or collapsed stocks. While coastal fisheries of demersal fish, especially Atlantic cod (*Gadus morhua*), continued with gillnets and longlines (Fig. S1), fishing for northern shrimp (*Pandalus borealis*) ceased entirely after the trawling ban. Subsequently, shrimp in those two fjords have not experienced any fishing-related mortality or disturbance of their habitat in 50 years (except for the emergence of a pot fishery in a small area of Porsanger, Fig. S1). In contrast, bottom trawling for shrimp has continued in other fjords in northern Norway, notably the area of Kvænangen (Figs. S1 and S2).

Northern shrimp is a protandrous hermaphroditic species distributed across the northern Atlantic and Pacific Ocean (Shumway et al., 1985), occurring mostly on muddy soft-bottom habitat in 50–500m depth and sustaining several major fisheries. Globally, 197,100 t were landed in 2019, down from a peak of almost 447,000 t in 2004 (Hvingel et al., 2021). In the study area, landings fluctuated between 100 and 200 t, almost entirely originating from Kvænangen fjord (Fig. S1) where a shrimp fishery has been active since the 1930s. Fluctuations in shrimp catches have been attributed to direct fishing pressure, environmental changes and ecosystem dynamics, with shrimp benefiting from overfishing of important predators of shrimp such as Atlantic cod (Frank et al., 2005; Pérez-Rodríguez et al., 2012). In Norway, the northern shrimp fishery has developed over a century from a small-scale coastal fishery to an offshore fishery dominated by catches from the Barents Sea and the Svalbard area (Melaa et al., 2022). However, a coastal fishery consisting mostly of vessels below 15m length has remained active in northern Norway and along the Skagerrak coast, filling a market niche by supplying fresh boiled shrimp in contrast to frozen shrimp produced by offshore trawlers. The current stock definition lumps all coastal shrimp populations north of 62° together with the large Barents Sea stock, despite evidence of distinct genetic structure (Hansen et al., 2021). The coastal shrimp fishery in the Barents Sea is not regulated by quotas but only subject to gear regulations (mandatory sorting grid, no trawling shallower than 170m). As an open access fishery, catches are mostly controlled by economic constraints, whereby fishers abandon shrimp grounds when the density becomes unprofitable. Most of the inshore production in northern Norway originates from relatively few and mostly small shrimp grounds in fjords like Kvænangen.

Here, we used highly resolved data from scientific bottom trawl surveys in the three large fjord systems of Kvænangen, Tana and Porsanger to compare the density, sex composition and individual size of northern shrimp and Atlantic cod across fjords. The zero hypothesis was that shrimp and cod populations across fjords form one stock with identical characteristics, despite differences in trawling, other anthropogenic impacts and fjord ecology. We used geostatistical models to

explore the variation in population density, sex composition and individual size, and their link to environmental and ecological variables. The analysis provides a comprehensive assessment of northern shrimp and cod in fjord ecosystems that is unique both in terms of its fine-scale spatial resolution and the opportunity to infer long-term impacts of banning bottom trawling.

## 2. Methods

### 2.1. Study area

Kvænangen, Porsanger and Tana fjords are amongst the northernmost fjords of Norway. Kvænangen is approximately 60 km long and has a complex bathymetry, with an outer channel under strong influence from coastal currents because of depths down to 400–450m and no entrance sill, and several deep basins in the inner fjord. Porsanger fjord is one of the largest fjords in northern Norway, stretching over 120 km in north-south direction and opening to the Barents Sea only in its outermost part. The midsection of the fjord features a deep channel on the east border down to 300m depth, where past commercial shrimp grounds are found. The inner section of the fjord is also separated by a sill and distinguishes itself by substantially colder water temperatures and a partial ice cover during the winter on the eastern side, resulting in an Arctic species community distinct from the rest of the fjord (Søvik et al., 2020). Tana fjord is situated east of Porsanger fjord, has no sill and consists of an outer deep basin open to the Barents Sea, and three inner branches with complex bathymetry.

### 2.2. Survey design and data

Data was collected with the commercial shrimp trawler “Katla” (LK7560, 14.95m vessel length) during one spring (March 2019) and two autumn (October 2018 and 2019) surveys. On each survey, all three fjords were sampled with bottom trawl stations placed within trawlable areas (Fig. 1). Bottom habitat accessible to bottom trawling was identified prior to the surveys based on publicly available maps of shrimp grounds from the Norwegian Directorate of Fisheries ([www.fiskeridir.no](http://www.fiskeridir.no)), bathymetry, and sediments Geological Survey of Norway ([www.ngu.no](http://www.ngu.no)). A fixed number of stations per fjord were allocated in a random-stratified design, proportional to size of areas deeper and shallower than 170m (limit for commercial trawling). Additional stations were added to replace target stations where conditions were found to be unsuitable for trawling during the survey. In total, samples were collected at 234 stations, ranging from 19 to 32 per fjord and survey, during daylight hours only (between 08:00 and 18:00 local time) (Table 1).

A shrimp trawl 1600 m with 15 mm mesh size in the codend and without a fish sorting grid was used (dispensation approved by the Norwegian Directorate of Fisheries). At each station, the vessel trawled with 1.5–1.7 knots for 15 min after the gear made bottom contact, resulting in towing distances of  $0.39 \pm 0.02$  nmi (mean and standard deviation). Catches were sorted by species or lowest identifiable taxonomic group, and total weight and number of all taxa were registered. The carapace or total length of a subsample of up to 300 individual shrimp and 20 cod, respectively, was measured, and sex and maturity stage of both species were registered (stages and staging procedure for shrimp are described in Fig. S3). Two separate cod stocks are present in the fjords, Northeast Arctic and coastal cod, but were not distinguished in this study.

### 2.3. Statistical analysis

The following response variables and their link to available covariates were investigated with statistical models: 1) density of shrimp, 2) density of cod, 3) proportion of male shrimp in population, and 4) size of shrimp in population (Table 2). Initial exploration with generalized

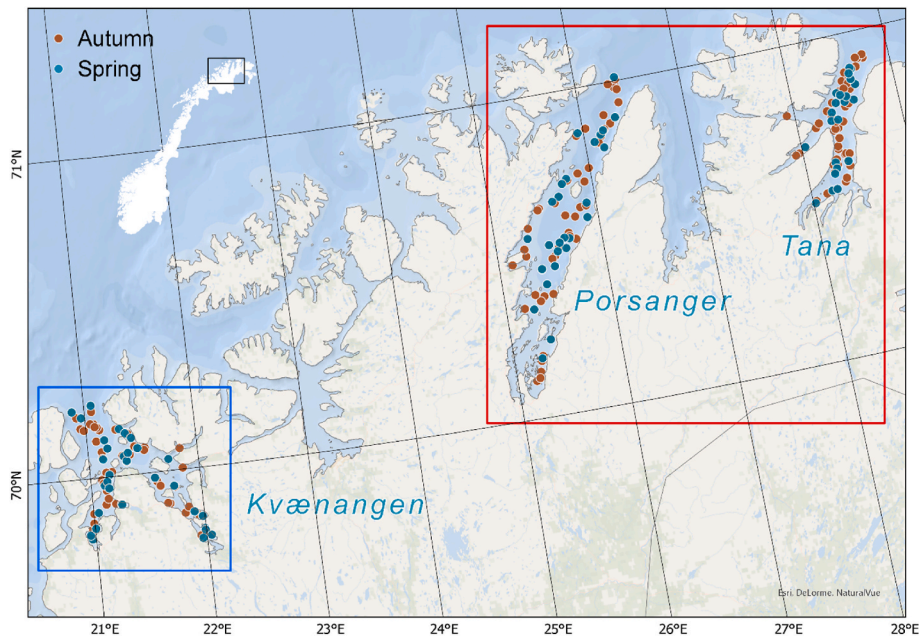


Fig. 1. Overview of survey area and bottom trawl stations in 2018–2019. Colors indicate season and rectangles the fjord(s) open (blue) and closed (red) to shrimp trawling. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Number of bottom trawl stations and bottom depth (mean and range) in meters by survey in 2018–2019.

Year	Season	Number of stations			Mean depth (range)		
		Kvænangen	Porsanger	Tana	Kvænangen	Porsanger	Tana
2018	Autumn	24	25	19	223 (73-409)	165 (36-298)	248 (168-324)
2019	Spring	32	30	20	231 (54-396)	178 (39-292)	238 (130-326)
2019	Autumn	27	28	29	228 (45-411)	176 (44-298)	229 (158-318)

Table 2

The statistical models used in the analysis detailing the response variable, the fixed effects (categorical and continuous) that were tested, offsets used, and the random effects component included.

Model	Response variable	Fixed effects	Offset	Random effects
1	Shrimp catch weight (kg)	Fjord, season, bottom depth (m), cod density (kg/nmi),	Tow distance	Spatial random field
2	Cod catch weight (kg)	Fjord, season, bottom depth (m), shrimp density (kg/nmi)	Tow distance	Spatial random field
3	Male proportion in shrimp population	Fjord, season, bottom depth (m), shrimp density (kg/nmi),	-	Spatial random field
4	Shrimp density (kg/nmi)	Fjord, season, bottom depth (m), shrimp density (kg/nmi), maturation stage	-	Spatial random field

additive models (GAM) resulted in relatively poor fits and clear indications of spatial correlation in the residuals that could not be accounted for with the available fixed effects. For all further statistical analysis, therefore, generalized additive mixed effect models (GAMMs) with spatial Gaussian Markov random fields were used to analyze density and demography of shrimp as well as density of cod, focusing on potential differences between trawled and non-trawled areas. These types of models have been shown to perform well in capturing the observed variation and spatial correlation in survey data, both for purposes of species distribution modelling and abundance index estimation

(Breivik et al., 2021; Cao et al., 2017; O’Leary et al., 2022). All models were implemented in R 4.2.1 (R: Development Core Team, 2021) using the sdmTMB (Anderson et al., 2022) and tidyverse (Wickham et al., 2019) packages.

All models used in the present study were of the form:

$$E[y_{i,a}] = \mu_{i,a}$$

$$\mu_{i,a} = f(X_{i,a}\beta + O_i + \omega_i)$$

with  $y_{i,a}$  representing the response data for station  $i$  in fjord  $a$ ,  $\mu$  the mean,  $f$  a link function,  $X_{i,a}\beta$  the design matrix for categorical or continuous fixed-effect coefficients,  $O_i$  an offset for trawling distance (only applicable for density as response), and  $\omega_i$  a spatial random field. The spatial random field was modelled as spatially correlated random effects  $\omega_i$  with a Matérn covariance matrix  $\Sigma_k \omega_i = f(x_i, y_i) \sim GF(0, \Sigma_\omega)$ . Stochastic partial differential equations (SPDE) were used to estimate the Gaussian random field. Matérn range and marginal standard deviation of spatial random fields were estimated as functions of decorrelation rate  $\kappa$  and spatial variance  $\tau^2$  as  $range = \frac{\sqrt{8}}{\kappa}$  and  $\sigma = \frac{1}{4\pi e^2 \log(\tau) + 2 \log(\kappa)}$ , respectively. For further details see Anderson et al. (2022).

Backward model selection was applied to sets of response-specific fixed effects, as detailed in Tables 2 and in the sections below. From the full models defined below, the ones explaining the data best were determined through model validation and backward model selection using AIC. All continuous effects were standardized using z-score normalization to facilitate model convergence and effect size comparison. Smooth splines were tested for all continuous fixed effects,



modelled as penalized thin plate splines restricted to five degrees of freedom to avoid overfitting. Model performance was evaluated through simulated residual distributions using the DHARMA package (Hartig, 2021).

#### 2.4. Density of shrimp and cod (M1 and M2)

Density was used here synonymously with catch rate (kg/nmi), i.e. defined as the observed catch weight divided by the trawled distance. Densities of shrimp and Atlantic cod were modelled with a compound Poisson-gamma tweedie distribution (Dunn and Smyth, 2005) and log-link:  $Tweedie(\mu, p, \varphi)$ , using catch weight as response variable and towing distance as offset to estimate standardized catch rates. The power parameter  $p$  was restricted to  $1 < p < 2$ , resulting in a continuous distribution for positive values and a positive mass at 0. The distribution was selected because of the properties of the data, containing several zero observations combined with continuous positive catch weights.

The full model evaluated for shrimp and cod densities consisted of categorical effects for fjord and season (autumn or spring), and bottom depth and predator (cod) and prey (shrimp) densities, respectively, as continuous effect with a smooth spline. Smoothing specification of continuous effects was based on initial data exploration and confirmed through model selection and validation.

#### 2.5. Population structure: sex and size composition (M3 and M4)

The sex and size composition of the shrimp populations were modelled with proportion of male shrimp and carapace length as response variables. Male shrimp are defined as one stage, in contrast to multiple stages for females. They are also the first stage that can be identified and represent typically a major proportion of the abundance. Male shrimp proportion was modelled as a beta distribution with logit link:  $Beta(\mu\varphi, (1 - \mu)\varphi)$ , with  $\mu$  as mean and  $\varphi$  as precision parameter (Ferrari and Cribari-Neto, 2004). Length was assumed to be normally distributed:  $Normal(\mu, \sigma^2)$ , with  $\mu$  as mean and  $\sigma^2$  as variance.

The full model evaluated for male proportion and carapace length consisted of categorical effects of fjord, and bottom depth and shrimp density as continuous effect with a smooth spline. Interactions between area and season were added after initial exploration showed strong seasonal patterns in both male proportion and length. For carapace length, developmental stage was included as continuous effect to account for the link between development and growth.

#### 2.6. Spatial mesh and predictions

The mesh was created with vertices of a 50 km maximum edge distances and a cutoff for minimum allowed distance between observations at 10 km within nonconvex boundaries for each fjord to avoid correlation across fjords, using the R-package INLA (Bakka et al., 2018). Distances were determined based on data exploration and model selection.

An equally spaced interpolation grid with grid cells of 0.5 km<sup>2</sup> was used to predict the estimated quantities in space. Bottom depth for all prediction points was derived from GEBCO bathymetric data ([www.gebco.net](http://www.gebco.net)). All other covariates except for area effects and spatial random fields were set to their average where not otherwise specified. Marginal effects of covariates were produced through simulation (1000 sets) and were presented as median with 5% and 95% percentiles.

Detailed model estimates and validation plots are provided in Supplementary Model Information.

### 3. Results

#### 3.1. Shrimp density (M1)

On all three surveys substantial variation in shrimp density was

found, with local clusters of high densities linked to the deeper basins, especially in the Kvænangen and Tana fjords, and in the relatively shallow eastern basin of inner Porsanger fjord (Fig. 2). Statistical analysis revealed a clear link between shrimp density and bottom depth, whereas there was no significant effect ( $p > 0.05$ ) of trawling on the observed densities (Fig. 3). Predator density and season were found to be not relevant and were therefore not included in the final model (Tables M1 and M2). In contrast, the spatial random field explained a major part of the observed spatial variation (Fig. 2, Fig. S4, Table M1). Bottom depth predicted shrimp density in deeper areas of the fjord systems adequately, but the fixed effects alone underestimated shrimp density in some shallower areas, notably in the innermost section of Porsanger fjord (Fig. 3, Fig. S5).

#### 3.2. Predator density (M2)

In contrast to spatially clustered shrimp densities, Atlantic cod was found to be evenly distributed in the fjords (Fig. 4), except for few minor hotspots and the inner basin of Porsanger fjord where cod was absent. Based on the selected model there were weak but relevant relationships with season and shrimp density (Fig. 5, Table M3). The relationship between cod and shrimp density was nonlinear, increasing to a peak at intermediate shrimp densities before decreasing again, driven by observations of high shrimp densities in inner Porsanger fjord where cod was absent. The spatial random field captured almost no additional spatial variation (Fig. S6), improving the model fit only slightly (Table M3, Fig. S7), as also reflected in a very low Matérn range and SD of the spatial random field (Table M4). The area open to trawling showed a tendency towards higher predator density, although this effect was not significant (Fig. 5). The size distribution of cod was very similar among fjords (Fig. S8), with 90% of individuals between 10 and 80 cm length (mean 28 cm).

#### 3.3. Shrimp population structure: stage and size

##### 3.3.1. Sex distribution (M3)

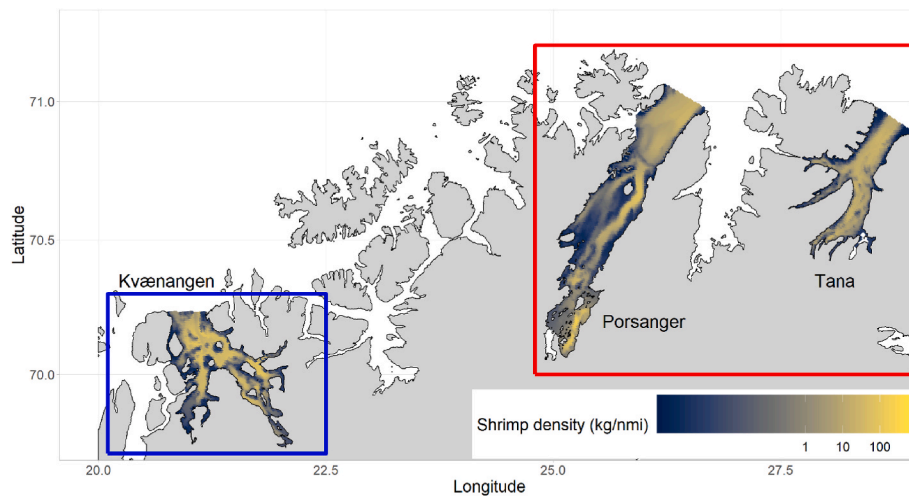
The population structure across fjords and season was consistent in general, but included some differences; notably, larger sizes in Kvænangen in autumn and the appearance of a new cohort in spring, and a seasonal pattern in the occurrence of female stages that was the opposite in innermost Porsanger fjord compared to all other areas (Fig. S9). Males (stage 2) were clearly dominating the abundance (>50% of all shrimp in numbers) in autumn in all fjords, but their proportion was significantly ( $p < 0.05$ ) decreased in spring across all fjords (Figs. 6 and 7).

Season was found to be the most important variable explaining variation in male proportion (Table M5), and seasonal difference was much more pronounced in the two fjords closed for trawling, as expressed by a statistically significant interaction between season and the two fjords (Table M6). The male proportion in Porsanger and Tana tended to be higher in autumn and lower in spring than in Kvænangen (Fig. 7). The proportion of males was, however, not significantly different among fjords, as the two fjords closed for trawling were very similar, especially in spring. There was a significantly ( $p < 0.05$ ) positive correlation with total shrimp density (Fig. 7). Removing bottom depth, on the other hand, was improved the model fit (Table M5).

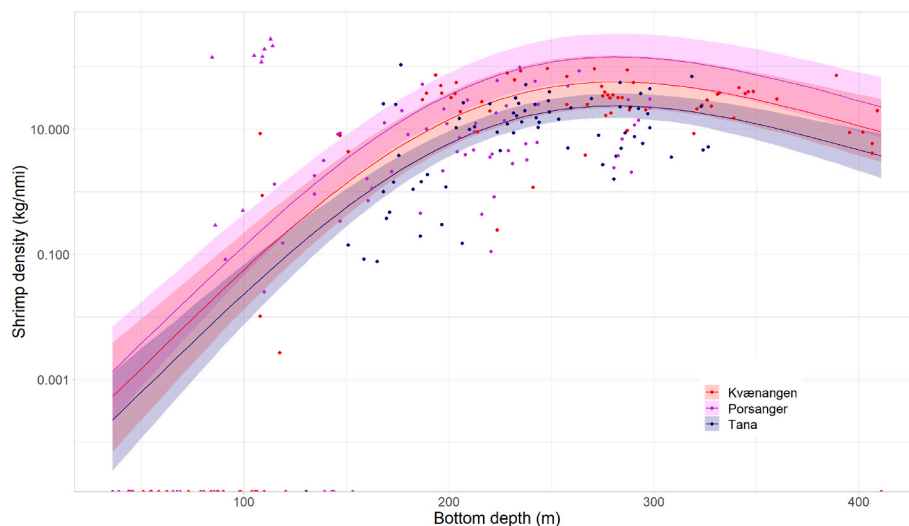
There was spatial variation reflected in the spatial random field that was not explained by the fixed effects (Table M5, Fig. S10), with elevated presence of males in central Kvænangen and towards inner parts of Porsanger and Tana fjord. The fixed effects were strongly dominated by the seasonal dynamics (Fig. S11). The model showed a slight tendency to underestimate the occurrence of very low proportions of males in the population (Fig. 7 and M4).

##### 3.3.2. Size distribution (M4)

Model selection showed that variation in individual size was foremost explained by season as categorical variable and stage (Tables M7



**Fig. 2.** Density of shrimp (kg/nmi) as predicted by the selected model. Predicted values are the joint prediction of fixed effects and spatial random fields. Boxes indicate the fjord(s) open (blue) and closed (red) to trawling. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 3.** Combined marginal effects of fjord and bottom depth on shrimp density, showing median (lines) and 5% and 95% percentiles (shaded areas) by depth for Kvænangen (red), Porsanger (purple) and Tana (dark blue) fjords. Dots are observed densities at all survey stations except for inner Porsanger fjord that are shown as triangles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

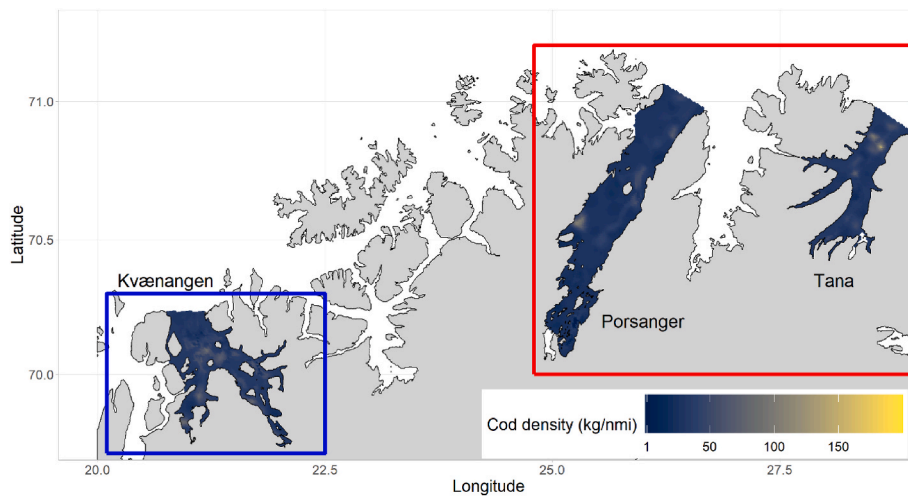
and 8), with an interaction between season and fjord. The fixed effects explained the observed variation insufficiently (Fig. S12), and substantial spatial variation was captured by the spatial random field (Fig. 8, Table M7), both within and among the fjords. The joint prediction estimates showed a tendency towards larger shrimp sizes in Kvænangen, especially in autumn (Fig. S12), but also in parts of the fjords closed for trawling, specifically Tana fjord and parts of inner Porsanger fjord (Fig. S13). Because of this large variation within the fjords that were not trawled, the fjord effect was nonsignificant. The effects of stock density and bottom depth on size were weak but marginally improved the model fit (Fig. S14, Table M7).

#### 4. Discussion

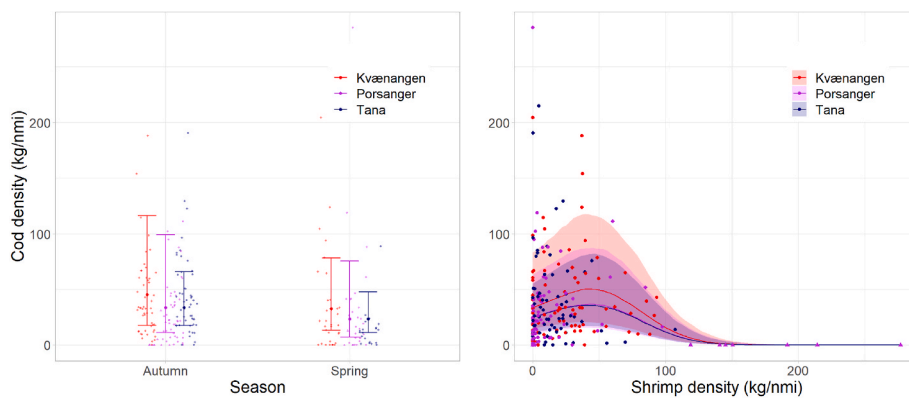
We compared northern shrimp and Atlantic cod density and population structure in a fjord with a continuous trawl fishery for shrimp with two fjords that were closed for trawling for 50 years. The result showed substantial spatial intra- and interfjord variation but no fjord-specific differences in shrimp density that could be linked to the trawl ban,

similar to findings in other studies (Bernardes et al., 2020; Coleman et al., 2004). Rather, indications of equal to higher densities and larger sizes in the trawled fjord Kvænangen suggest other ecosystem processes as driver of shrimp dynamics and, possibly, positive links between trawling and shrimp productivity. Densities and size composition of the main shrimp predator, cod, were homogeneous among fjords, and did therefore not directly indicate differences in predation pressure. The lack of significant differences in shrimp density could be the result of released density dependence or increased benthic productivity caused by trawling in Kvænangen fjord, in addition to underlying differences in the three ecosystems. Strong spatial variability in shrimp density and size suggests that unobserved environmental and ecological processes are important for shrimp distribution, density, and population structure. Cod and shrimp populations may therefore be shaped by fine-scale differences in fjord ecology where bottom trawling is one contributing factor among many.

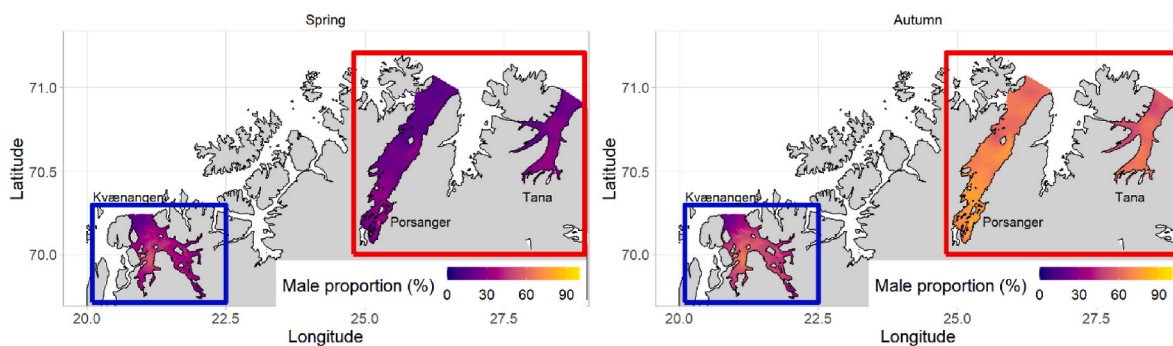
Atlantic cod is the most important predator on northern shrimp (Berenboim et al., 2000; Hedeholm et al., 2017), and in Porsanger fjord, prior studies determined shrimp as the most important prey item for cod



**Fig. 4.** Density of Atlantic cod (kg/nmi) as predicted by the selected model. Predicted values are the joint prediction of fixed effects (shrimp density, season set to autumn) and spatial random fields. Mean predictions for spring were just slightly downscaled (Fig. 5) and not shown. Boxes indicate the fjord(s) open (blue) and closed (red) for trawling. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



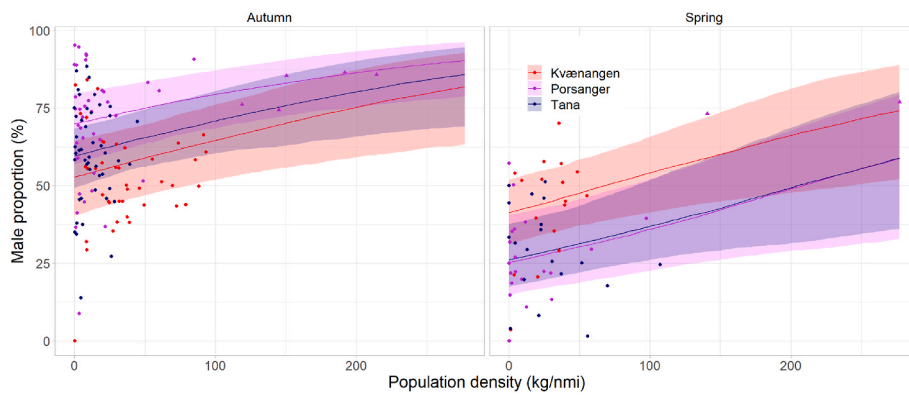
**Fig. 5.** Combined marginal effects of fjord and season (left) and trawling and shrimp density on Atlantic cod density, showing median (lines) and 5% and 95% percentiles (shaded areas) by depth for Kvænangen (red), Porsanger (purple) and Tana (dark blue) fjords. Dots are observed densities at all survey stations (horizontally jittered in left figure for visualization purposes). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



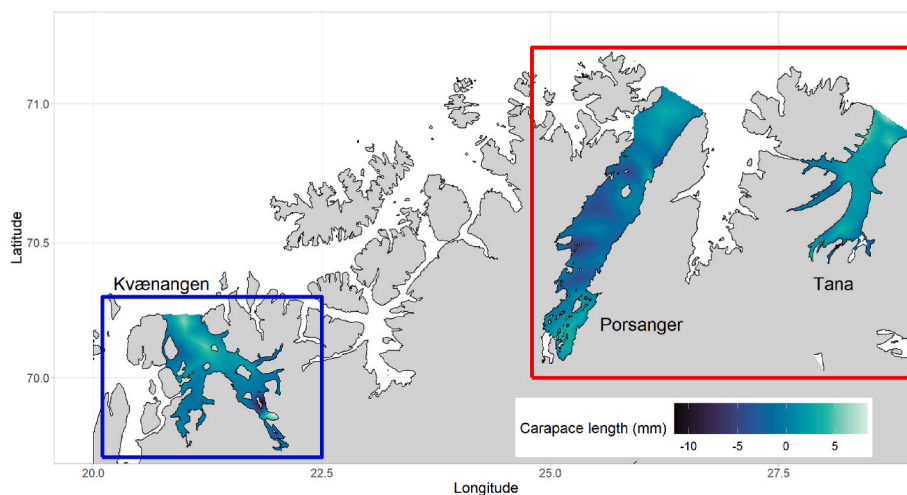
**Fig. 6.** Male proportion in the population in spring (left) and autumn (right) as predicted by the selected model. Predicted values are the joint prediction of fixed effects and spatial random fields. Boxes indicate the fjord(s) open (blue) and closed (red) for trawling. Male proportion was modelled as the proportion of males (stage 2) of the observed number of shrimp per location. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Pedersen et al., 2018). Here we found a non-linear (convex) relationship between cod and shrimp, with very high shrimp density and no cod in the inner part of Porsanger fjord. The absence of a clear link between cod and shrimp density in most of the study area may indicate that cod density is a poor predictor of predation on shrimp in our study area, even if the majority of the observed cod was within the size range known to prey on shrimp (Holt et al., 2019). On the other hand, a cluster of very high shrimp densities in absence of cod in inner Porsanger suggests that

cod plays a role in regulating the shrimp population in the other areas. Several possible reasons can mask the predator-prey relationship: i) confounding effects as shrimp density may be reduced by cod presence while high shrimp density could attract higher cod densities, ii) predation may depend on the presence of other prey species, iii) current cod abundance is too low to make significant impacts on the shrimp density, and iv) cod was absent from high-density shrimp areas due to environmental constraints. Occurrence of alternative prey, notably capelin



**Fig. 7.** Combined marginal effects of fjord, population density and season on the male proportion in the shrimp population, showing median (lines) and 5% and 95% percentiles (shaded areas) by density for Kvænangen (red), Porsanger (purple) and Tana (dark blue) fjords. Dots are all observed male proportions at all survey stations. Male proportion was modelled as the proportion of males (stage 2) of the observed number of shrimps per trawl haul, population density is the observed biomass standardized to trawling distance. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 8.** Marginal effects of spatial random field on carapace length of shrimp in the population as predicted by the selected model. Boxes indicate the fjord open (blue) and closed (red) for trawling. Note that the scale includes negative values because spatial random field are normally distributed random effects with mean of 0 that account for both smaller and larger sizes than expected based on fixed effects alone. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(*Mallotus villosus*), varies among the fjord ecosystems. Porsanger fjord has its own endemic capelin population, as confirmed by our survey (Søvik et al., 2020), that likely fluctuates over time similar to Barents Sea capelin, with consequences both for cod abundance and shrimp predation. Conversely, other species also prey on shrimp, and even though this predation occurs overall on a lower level, it may nevertheless be relevant, especially in areas with little or no cod presence (e.g. cottids in the eastern basin of innermost Porsanger fjord). This applies also for other potential shrimp predators such as saithe (*Pollachius virens*) that were underrepresented in our data because of poor catchability in bottom trawls. The relatively low trawling speed may have also reduced catchability of cod, although this effect can be expected to be equal across fjords and not affect our results. In view of relatively homogenous cod densities, differences in trophic interactions and realized predation mortality could explain the comparable shrimp densities of fished and unfished populations, as higher consumption of cod in fjords closed for trawling could scale to a similar magnitude as the shrimp catches in Kvænangen. The predator-prey relationship entails, therefore, management implications, as a reopened trawl fishery for shrimp might decrease the foraging opportunities for cod and undermine efforts to rebuild the local coastal cod populations. Diet composition across fjord ecosystems should therefore be further investigated and predator-prey interactions possibly included in future management plans for cod and shrimp.

Although top-down regulation through fishing and predation likely shapes shrimp dynamics, bottom-up drivers of stock productivity may play an important role in explaining shrimp density and dynamics and variation thereof. The studied fjords are comparable due to shared latitude, climate and their link to the Barents Sea, but there are physical

differences that may carry over to ecosystem functioning and productivity. While both Tana and Kvænangen fjords have wide openings and no sills, exposing them to the Barents Sea, this only applies for the outermost area of Porsanger fjord. The larger part of Porsanger fjord is separated by two sills into two distinct segments, including the innermost part of the fjord with a distinct Arctic ecosystem. There are also differences in freshwater inflow, with Tana river creating a strong surface current flowing out of Tana fjord possibly flushing hatched larvae out of the fjord (Søvik et al., 2020). Differences in hydrography and currents may therefore affect larval drift and retention, a key driver of recruitment variability in shrimp and, thus, population dynamics. The observation of a new cohort in Kvænangen but not in the other two fjords in spring 2019 (Fig. 6) may be evidence of distinct recruitment dynamics. Furthermore, the low temperature (around 0 °C) in the innermost part of Porsanger fjord causes slower growth and delayed sex change, explaining the high abundance of males in this basin. Many females in the resting stage (7) in autumn suggests a reproductive cycle of 2, perhaps 3 years. This highlights environmental variables such as temperature as important driver of life-history and, thus, population dynamics that should be included in future analysis. Pandalid shrimps can be, furthermore, affected by aquaculture effluents and incorporate organic fish farm waste into their diet (Olsen et al., 2012). Kvænangen has the highest number of salmon farms of the three fjords with 12 compared to 2 in Porsanger and none in Tana as of 2020 (Aquaculture register, Norwegian Directorate of Fisheries). The effects of this potential food source and the resuspension of organic particles caused by bottom trawling are unknown and difficult to quantify but can – together with differences in hydrography – affect habitat suitability and food availability for shrimp.



Since the introduction of the trawl ban in the 1970s, the ecosystems in the study fjords have undergone major changes. Besides likely shifts in species composition due to climate change and anthropogenic activities, the introduction of red king crab (*Paralithodes camtschaticus*) has reshaped Porsanger, Tana and other fjords east of 26°E fundamentally (Falk-Petersen et al., 2011; Fuhrmann et al., 2015), whereas unrestricted fishing has kept Kvænangen are largely free of king crab. Although shrimp are not prey, the transformative presence of king crab (Christie et al., 2019; Pedersen et al., 2018) most likely has affected shrimp dynamics through competition and other trophic feedbacks, causing differences in ecosystem functioning that may explain part of the variation in shrimp density and stock composition.

Impacts of fishing on population dynamics are complex and may result in (over-)compensatory effects that increase stock productivity and, thus, possibly result in similar or higher densities in a trawled area compared to an area without trawling. Density dependence in recruitment and growth are known to determine the dynamics of fish stocks (Lorenzen and Camp, 2018; Zimmermann et al., 2018), mostly due to released competition for resources when parts of the stock biomass are removed. Dynamics of fished shrimp population in Kvænangen fjord may therefore differ from the other two fjords, with a faster life history and higher productivity. The lack of significant differences in density and the tendency towards larger body size in the trawled fjord may provide evidence for these differences in shrimp dynamics. Density-dependent effects of fisheries removals may be magnified by trawling effects on bottom substrate and benthic species composition, potentially increasing the food availability for shrimp, contrasting detrimental impacts on benthic habitats (Hiddink et al., 2017; Sköld et al., 2018).

Most coastal fish and shellfish stocks in Norway are managed as relatively uniform (meta-)populations despite more complex population structures being common (Johansen et al., 2020; Knutsen et al., 2007). This applies to northern shrimp where genetic analyses have revealed that coastal shrimp are genetically distinct from the offshore stock in the Barents Sea (Hansen et al., 2021). Coastal shrimp including stocks in northern Norway appear to be genetically linked to the population found in the Skagerrak area, and only in Porsanger fjord and eastwards, genetic markers of the Barents Sea population assert themselves, with gradients within the fjords. This can likely be explained by the complex coastal topography and larval drift patterns, predominantly shaped by the Norwegian coastal current acting as a main pathway for genetic connectivity. The closer genetic relationship of Kvænangen shrimp with shrimp in the Skagerrak than those in Porsanger and Tana fjords adds another layer of complexity when comparing the population dynamics across the study area. Because life history and growth of shrimp in the Skagerrak has a faster pace compared with shrimp in the Barents Sea, some of the observed population characteristics in the three study fjords might be explained by their genetic composition. This includes notably the indications of faster growth and, thus, sex transition in Kvænangen compared to Porsanger and Tana. An earlier study showed that shrimp change sex around February–March in Northern Norway (Rasmussen, 1953), but our analysis suggests that there might be fjord-specific variation. Disentangling the genetic factors from other previously discussed drivers such as density dependence, predation and environmental effects should therefore be a focus of future research. The innermost Porsanger fjord provides here an important reference that illustrates how absence of both fishing and major predators can result in much higher shrimp densities than observed elsewhere.

The range of interlinked explanations for the unclear or absent effects of a trawling ban on the shrimp stocks in two Norwegian fjords represent challenging unknowns for their management and a possible reopening of a trawl fishery in Porsanger and Tana fjords. Our study provides only a snapshot in time of the densities and, thus, biomass at the time of the surveys. This does therefore not allow for deriving population dynamics parameters to estimate sustainable yield in the fjords. A density dependent response to renewed fishing might support

shrimp productivity and in the long run result in similar population dynamics as in the currently fished areas. But this ignores possible differences in predation, food availability, other anthropogenic stressors, environment, and genetics. Applying identical harvest strategies across fjords despite likely differences in ecosystem functioning and population dynamics entails therefore a risk of depleting the currently unfished stocks and negatively affecting other species such as cod that rely on shrimp as prey. These considerations call for a precautionary approach, where after a possible reopening, fishing pressure should slowly and gradually increase. Since the 1990s, mandatory fish sorting grids for shrimp trawls and temporary area closures when bycatch exceed limits have largely resolved past bycatch issues that motivated the trawl ban. However, impacts of trawling on benthic species vulnerable to trawling are an additional management concern, together with other anthropogenic activities such as aquaculture that have expanded in the study area and represent further stressors for the fjord ecosystems. Our study underlines the need for fisheries management in the coastal zone that accounts for ecosystem dynamics in space and balances potentially conflicting exploitation and conservation concerns.

The exceptionally fine-scaled dataset analyzed here revealed the complex spatial variation of population dynamics in coastal shrimp populations, both among and within fjords, underlining the importance of spatially explicit methods in stock assessment and management as shown for other shrimp stocks (Cardinale et al., 2023). This applies especially for shellfish species that have become increasingly important globally (Boenish et al., 2022) but tend to be poorly managed, including in Norway where many shellfish stocks are unassessed and under-regulated (Zimmermann et al., 2022). The intra- and inter-fjord variation found in our study confirms the need to include spatial and ecological consideration in coastal fisheries management. In northern Norway, this may include the evaluation of separate management regimes for coastal shrimp apart from the large Barents Sea offshore stock, potentially on the spatial scale of single fjords.

#### CRediT authorship contribution statement

**Fabian Zimmermann:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jessica Tengvall:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis. **Hans Kristian Strand:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Kjell Nedreaas:** Writing – review & editing, Investigation. **Trude H. Thangstad:** Writing – review & editing, Visualization, Data curation. **Berengere Husson:** Writing – review & editing, Writing – original draft, Validation. **Guldborg Søvik:** Writing – review & editing, Writing – original draft, Validation, Project administration, Funding acquisition, Data curation, Conceptualization.

#### Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Fabian Zimmermann reports financial support was provided by Norges Forskningsrad. Fabian Zimmermann reports financial support was provided by the Norwegian Ministry of Trade, Industry and Fisheries.

#### Data availability

Data will be made available on request.

#### Acknowledgments

The authors thank the skipper of “Katla”, D.O. Molan, and his crew, for the great support, the Norwegian Directorate of Fisheries for their collaboration and financial support, and all survey participants for their



contribution to data collection. We acknowledge funding by the Research Council of Norway (“CoastRisk”, project number 299554) and the Norwegian Ministry of Trade, Industry and Fisheries.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2023.108435>.

## References

- Abbott, J.K., Haynie, A.C., 2012. What are we protecting? Fisher behavior and the unintended consequences of spatial closures as a fishery management tool. *Ecol. Appl.* 22, 762–777.
- Anderson, S.C., Ward, E.J., English, P.A., Barnett, L.A.K., 2022. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. *bioRxiv*, 485545, 2022.2003.2024.
- Bakka, H., Rue, H., Fuglstad, G.-A., Riebler, A., Bolin, D., Illian, J., Krainski, E., Simpson, D., Lindgren, F., 2018. Spatial modeling with R-INLA: a review. *WIREs Computational Statistics* 10, e1443.
- Berenboim, B., Dolgov, A., Korzhhev, V., Yaragina, N., 2000. Sea shrimp (*Pandalus borealis*) as determined by multispecies models. *J. Northwest Atl. Fish. Sci.* 27, 69–72.
- Bernardes, V.P., Sousa, A.N., Bernardo, C.H., Teixeira, G.M., Costa, R.C., Mantelatto, F.L., Fransozo, A., 2020. Comparison of the spatio-temporal distribution of the roughneck shrimp *Rimapenaeus constrictus* (Stimpson, 1874) (Crustacea, Penaeoidea) from monthly samples collected 20 years apart: effects of a marine protected area in southeastern Brazil. *Mar. Ecol.* 41, e12605.
- Boenish, R., Kritzer, J.P., Kleisner, K., Steneck, R.S., Werner, K.M., Zhu, W., Schram, F., Rader, D., Cheung, W., Ingles, J., Tian, Y., Mimikakis, J., 2022. The global rise of crustacean fisheries. *Front. Ecol. Environ.* 20, 102–110.
- Breivik, O.N., Aanes, F., Sovik, G., Aglen, A., Mehl, S., Johnsen, E., 2021. Predicting abundance indices in areas without coverage with a latent spatio-temporal Gaussian model. *ICES J. Mar. Sci.* 78, 2031–2042.
- Cao, J., Thorson, J.T., Richards, R.A., Chen, Y., 2017. Spatiotemporal index standardization improves the stock assessment of northern shrimp in the Gulf of Maine. *Can. J. Fish. Aquat. Sci.* 74, 1781–1793.
- Cardinale, M., Zimmermann, F., Sovik, G., Griffiths, C.A., Bergenius Nord, M., Winker, H., 2023. Spatially explicit stock assessment uncovers sequential depletion of northern shrimp stock components in the North Sea. *ICES J. Mar. Sci.*
- Christie, H., Gunderson, H., Rinde, E., Filbee-Dexter, K., Norderhaug, K.M., Pedersen, T., Bekkby, T., Gitmark, J.K., Fagerli, C.W., 2019. Can multitrophic interactions and ocean warming influence large-scale kelp recovery? *Ecol. Evol.* 9, 2847–2862.
- Coleman, F.C., Figueira, W.F., Ueland, J.S., Crowder, L.B., 2004. The impact of United States recreational fisheries on marine fish populations. *Science* 305, 1958.
- Di Lorenzo, M., Claudet, J., Guidetti, P., 2016. Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. *J. Nat. Conserv.* 32, 62–66.
- Dimarchopoulou, D., Dogrammatzi, A., Karachle, P.K., Tsikiras, A.C., 2018. Spatial fishing restrictions benefit demersal stocks in the northeastern Mediterranean Sea. *Sci. Rep.* 8, 5967.
- Dunn, P.K., Smyth, G.K., 2005. Series evaluation of Tweedie exponential dispersion model densities. *Stat. Comput.* 15, 267–280.
- Duplisea, D.E., Jennings, S., Warr, K.J., Dinmore, T.A., 2002. A size-based model of the impacts of bottom trawling on benthic community structure. *Can. J. Fish. Aquat. Sci.* 59, 1785–1795.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S. J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216–220.
- Eigaard, O.R., Bastardie, F., Hintzen, N.T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G.E., Egekvist, J., Fock, H.O., Geitner, K., Gerritsen, H.D., González, M.M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, J.R., Papadopoulou, N., Posen, P.E., Pulcinella, J., Russo, T., Sala, A., Silva, C., Smith, C.J., Vanellander, B., Rijnsdorp, A.D., 2016. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. *ICES J. Mar. Sci.* 74, 847–865.
- Falk-Petersen, J., Renaud, P., Anisimova, N., 2011. Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea—a review. *ICES J. Mar. Sci.* 68, 479–488.
- Fenberg, P.B., Caselle, J.E., Claudet, J., Clemence, M., Gaines, S.D., Antonio García-Charton, J., Gonçalves, E.J., Grorud-Colvert, K., Guidetti, P., Jenkins, S.R., Jones, P. J.S., Lester, S.E., McAllen, R., Moland, E., Planes, S., Sørensen, T.K., 2012. The science of European marine reserves: status, efficacy, and future needs. *Mar. Pol.* 36, 1012–1021.
- Ferrari, S., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. *J. Appl. Stat.* 31, 799–815.
- Fogarty, M.J., Botsford, L.W., 2007. Population connectivity and spatial management of marine fisheries. *Oceanography* 20, 112–123.
- Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621.
- Fuhrmann, M.M., Pedersen, T., Ramasco, V., Nilssen, E.M., 2015. Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. *J. Sea Res.* 106, 1–13.
- Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., Macpherson, E., Micheli, F., Pais, A., Panzalis, P., Rosenberg, A.A., Zabala, M., Sala, E., 2014. Large-scale assessment of Mediterranean marine protected areas effects on fish assemblages. *PLoS One* 9, e91841.
- Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13, 117–137.
- Hansen, A., Westgaard, J.-I., Sovik, G., Hanebrekke, T., Nilssen, E.M., Jorde, P.E., Albretsen, J., Johansen, T., 2021. Genetic differentiation between inshore and offshore populations of northern shrimp (*Pandalus borealis*). *ICES J. Mar. Sci.* 78.
- Hartig, F., 2021. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.4.1.
- Hedeholm, R.B., Mikkelsen, J.H., Svendsen, S.M., Carl, J., Jensen, K.T., 2017. Atlantic cod (*Gadus morhua*) diet and the interaction with northern shrimp (*Pandalus borealis*) in Greenland waters. *Polar Biol.* 40, 1335–1346.
- Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Mazon, T., Hilborn, R., Collie, J.S., Pitcher, C. R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc. Natl. Acad. Sci. U.S.A.* 114, 8301–8306.
- Hiddink, J.G., Moranta, J., Balestrini, S., Sciberras, M., Cendrier, M., Bowyer, R., Kaiser, M.J., Sködl, M., Jonsson, P., Bastardie, F., Hinz, H., 2016. Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors. *J. Appl. Ecol.* 53, 1500–1510.
- Hilborn, R., Micheli, F., Leo, G.A.D., 2006. Integrating marine protected areas with catch regulation. *Can. J. Fish. Aquat. Sci.* 63, 642–649.
- Hilborn, R., Stokes, K., Maguire, J.-J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., 2004. When can marine reserves improve fisheries management? *Ocean Coast Manag.* 47, 197–205.
- Holt, R.E., Bogstad, B., Durant, J.M., Dolgov, A.V., Ottersen, G., 2019. Barents Sea cod (*Gadus morhua*) diet composition: long-term interannual, seasonal, and ontogenetic patterns. *ICES J. Mar. Sci.* 76, 1641–1652.
- Hvingel, C., Sainte-Marie, B., Kruse, G.H., 2021. Cold-water shellfish as harvestable resources and important ecosystem players. *ICES J. Mar. Sci.* 78, 479–490.
- Johansen, T., Besnier, F., Quintela, M., Jorde, P.E., Glover, K.A., Westgaard, J.-I., Dahle, G., Lien, S., Kent, M.P., 2020. Genomic analysis reveals neutral and adaptive patterns that challenge the current management regime for East Atlantic cod *Gadus morhua* L. *Evol Appl* 13, 2673–2688.
- Kaiser, M.J., 2005. Are marine protected areas a red herring or fisheries panacea? *Can. J. Fish. Aquat. Sci.* 62, 1194–1199.
- Knutsen, H., Olsen, E.M., Ciannelli, L., Espeland, S.H., Knutsen, J.A., Simonsen, J.H., Skreslet, S., Stenseth, N.C., 2007. Egg distribution, bottom topography and small-scale cod population structure in a coastal marine system. *Mar. Ecol. Prog. Ser.* 333, 249–255.
- Knutsen, J.A., Kleiven, A.R., Olsen, E.M., Knutsen, H., Espeland, S.H., Sørđalen, T.K., Thorbjørnsen, S.H., Hutchings, J.A., Fernández-Chacón, A., Huserbråten, M., Villegas-Ríos, D., Halvorsen, K.T., Nillos Kleiven, P.J., Langeland, T.K., Moland, E., 2022. Lobster reserves as a management tool in coastal waters: two decades of experience in Norway. *Mar. Pol.* 136, 104908.
- Kriegel, M., Elías Ilosvay, X.E., von Dorrien, C., Oesterwind, D., 2021. Marine protected areas: at the crossroads of nature conservation and fisheries management. *Front. Mar. Sci.* 8.
- Lorenzen, K., Camp, E.V., 2018. Density-dependence in the life history of fishes: when is a fish recruited? *Fish. Res.* 217.
- McCook, L.J., Ayling, T., Cappel, M., Choat, J.H., Evans, R.D., De Freitas, D.M., Heupel, M., Hughes, T.P., Jones, G.P., Mapstone, B., Marsh, H., Mills, M., Molloy, F. J., Pitcher, C.R., Pressey, R.L., Russ, G.R., Sutton, S., Sweatman, H., Tobin, R., Wachenfeld, D.R., Williamson, D.H., 2010. Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18278–18285.
- Melaa, K.W., Zimmermann, F., Sovik, G., Thangstad, T.H., 2022. In: *Historic Landings of Northern Shrimp (Pandalus borealis) in Norway — Data Per County for 1908-2021, Rapport fra havforskningen* 2022-24.
- O’Leary, C.A., DeFilippo, L.B., Thorson, J.T., Kotwicki, S., Hoff, G.R., Kulik, V.V., Ianelli, J.N., Punt, A.E., 2022. Understanding transboundary stocks’ availability by combining multiple fisheries-independent surveys and oceanographic conditions in spatiotemporal models. *ICES J. Mar. Sci.* 79, 1063–1074.
- Ohayon, S., Granot, I., Belmaker, J., 2021. A meta-analysis reveals edge effects within marine protected areas. *Nature Ecol. Evol.* 5, 1301–1308.
- Olsen, S.A., Ervik, A., Grahl-Nielsen, O., 2012. Tracing fish farm waste in the northern shrimp *Pandalus borealis* (Krøyer, 1838) using lipid biomarkers. *Aquac. Environ. Interact.* 2, 133–144.
- Ovando, D., Caselle, J.E., Costello, C., Deschenes, O., Gaines, S.D., Hilborn, R., Liu, O., 2021. Assessing the population-level conservation effects of marine protected areas. *Conserv. Biol.* 35, 1861–1870.
- Parker, R.W.R., Tyedmers, P.H., 2015. Fuel consumption of global fishing fleets: current understanding and knowledge gaps. *Fish. Fish.* 16, 684–696.
- Pedersen, T., Fuhrmann, M.M., Lindström, U., Nilssen, E.M., Ivarjord, T., Ramasco, V., Jørgensen, L.L., Sundet, J.H., Sivertsen, K., Källgren, E., Hjelset, A.M., Michaelsen, C., Systad, G., Norrbinn, F., Svenning, M.A., Bjørge, A., Steen, H., Nilssen, K.T., 2018. Effects of the invasive red king crab on food web structure and ecosystem properties in an Atlantic fjord. *Mar. Ecol. Prog. Ser.* 596, 13–31.

- Pérez-Rodríguez, A., Koen-Alonso, M., Saborido-Rey, F., 2012. Changes and trends in the demersal fish community of the Flemish Cap, Northwest Atlantic, in the period 1988–2008. *ICES J. Mar. Sci.* 69, 902–912.
- R: Development Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rasmussen, B., 1953. On the Geographical Variation in Growth and Sexual Development of the Deep Sea Prawn (*Pandalus borealis* Kr.). Fiskeridirektoratets skrifter. Serie Havundersøkelser 10.
- Rassweiler, A., Costello, C., Siegel, D.A., 2012. Marine protected areas and the value of spatially optimized fishery management. *Proc. Natl. Acad. Sci. U.S.A.* 109, 11884–11889.
- Sala, E., Mayorga, J., Bradley, D., Cabral, R.B., Atwood, T.B., Auber, A., Cheung, W., Costello, C., Ferretti, F., Friedlander, A.M., Gaines, S.D., Garilao, C., Goodell, W., Halpern, B.S., Hinson, A., Kaschner, K., Kesner-Reyes, K., Leprieur, F., McGowan, J., Morgan, L.E., Mouillot, D., Palacios-Abrantes, J., Possingham, H.P., Rechberger, K. D., Worm, B., Lubchenco, J., 2021. Protecting the global ocean for biodiversity, food and climate. *Nature* 592, 397–402.
- Shumway, S.E., Perkins, H.C., Schick, D.F., Stickney, A.P., 1985. Synopsis of Biological Data on the Pink Shrimp, *Pandalus borealis* Krøyer, 1838. FAO Fisheries Synopsis 144, p. 59ff.
- Sköld, M., Göransson, P., Jonsson, P., Bastardie, F., Blomqvist, M., Agrenius, S., Hiddink, J.G., Nilsson, H.C., Bartolino, V., 2018. Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat. *Mar. Ecol. Prog. Ser.* 586, 41–55.
- Sørdalen, T.K., Halvorsen, K.T., Olsen, E.M., 2022. Protection from fishing improves body growth of an exploited species. *Proc. R. Soc. A B* 289, 20221718.
- Søvik, G., Nedreaas, K.H., Zimmermann, F., Husson, B., Strand, H.K., Jørgensen, L.L., Strand, M., Thangstad, T.H., Hansen, A., Båtevik, T., 2020. Kartlegging av fjordøkosystemene i Tana-og Porsangerfjorden-Råd og kunnskapsbidrag fra Havforskningsinstituttet i forbindelse med vurdering av en eventuell åpning av direktefiske etter reker med bunntrål i Tana-og Porsangerfjorden. Rapport fra havforskningen 2020-39.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D.A., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., 2019. Welcome to the tidyverse. *J. Open Source Softw.* 4, 1686.
- Zimmermann, F., Kleiven, A.R., Ottesen, M.V., Søvik, G., 2022. Inclusion of recreational fishing in data-limited stocks: a case study on Norway lobster (*Nephrops norvegicus*) in Norway. *Can. J. Fish. Aquat. Sci.* 79, 969–978.
- Zimmermann, F., Ricard, D., Heino, M., 2018. Density regulation in Northeast Atlantic fish populations: density dependence is stronger in recruitment than in somatic growth. *J. Anim. Ecol.* 87, 672–681.