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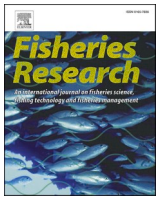

Quantifying depletion rates of benthic macrofauna from the Danish Seine – A 'low impact' mobile bottom-contacting fishing gear

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ABSTRACT

The Danish 'anchor' seine is a widely used commercial fishing gear, assumed to have relatively low seabed impact due to shallow sediment penetration. However, this assumption has lacked empirical testing. Here, we quantify benthic macrofaunal depletion from Danish seines for the first time via a Before-After-Control-Impact (BACI) experiment involving single and multiple hauls. By attaching GPS loggers to the seine gear, we analysed separate benthic effects of the two main seine components (rope and ground gear) using targeted sampling within the respective footprints. From 120 Van Veen grab samples, we observed little or no depletion in macrofaunal density, biomass, or species richness for either gear component or haul treatment. However, multiple hauls led to marked depletion of erect tube-building *Phoronis* spp., which declined by 90 % in the rope and 64 % in ground gear footprints. Overall, macrofauna depletion was greater when subjected to multiple hauls, with clearer negative effects in rope impacted areas. Conversely, metrics such as density and biomass unexpectedly increased in ground-gear impacted areas, possibly due to scavenging species or natural variability in macrofauna distributions. We further estimated a whole-gear single-haul biomass depletion rate of 0.068, though this estimate is based on large-bodied fauna (>4 mm) and was associated with high uncertainty. Despite considerable sampling effort, the contrasting results and chiefly species-specific effects indicate an overall low benthic impact from the Danish seine. This outcome supports the general assumption of its relatively low impact, and as a potential alternative to more damaging beam trawls that target the same species in similar habitats.

1. Introduction

Mobile bottom-contacting fishing gears account for almost one quarter of wild marine fish landings worldwide and are widely used across the world's continental shelves (Eigaard et al., 2017; Amoroso et al., 2018). The seabed impacts of bottom trawling with e.g. otter and beam trawls is relatively well studied, and there is consensus on the environmental burden of these activities (e.g., Kaiser et al., 2006; Hiddink et al., 2017; Sciberras et al., 2018). Although the use of Danish seines is less widespread (Rickwood et al., 2025), these gears are regionally important and are also thought to exert a comparatively low level of physical impact on the seabed and to the associated benthic macrofauna (Suuronen et al., 2012; Dinesen et al., 2018). As a result, gears such as Danish seines could potentially offer a more sustainable alternative to bottom trawls for a range of fisheries (Suuronen et al., 2012). Despite this, the widespread assumption of low impacts to benthic communities is yet to be empirically examined, and an improved understanding and quantification of the benthic effects of such gears is needed to inform an Ecosystem Approach to Fisheries Management (EAFM).

The resulting ecological effects of bottom-towed gears on the seabed are thought to be directly related to the frequency of the fishing, seafloor

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habitat type, and the sediment penetration depth of the gear (Hiddink et al., 2017; Pitcher et al., 2022). By nature of their varying design and dimensions, and thus penetration depth, different types of bottom-towed gears have differential impacts on characteristics such as benthic biomass and community longevity, and indeed the overall status of seafloor habitats (Rijnsdorp et al., 2020). In a North Sea study by Rijnsdorp et al. (2020), otter trawling for crustaceans was evaluated to have the greatest impact on benthic fauna, while Danish seines had among the lowest impacts. While the estimates of Rijnsdorp et al. (2020) for commonly used gears such as beam trawls were based on observations of fishing frequency (VMS data) and empirical evidence of gear penetration and macrofauna depletion (Hiddink et al., 2017), the estimates provided for less commonly used gears such as Danish seines relied on a range of assumptions due to key data gaps, e.g., the gear penetration depth and depletion rate.

In addition to the reduction of benthic macrofauna abundance and biomass, bottom-towed gears can also alter benthic ecosystem structures and functioning (Tillin et al., 2006). Trawling can affect ecosystem functioning through the loss of species with important life-history traits (Norling et al., 2007). These characteristics are also commonly referred to as biological traits, and analysis of such traits can be used to identify and infer the changes to ecosystem functioning caused by fishing (Tillin et al., 2006). Using biological traits to characterise the community can therefore provide a complementary approach to taxonomic and community-level analyses and improve our understanding of how gears such as trawls and demersal seines can impact the ecological integrity of the benthic ecosystems.

The primary objective of this study was to quantify the impact of the Danish seine on benthic macrofauna via experimental seining. In Denmark, the Danish seine ground gear is attached to the net and accounts for about 1 % of the total gear footprint (Noack et al., 2019). This component is considered the deepest penetrating component of the gear (Eigaard et al., 2016). Very little, or no penetration, is thought to occur from the Danish seine ropes (Noack et al., 2019), which account for ~99 % of the total footprint. Accordingly, it is expected that the macrofauna depletion rate is lesser within the areas impacted by the seine ropes (Eigaard et al., 2016). To test this, we undertook targeted sampling within the areas of seabed impacted by the two respective main gear-components, under single and multiple hauling intensity of the gear in two nearby areas. This allowed us to i) assess whether the depletion of benthic macrofauna varied across the full Danish seine footprint, to ii) assess whether multiple impacts of the Danish seine reduced benthic macrofaunal metrics to a greater extent, and iii) to combine the two component-specific effects and produce an empirically derived whole-gear depletion rate for the Danish seine. This study presents the results of two gear-component specific Before-After-Control-Impact (BACI) experiments that took place in sandy coastal locations in northeast Jutland, Denmark, using a commercial Danish seine vessel.

2. Material and methods

2.1. The Danish seine

The Danish seine was developed in Denmark in 1848, where a beach seine was adapted to catch plaice (*Pleuronectes platessa*) from a rowing boat. The boat operating the Danish seine has since evolved into a bigger, engine powered vessel, which many countries worldwide have adapted for use in their vessel-based seine fisheries (Walsh and Winger, 2011). The assumed low seabed impact of the Danish seine is, in part, due to the hauling procedure, where the gear is retrieved from an anchored position using hydraulics as opposed to being towed directly by the vessel-engine, like for otter trawls and beam trawls (Noack et al., 2017). This difference in towing principles (hydraulics *vs.* vessel movement) is also the main reason why Danish seiners have higher catch quality and survival of discards (Dinesen et al., 2018; Noack et al., 2020) as well as much higher fuel efficiency than otter and beam trawlers fishing for the same species (Bastardie et al., 2022).

The basics of a Danish seine-haul is that a net (the seine) is towed by two long ropes, attached on each wing end of the seine, to an anchored vessel. The two ropes are laid out in a roughly triangular area from an anchor point and are winched in from the vessel, which reduces the area between the ropes until the net closes around the catch (Fig. 1). The procedure creates a relatively large footprint on the seabed (~5 km^2 in total and ~1 km^2/hour) (Eigaard et al., 2016; Noack et al., 2019). That said, ~99 % of the footprint is from the ropes moving across the seabed, and ~1 % from the ground gear and the attached seine net (Noack et al., 2019). The two gear components interact with the seabed differently, which creates a heterogeneous footprint and physical effect.

2.2. Study area

The fishing experiment took place in Ålbæk Bay, located southeast of the northern tip of Jutland, Denmark (Fig. 2A), a shallow (<20 m) and semi-sheltered bay in the northern Kattegat. The location was selected due to an absence of commercial fishing with bottom-towed gears in the nine years prior to the study, as determined by Vessel Monitoring System (VMS), Automatic Identification System (AIS), and information from local fishers. The absence of bottom trawling in the experimental area is due to many underwater wooden posts that remain from abandoned fyke nets, which represent a large risk of tearing the seine gear. Two adjacent sites were scanned for wooden posts and selected for experimental trawling (Fig. 2B) in comparable coastal conditions to nearby fishing grounds of similar distance from shore, depth, substrate and exposure. The experimental sites each covered ~5.5 km^2 and were oriented perpendicular to the coast, which resulted in a depth range between 6 and 10 m. The sediment type at both locations was sand. At the northerly site, the Danish seine was deployed once and referred to hereafter as the 'single haul' site. At the southerly site, the Danish seine was deployed three times in succession and referred to as the 'multiple haul' site (Fig. 2C).

2.3. Experimental design and data collection

The BACI design applied here aims to isolate the effect of fishing by using a factorial design that includes a comparison in time (before and after experimental fishing) and space (impacted and control sites). A significant interaction between time (e.g., before, after) and treatment (e.g., control, impact) indicates an effect of fishing (Green, 1979). However, a potential issue is that it is possible for significant interactions to occur when there has been a greater change in the control treatment (Chevalier et al., 2019), unrelated to a potential fishing effect. According to Underwood (1992), to satisfy a causal relationship from a known disturbance, the change over time should be greater in the impact treatment than in the control treatment. To negate this, and to provide quantification of any significant BACI interaction, we followed the approach from Chevalier et al. (2019) and applied two additional metrics; the Control-Impact (CI) Contribution and the CI Divergence (described in the 'Data Analysis' section).

To improve our understanding of how Danish seines interact with benthic fauna, our BACI sampling design included targeted sampling of each of the main gear components, i.e., the rope and ground gear (Fig. 2C). This was achieved by attaching floating Global Positioning System (GPS) loggers to both the wing ends of the seine net (Noack et al., 2019). Benthic samples were collected once before and once after fishing at both the single and multiple haul site. Each site was divided into five zones comprising two control zones (areas just north and south of the gear footprint), two rope zones (the footprint on either side of the ground gear), and the ground gear zone (the middle part of the footprint) (Fig. 2). Experimental fishing was carried out at both sites on the 21st June 2019 by the commercial Danish seine vessel S15 *Vera Maria* (length 16.3 m, engine power: 140 kW). Benthic macrofaunal samples

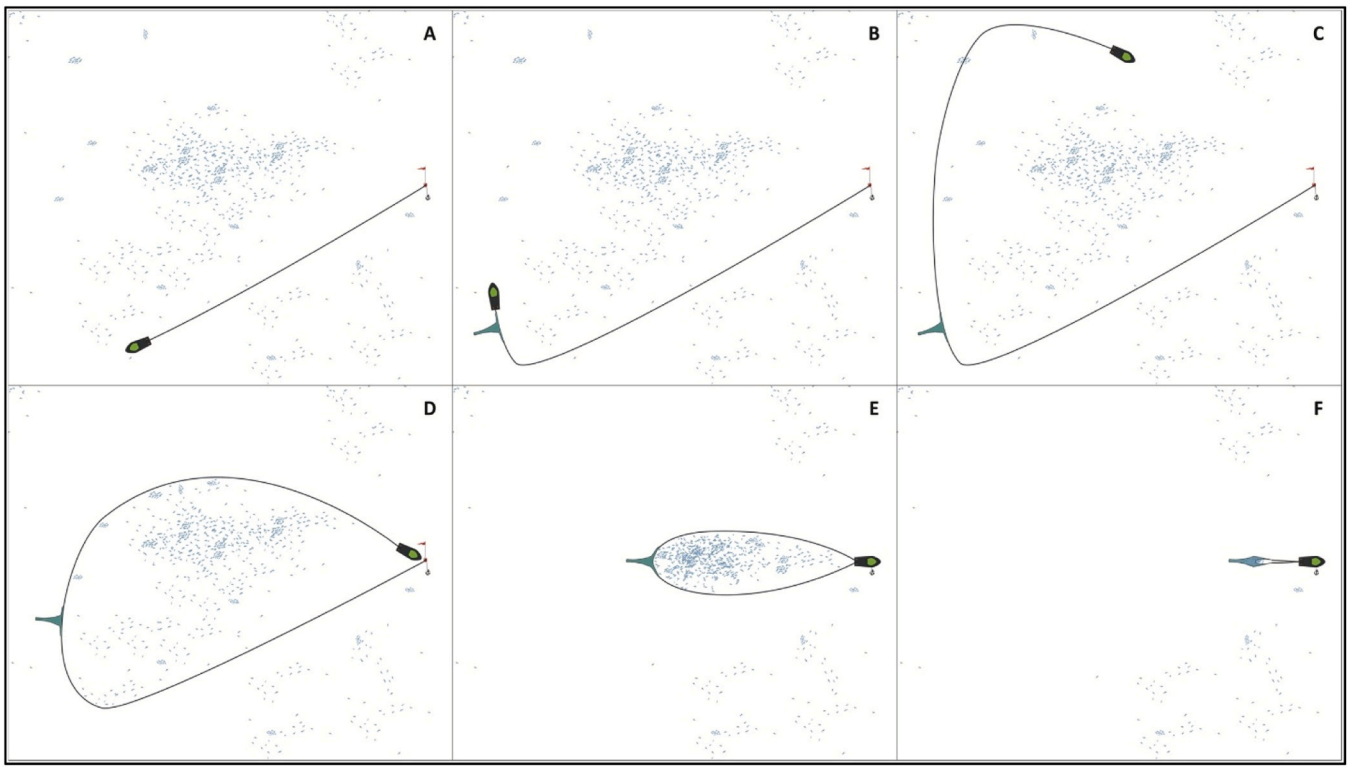

Fig. 1. The main phases of the Danish seine fishing process (A) setting rope 1, (B) deploying the ground gear and net, (C) setting rope 2, (D) returning to the anchor, (E) herding phase, and (F) catching phase. (Reproduced with permission from Noack et al., 2019).

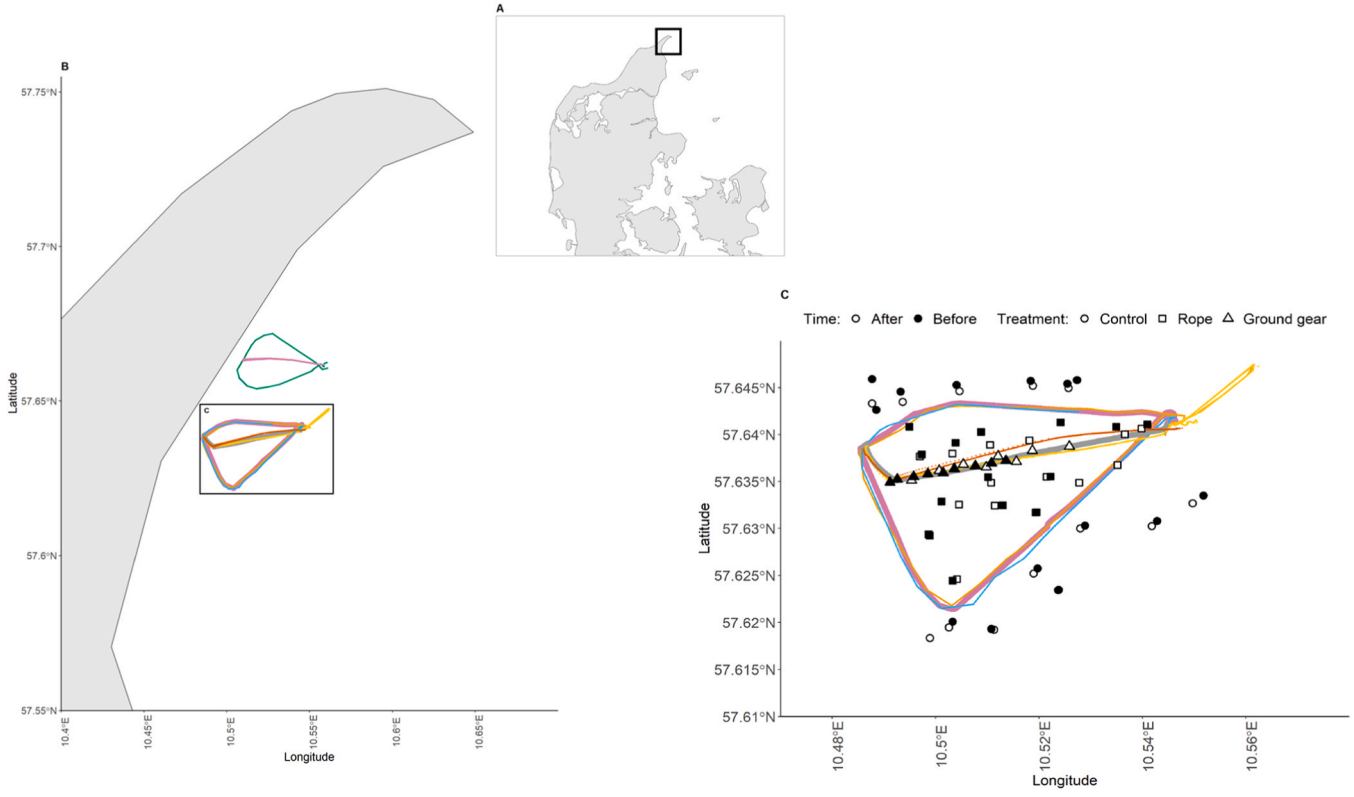

Fig. 2. (A) study location in Ålbæk Bay, (B) location of respective experimental sites and the gear footprints of the experimental hauls, (C) the multiple haul site showing before (blue) and after (red) seining sampling points. The sampling points are spread within two rope areas, along the central track of the ground gear, and across two control areas located north and south of the gear footprint.

were collected using a Van Veen grab (sampling area: 0.1 m^2) on the 18th and 19th June 2019 (before fishing) and 26th and 27th June 2019 (after fishing). The 'after' sampling took place several days after the trials to reduce potential bias introduced by scavenging species in the period immediately after fishing.

The Danish seine net used in the experiment had 455 meshes around the fishing circle (nominal mesh size 120 mm), and a ground gear of approximately 43.8 m made of Taifun wire (diameter: 14 mm, weight in air: 0.25 kg·m^{-1}, weight in water: 0.15 kg·m^{-1}). The gear was additionally weighted with 90 kg of lead and had rubber bobbins (15 cm diameter, 4 cm thick) interspaced with four cookies (5 cm diameter, 2 cm thick) attached along the ground rope. The ropes of the seine gear were made of leaded seine ropes "Icelandic seine rope" (diameter 26 mm, weight in air 0.56 kg·m^{-1}, weight in water 0.12 kg·m^{-1}). To determine the seabed impacts of the rope and ground gear separately, GPS loggers (Canmore G-PORTER GP-102 +; accuracy: 2.5 m) were attached to the gear during hauling. This approach allows for accurate mapping of the gear footprint following the methodology described in Noack et al. (2019). In the interest of having paired 'before' and 'after' samples, we used pre-defined anchor points for each site and overlaid theoretical modelled gear footprints based on the methods of Noack et al. (2019).

Each sediment sample collected was then sieved on board through 4- and 1-mm sieves to divide the faunal sample into two size fractions. Large benthic macrofauna (≥4 mm) have been shown to be comparatively more sensitive to fishing disturbance (McLaverty et al., 2020), although this approach has not been tested for a BACI experiment. Benthic macrofauna were preserved in borax-saturated 4 % formaldehyde prior to taxonomic identification and enumeration in the laboratory. Biomass (wet weight) was determined for the large 4 mm fraction of the community only. At the single haul site, 8 samples were taken from the control and ground gear treatments, and 7 samples were taken from within the rope treatment, with 3 or 4 replicates per zone (N = 23) at each time. At the multiple haul site, 6–9 replicates were taken per zone (N = 37). To visually examine the seabed impact of the seine, side-scan sonar (Edgetech 4125 SAR 600/1600) was used to scan a section of each site before and after fishing. The side scan sonar was towed 3–4 m above the seabed with a range of 55 m on either size. A scanning frequency of 600 kHz was used at a towing speed of 1 kn.

2.4. Data analyses

2.4.1. Univariate analysis

Generalised linear models were fitted using a Bayesian framework to assess gear component-specific effects of the Danish seine on 10 different benthic macrofaunal indicators. We examined the response of three community indicators - density, species richness and biomass –with density and species richness additionally analysed across two size groups/fractions: the full community (>1 mm) and large fauna (>4 mm). We also analysed responses of two common surface dwelling tube-building species, the sandmason worm (*Lanice conchilega*) and the horseshoe worm (*Phoronis* spp.), chosen as these emergent or erect surface-dwelling species are potentially sensitive to sediment surface disturbance from the Danish seine. We further explored potential impacts on functionally similar species in terms of those with 'tube builder' traits, and also those with scavenging and suspension feeder traits, based on their well-documented sensitivity to bottom trawling (Kenchington et al., 2006; Reiss et al., 2009; Sköld et al., 2018; Hiddink et al., 2020; McLaverty et al., 2021, Bromhall et al., 2022).

All models included the BACI factorial predictors (Time, Treatment, and Site), and followed the basic structure:

$$\log(u_i) = \beta_0 + \beta_1 Time_i + \beta_2 Treatment_i + \beta_3 Site_i + \beta_4 (Time * Treatment)_i + \beta_5 (Time * Site)_i + \beta_6 (Treatment * Site)_i + \beta_7 (Time * Treatment * Site)_i \quad (1)$$

where $u_i = E(Y_i)$ is the expected value of the response variable (e.g. density, biomass, tube builders, etc.), β_0 the intercept, and $\beta_1 - \beta_7$ the fixed effects coefficients. Appropriate exponential family distributions were fitted depending on the response type:

- Poisson: $Y_i \sim Poisson(u_i)$
- Negative Binomial: $Y_i \sim NegBin(u_i, \theta), Var(Y_i) = u_i + \frac{u_i^2}{\theta}$
- Gamma: $Y_i \sim Gamma(u_i, \phi), Var(Y_i) = \frac{u_i^2}{\phi}$

Models were first fitted with a Poisson distribution for count data and gamma distribution for biomass data, with a negative binomial distribution was used in place of Poisson where overdispersion was detected (Supplementary Figure 1). A log-link function was used in all cases to relate the expected response to the linear predictor.

Additional covariates were also tested for inclusion in the model such as water depth (m), *L. conchilega* tube biomass (g), given that habitat forming species such as *L. conchilega* can affect local species richness and density (Callaway, 2006). Density was also included as a predictor in models of species richness *as per* (Gislason et al., 2017). Additionally, the inclusion of random intercepts were also examined. Selection of the most parsimonious model was based on 'leave-one-out' (LOO) cross-validation (Vehtari et al., 2017) and Watanabe-Akaike Information Criterion (WAIC) (Watanabe, 2010). As no prior information was available on the impact from the Danish seine, we defined weakly-informative priors with a normal distribution for the parameters and intercept and a half-Cauchy prior for the dispersion parameter of the Gamma and negative binomial models Gelman et al., 2008). The final suite of models analysed, as well as prior distributions, are listed in Supplementary Table 1.

Models were run using the R package 'brms' (Bürkner, 2017) using 20,000 iterations across 4 chains with a 'burn-in' of 10,000, yielding a total of 40,000 post 'warm-up' iterations per model. We checked for zero inflation or deflation and spatial autocorrelation, with none detected (Supplementary Figure 2A). Moran I's tests using the DHARMa package Hartig, 2019) were used to validate the models (Supplementary Figure 2B).

2.4.1.1. Before-after-control-impact ratios. To estimate potential fishing impacts, we followed Conner et al. (2016) by employing Markov Chain Monte Carlo (MCMC) sampling to compute BACI ratios for each response variable. The advantage of this approach is that BACI ratios compare change over time at the impact site to that of change over time at the control site, and can distinguish whether observed differences are due to fishing or natural changes. We calculated BACI ratios separately for rope and ground gear components at both single and multiple haul sites, giving four BACI ratios per indicator i.e. a rope and ground gear impact at the single haul site, and the same at the multiple hauls site. Posterior samples for each time and treatment were extracted for each model, with N number of samples equal to the post-warm up iterations (Supplementary Table 1). The 'before' and 'after' ratios were calculated as follows:

$$R_{i|Before} = \frac{\widehat{Y}_{i|I_{Before}}}{\widehat{Y}_{i|C_{Before}}}; R_{i|After} = \frac{\widehat{Y}_{i|I_{After}}}{\widehat{Y}_{i|C_{After}}}; i = 1, \ldots, N\# \quad (2)$$

Where $R_{i\,|Before}$ is the 'before ratio' and $R_{i\,|After}$ is the 'after ratio' for the *i*-th iteration for each of the impact treatments (rope or ground gear) at each of the sites (Single or Multiple haul). $\widehat{Y}_{i|I}$ and $\widehat{Y}_{i|C}$ represent the fitted values on the response scale for the *i*-th iteration of the impact and control, respectively. The BACI ratios were then calculated by:

$$R_{i|BACI} = \frac{R_{i|After}}{R_{i|Before}}; i = 1, \ldots, N\# \quad (3)$$

yielding a posterior distribution of *N* BACI ratios for each model. A BACI

ratio of 1 indicates the 'before' and 'after' ratios are equal, and no difference between the impact and control sites over time. A BACI ratio of < 1 therefore suggests a decline at the impact site relative to the control (a negative fishery effect), while > 1 indicates an increase. This is shown via a mean effect response, which is the average proportional change in the BACI ratio (in %). For example, a mean effect response of −10 % indicates a 10 % reduction in a given indicator after fishing. These values are supported by a 95 % credible interval (referred to as 'Cred') showing the uncertainty range of that estimate. The BACI ratio probability expresses the likelihood (in %) of an observed negative fishery effect. The values are estimated as the proportion of BACI ratios (out of *N* ratios) corresponding to a ratio < 1. Accordingly, BACI ratios closer to 100 % suggest a high probability of a negative fishery effect, while values closer to 0 % suggest a low probability of a negative fishery effect, and can be inferred that the indicator value has increased over time. Probabilities close to 50 % indicate high uncertainty (i.e. an equal chance of a positive or a negative effect).

2.4.1.2. Complimentary metrics: CI contribution and CI divergence. To aid interpretation of BACI interactions and assess whether changes are due to fishing rather than natural variation, we used two additional metrics as recommended by Chevalier et al. (2019). The first metric, CI-Contribution, identifies which treatment (control or impact) shows the greatest absolute change over time. The value of this is that a greater change in the impact site (i.e. via the rope/ground gear) would meet Underwood's criteria for a causal effect (Underwood, 1992), thus supporting the hypothesis of a fisheries effect. Probabilities approaching 100 % indicate a larger change in the impact site (a fishery effect), while values approaching 0 % indicate a greater change in the control (non-fishery effect due to e.g. natural variability or a compromised control site). A probability of 50 % indicates similar changes in both sites. The CI-Contribution was calculated as follows:

$$CI-Contribution=\left|\widehat{Y}_{i|I_{After}}-\widehat{Y}_{i|I_{Before}}\right|-\left|\widehat{Y}_{i|C_{After}}-\widehat{Y}_{i|C_{Before}}\right|\quad i=\ 1,\ \ldots,N\# \tag{4}$$

The second metric, CI-Divergence, measures whether impact and control sites diverge or converge over time. A large divergence in indicator values would indicate a fisheries effect, while a convergence would indicate otherwise. Accordingly, we interpret the CI-Divergence in a similar manner to the CI-Contribution, with probabilities approaching 100 % indicating increasing differences between sites (fisheries effect), and values approaching 0 % indicates the treatments becoming more similar (no effect of fishing). Similar levels of change in the sites would be reflected by a CI-Divergence of 50 %. CI-Divergence was calculated as follows:

$$CI-Divergence=\left|\widehat{Y}_{i|I_{After}}-\widehat{Y}_{i|C_{After}}\right|-\left|\widehat{Y}_{i|I_{Before}}-\widehat{Y}_{i|C_{Before}}\right|;i=1,\ \ldots,N\ \#\tag{5}$$

The method of combining mean effect sizes, BACI ratios, and CI-Contribution and CI-Divergence estimates is intended provide a thorough and robust approach to assessing potential fishery effects from before/after experiments, and to provide different metrics that can help interpret the observed responses. To take an example, a high probability of a negative fisheries effect would be observed via a negative mean effect response (a decline in the indicator), the 95 % credible interval not overlapping with zero, a high BACI ratio probability (near 100 %), and similarly high CI-contribution and CI-Divergence values. On the other hand, strong evidence of a positive effect of fishing would be indicated by a positive mean effect response, the 95 % credible interval not overlapping with zero, low BACI ratio probability (near 0 %), and high (near 100 %) CI-contribution and CI-Divergence probabilities. In each case, 40,000 post warm-up MCMC samples were used to calculate probabilities.

2.4.1.3. Whole-gear depletion rate. Based on the component-specific effects estimated in this experiment and the component-specific footprint proportions (rope 99 % and ground gear 1 %) estimated in Noack et al. (2019), a whole-gear single-pass depletion rate of biomass was calculated for the 4 mm proportion of the fauna:

Whole-gear (DRS) = Effect (RS) x Proportion (RF) + Effect (GS) x Proportion (GF)(6)

Where DRS = Depletion Rate Single-pass, RS = Rope Single-pass, RF = Rope Footprint, GS = Ground gear Single-pass, and GF = Ground gear Footprint. The use of biomass, as opposed to density, for the calculation of this metric is in line with other estimates of gear depletion rates used in the ICES area (Rijnsdorp et al., 2020).

2.4.2. Multivariate analysis

To assess the effects of Dansh seining on benthic macrofaunal community characteristics, we analysed potential changes to species and trait composition using a combination of Bayesian ordination and multivariate regression analysis. Species community composition consisted of counts of taxa that were present in more than three samples (i.e. rare taxa removed). Biological traits were coded for each taxa at the genus or higher taxonomic level using the EU BENTHIS database (Bolam et al., 2017) and calculated following Bolam et al. (2014).

First, we performed a Bayesian unconstrained ordination by fitting a pure latent variable model (LVM). The LVM represents a model-based ordination approach that treats ordination scores as unobserved random effects, i.e., 'latent variables' (Hui et al., 2015). Therefore, this approach estimates the correlation between species without any predictor variables. In addition, the LVM identifies any indicator species associated with different clusters (Hui et al., 2015). To consider differences in both density and species composition, we omitted the row effect (Hui, 2016). We then fitted three Correlated Response Models (CRM), which included the latent variables and one of our other predictors (BACI interaction; Depth; *Lanice conchilega* tube biomass).

Unconstrained ordinations from the LVM were compared to the residual ordinations from the CRMs to determine whether community patterns were explained by any of the predictors. Initially we used a Poisson distribution to model species density, but information criteria and model validation plots indicated that a negative binomial distribution would provide an improved model fit (Supplementary Figure 1 and 2). The boral package for R (Hui, 2016) was used to implement the LVMs and CRMs. All statistical analyses were carried out in R programming language (R Core Team, 2020).

3. Results

The processing of 120 benthic samples identified 18,504 individuals from 133 different taxa. Of these, 79 % of taxa were represented in the small fraction (106 taxa), 72 % of taxa represented in the large fraction (96 taxa), with 13 % unique to the large fraction (17 taxa). The most abundant taxa in the pooled community were *Urothoe poseidonis* (Malacostraca), *Fabulina fabula*, *Spisula subtruncata* (both Class Bivalvia), *Spiophanes bombyx*, *Scoloplos armiger*, *Chaetozone setosa*, *Eunoe nodosum*, *Lanice conchilega*, and *Magelona mirabilis* (all Phylum Annelida).

3.1. Univariate

3.1.1. Single haul – seine rope

Observed changes to benthic indicators after fishing are provided as mean effect responses and shown in Table 1 and Fig. 3A for the single haul experiment. These responses reveal that a single pass of the Danish seine rope resulted in a −3 % decline in species richness (Cred:-27–52 %), −11 % decline in large fauna density (Cred:-32–52 %), −9 % decline in large fauna species richness (Cred:-31–65 %), and −8 % decline in large fauna biomass (Cred:-76–150 %), relative to the control site.

However, in each case the associated 95 % credible intervals

Table 1
Summary results from the single haul experiment. Potential fishery effects are shown via the mean response size and 95 % Bayesian credible interval, BACI Ratio (i.e. the probability of a negative effect of fishing), CI-Contribution (i.e. probability of a fishery induced change in the impact treatment) and CI-Divergence (i.e. the probability that treatments became more different due to fishing).

Intensity - gear component	Variable	Mean effect response (95 % Credible interval)	BACI ratio - *Prob. of a negative fishery effect*	CI Contribution - *Prob. of a positive CI Contribution*	CI Divergence - *Prob. of a positive CI Divergence*
Single haul - rope	*Community indicators*				
	Density	8 % (-32–52 %)	35 %	54 %	39 %
	Density (large taxa)	-11 % (-32–52 %)	69 %	51 %	38 %
	Species richness	-3 % (-27–25 %)	62 %	57 %	39 %
	Species richness (large taxa)	-9 % (-31–65 %)	38 %	62 %	62 %
	Species/trait				
	Biomass (large taxa)	-8 % (-76–150 %)	67 %	65 %	38 %
	Lanice conchilega	-37 % (-83–59 %)	87 %	21 %	52 %
	Phoronis spp.	-35 % (-89–110 %)	83 %	80 %	25 %
	Tube builders	-4 % (-49–65 %)	61 %	57 %	45 %
Single haul - ground gear	Community indicator				
	Density	24 % (-14–72 %)	11 %	79 %	16 %
	Density (large taxa)	-8 % (-112–66 %)	65 %	68 %	66 %
	Species richness	-1 % (-24–28 %)	52 %	54 %	48 %
	Species richness (large taxa)	10 % (-29–63 %)	36 %	62 %	66 %
	Biomass (large taxa)	11 % (-69–185 %)	54 %	65 %	45 %
	Species/trait				
	Lanice conchilega	5 % (-70–167 %)	7 %	41 %	73 %
	Phoronis spp.	21 % (-78–281 %)	53 %	54 %	50 %
	Tube builders	70 % (-8–187 %)	4 %	88 %	25 %

overlapped with zero, signalling high uncertainty in the estimates (Fig. 3A). The BACI ratios indicated a low probability that the observed declines were a result of fishing, given that probabilities ranged between 38 % (large fauna species richness) and 69 % (large fauna density), and for context, a 50 % probability would represent an equal chance of a positive or a negative response. The complimentary metrics provided similarly limited support for a fishery effect, either in terms of a greater change in the impact treatment (CI-Contribution) or greater dissimilarity between treatments after fishing (CI-Divergence). The only indicator that did not decline was density (+8 %) (Fig. 3A).

At the species/trait level, potential fishery effects were more evident. The −37 % decline in *Lanice conchilega* and −35 % decline in *Phoronis* spp. density were associated with a BACI ratio probability exceeding 80 %. In the case of *Phoronis* spp., the greatest difference in density occurred in the impact treatment, providing support for a fishery effect (CI-Contribution = 80 %). However, *Phoronis* spp. density converged in the control and impact treatments (CI-Divergence = 25 %), suggesting insufficient evidence for full support of a fisheries effect. The results for *L. conchilega* were less compelling, with neither CI-Contribution nor CI-Divergence values supporting a fishery effect. While the density of tube builders decreased by −4 %, none of the associated metrics suggested the decline was fishery related. The raw observations before and after fishing, showing absolute change in each benthic indicator, are presented in Supplementary Figure 3.

3.1.2. *Single haul – ground gear*

In the area impacted by the ground gear, large fauna density declined by −8 % (Cred: −112–66 %), and species richness decline by −1 % (Cred: −24–28 %), meaning low confidence in the estimates. Conversely, indicators such as density, large taxa species richness, and biomass increased (Figs. 3a, 3d, 3e) by + 24 % (Cred: −14–72 %), + 10 % (Cred: −39–63 %) and + 11 % (Cred: −69–185 %), respectively. However, the associated credible intervals again suggested high uncertainty in the estimates (Table 1) and thus indicating an overall low benthic community impact from a single pass of the ground gear (Fig. 3A).

We observed a BACI ratio probability of 11 % for density, suggesting a possible positive effect of fishing. Although the increase in density was chiefly in the impact area (CI-Contribution: 79 %), density became more similar between treatments after fishing (CI-Divergence: 16 %), limiting support for a fishery effect. Similarly, we observed a + 70 % increase in tube builder density (Cred: −8–187 %) that was supported by both a BACI ratio probability of 4 %, and confirmation the increase was chiefly in the impact area (CI-Contribution 88 %). Nevertheless, tube-builder density also became more similar in the treatments after fishing (CI -Divergence of 25 %), reducing support for a fishery effect. Following a similar pattern, the densities of *L. conchilega* and *Phoronis* spp. increased by + 5 % and + 21 % respectively, but none of the associated metrics suggested these changes were due to fishing. Given that the observed increases in these indicators were unexpected, we further verified the accuracy of sampling points lying within the relatively small ground gear area by overlaying side-scan images of the site (Supplementary Figure 4 and text 1). These images confirmed a single scour mark across the site typical of the Danish seine ground gear during hauling, which also aligned with the location of the ground gear grab samples.

3.1.3. *Multiple hauls – seine rope*

Multiple hauls of the Danish seine rope led to a mean loss across most community indicators (Fig. 3B). Declines ranged from –4 % (Cred: −43–15) for large fauna density to −13 % (Cred: −55–140 %) for large fauna biomass (Table 2). However, the response values were again associated with high uncertainty, due to the 95 % credible intervals overlapping with zero. While the decline in density was supported by a high (80 %) probability, this was not consistent across the associated metrics (CI-Contribution 72 %, CI-Divergence 49 %). The exception to this was for large taxa species richness, which was associated with a mean effect response of + 6 %. This response, however, can be chiefly explained by a marked reduction in richness in the control site over time evidenced by the low (40 %) CI-Contribution value.

Evidence of fishery effects were, however, potentially clearer at the species and trait level. There was a high probability (99 %) that *Phoronis* spp. density declined after fishing, with a mean decrease of −90 % in density in the seine rope area, relative to the control. Large differences in the density of this species were observed after fishing between the treatments (CI-Divergence 95 %), and there was some evidence that the greater changed occurred in the rope treatment (CI-Contribution 72 %). In addition, there was a 98 % probability that tube builder density declined after multiple hauls of the rope, albeit to a lesser extent (-35 %

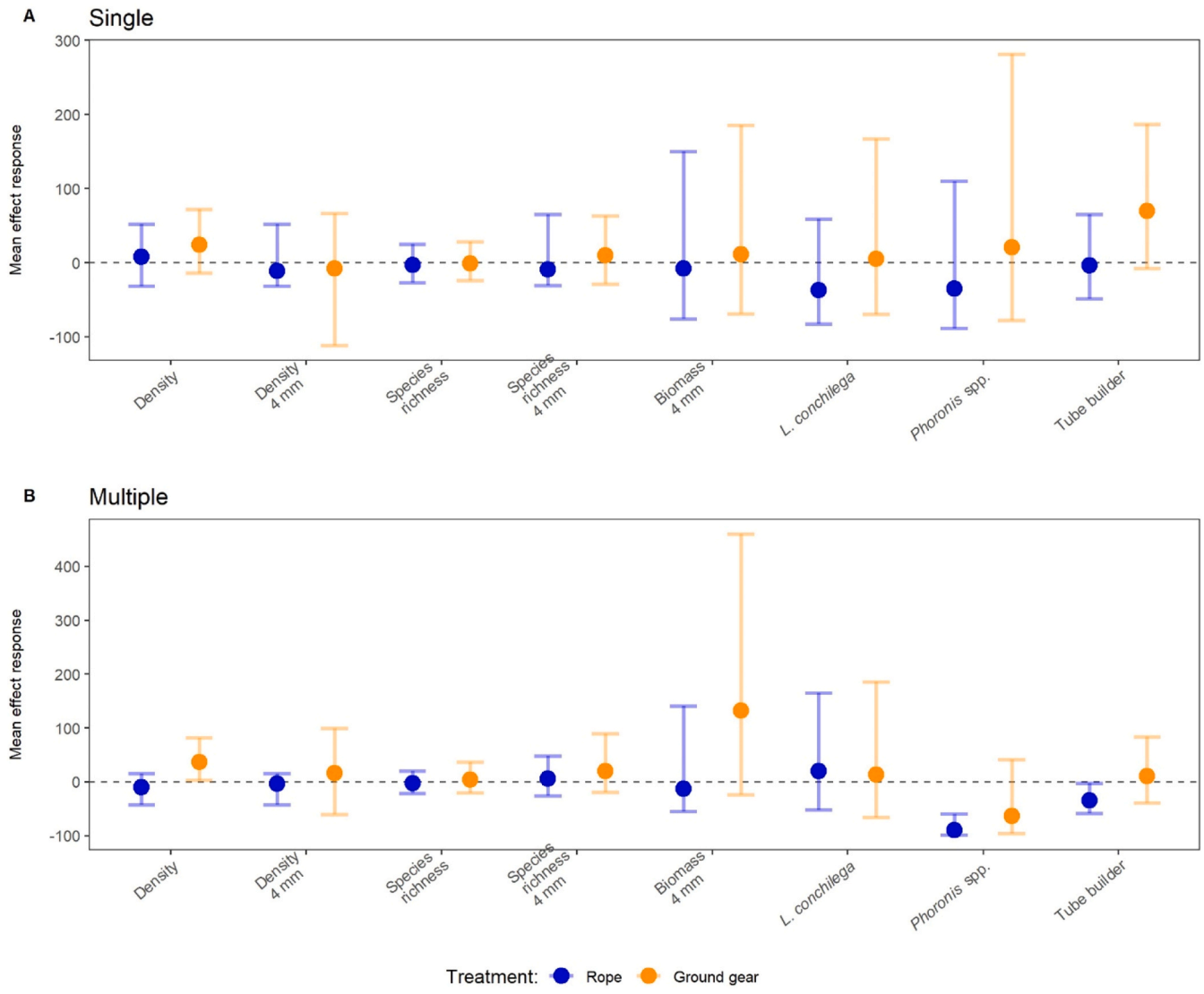

Fig. 3. Mean effect responses of benthic community indicators (with associated +/-95 % Bayesian credible intervals) to impact from the Danish seine rope and ground gear. Part (A) presents the results of the single haul experiment, and part (B) the multiple haul experiment.

CI: −59 to −3 %). The supporting metrics again showed strong evidence that fishing resulted in large differences in density between treatments (CI-Divergence 96 %), and some evidence that the impact treatment changed to a greater extent (CI-Contribution 77 %).

3.1.4. *Multiple hauls – ground gear*

In a similar response to the single haul experiment, increases in indicators values were observed from multiple passes of the ground gear (Fig. 3B). The estimated increases ranged from + 4 % (Cred: - 20–36 %) for species richness to + 132 % (Cred: −24–460 %) for biomass (Table 2). The probability that biomass increased after fishing was 92 % (BACI ratio of 8 %) with the greatest change occurring in the fished area (CI-Contribution 90 %), with some, albeit weak, evidence that biomass between treatments was less similar after the fishing experiment (CI-Divergence 69 %) (Table 2). Density also increased by + 36 %, supported by a high associated probability (2 %) of a positive effect. The increase in density mainly occurred in the impact area (CI-Contribution: 93 %), however, density became more similar between treatments after fishing (CI-Divergence: 25 %) reducing the support for a positive fisheries effect

On the contrary, there was a 94 % probability that *Phoronis* spp., decreased, with a mean decline of −64 %. Evidence of a negative fisheries effect was also endorsed by the CI-Divergence of 86 %, although not also reflected in the CI-Contribution value of 47 %. None of the estimates for *Lanice conchilega* or the tube building trait were associated with probabilities evidencing fishery effects.

The response of other traits examined, i.e. suspension feeders and scavengers, did not provide evidence of fishery effects. The results for these traits are provided in Supplementary Figure 7 and Supplementary Table 2.

3.1.5. *Whole-gear depletion rate*

The whole-gear single-pass biomass (fauna >4 mm) depletion rate of the Danish seine was estimated to be 0.068, although in each of the combined component-based depletion estimates (rope and ground gear) the associated 95 % credible interval included zero, signalling high uncertainty in the estimates.

3.2. *Multivariate*

Changes in community composition were observed after fishing in the area impacted multiple times by the seine rope. This response can be seen in the unconstrained ordination from the latent variable model (LVM), where the two clusters (before/after) for the rope treatment

Table 2
Summary of results of the multiple haul experiment. Potential fishery effects are shown via the mean response size and 95 % Bayesian credible interval, BACI Ratio (i.e. the probability of a negative effect of fishing), CI-Contribution (i.e. probability of a greater change in the impact treatment) and CI-Divergence (i.e. the probability that treatments became more different after disturbance).

Intensity - gear component	Variable	Mean effect response (95 % Credible interval)	BACI ratio - *Prob. of a negative fishery effect*	CI Contribution - *Prob. of a positive CI Contribution*	CI Divergence - *Prob. of a positive CI Divergence*
Multiple haul - rope	*Community indicators*				
	Density	-10 % (-43–15 %)	80 %	72 %	49 %
	Density (large taxa)	-4 % (-43–15 %)	61 %	47 %	58 %
	Species richness	-3 % (-22–20 %)	60 %	60 %	48 %
	Species richness (large taxa)	6 % (-26–48 %)	40 %	41 %	51 %
	Biomass (large taxa)	-13 % (-55–140 %)	46 %	52 %	61 %
	Species/trait				
	Lanice conchilega	20 % (-53–165 %)	40 %	58 %	60 %
	Phoronis spp.	-90 % (-99 to −60 %)	99 %	72 %	95 %
	Tube builders	-35 % (-59 to −3 %)	98 %	77 %	96 %
Multiple haul - ground gear	*Community indicator*				
	Density	36 % (3–81 %)	2 %	93 %	25 %
	Density (large taxa)	16 % (-61–99 %)	36 %	53 %	38 %
	Species richness	4 % (-21–36 %)	38 %	43 %	44 %
	Species richness (large taxa)	20 % (-20–89 %)	16 %	39 %	41 %
	Biomass (large taxa)	132 % (-24–460 %)	8 %	90 %	69 %
	Species/trait				
	Lanice conchilega	13 % (-67–185 %)	52 %	50 %	51 %
	Phoronis spp.	-64 % (-97–41 %)	94 %	47 %	86 %
	Tube builders	10 % (-39–83 %)	41 %	39 %	55 %

(shown in yellow) are not overlapping (Fig. 4A). The species mainly responsible for differences in the two clusters were the starfish *Asterias rubens* and the amphipod *Melita obtusata* which are driving the community composition before fishing (seen by their positive position furthest from y = 0)). Similarly, *Phoronis* spp., and the ribbon worm *Nemertea* indet., are driving the composition after fishing (seen by their negative position furthest from y = 0) (Fig. 4B). The cluster overlap visible in the residual ordination from the CRM (Fig. 4C) indicated that the observed differences in community composition were a fisheries effect. To the contrary, clustering in the residual ordination remained unchanged when depth or *Lanice conchilega* tube weight was added to the CRM, suggesting that these variables were unimportant for driving community patterns (Supplementary Figure 5). We did not observe similar separation of clusters in the LVM ordinations for single haul experiment or for the community composition of the large fauna (Supplementary Figure 6).

4. Discussion

The Danish seine is considered a 'low impact' mobile bottom-contacting fishing gear due to its light weight, lack of deep penetrating gear components, and its associated low fuel consumption (Suuronen et al., 2012; Dinesen et al., 2018; Bastardie et al., 2022). Given the low penetrative force, in theory, the depletion of benthic macrofauna should also be relatively low. Our study supports this assumption, by observing only small reductions in different community indicators (density, biomass and species richness) after impact from the Danish seine. Nonetheless, we also found that depletion rates could be high for individual species (*Phoronis* spp.) and similarly for individual biological traits ('tube-builders'). Moreover, our study detected differing effects from the two main gear components and unexpectedly found higher depletion of benthic fauna from the seine ropes than from the ground gear. In line with expectations, depletion was higher from multiple than single hauls. Our results therefore suggest that Danish seines may exert lower impacts on benthic communities compared to more widely used gears, such as beam trawls (Kaiser and Spencer, 1996) and otter trawls (Engel and Kvitek, 1998), that operate in similar habitat types.

4.1. Effect of the Danish seine ropes

We found a high probability (>98 %) that *Phoronis* spp. density and 'tube-builder' density were reduced by multiple hauls of the Danish seine ropes. These two results are inherently linked as *Phoronis* spp. is a tube building taxon. Although *Phoronis* spp. accounted for only 7 % of the total tube builder density, suggesting the observed effect on overall tube-builder density was largely independent of their presence. The sensitivity of *Phoronis* spp. to bottom trawling is closely linked to its life-history traits, as it exhibits non-mobile (sessile), surface dwelling, and erect characteristics (de Juan et al., 2007a; McLaverty et al., 2021). *Phoronis* spp. occupies a sediment position that places it in direct contact with bottom-contacting fishing gears, regardless of the gear penetration depth. Furthermore, *Phoronis* spp. has been shown to be sensitive to otter trawling (Hinz et al., 2009; Sköld et al., 2018) as well as to high fishing pressure exerted by Danish seiner fleets (McLaverty et al., 2024). Accordingly, *Phoronis* spp. may represent a habitat-specific indicator of trawling disturbance.

As the seine rope has a lower weight in water than the ground gear (0.12 $kg \cdot m^{-1}$ versus 0.15 $kg \cdot m^{-1}$) it was unexpected that greater changes to the benthic community would be observed in the rope impacted areas. Possible reasons for this could include high spatial variability in the community, or a bias introduced by an influx of scavenging species. However, our design aimed to account for this by allowing 3 days between fishing and subsequent sampling. An alternative mechanistic explanation is that in some areas the rope is hauled at higher speeds than the ground gear (O'Neill and Noack, 2021) potentially generating larger hydrodynamic forces. In addition to speed, the angle and orientation of the rope while hauling differs to that of the ground gear, which may alter the magnitude and direction of shear stresses.

High hydrodynamic forces are known to propel sediment and associated benthic organisms such as swimming crustaceans (amphipods and mysids) and tube-building polychaetes into the water column (O'Neill et al., 2013; O'Neill and Ivanović, 2016), with these smaller sessile taxa being at risk of being lost from the area. This was mirrored in the changes to community composition observed in rope impacted areas, where small-bodied worm-like taxa (*Phoronis* spp. and Nemertea indet.) significantly decreased post trawling.

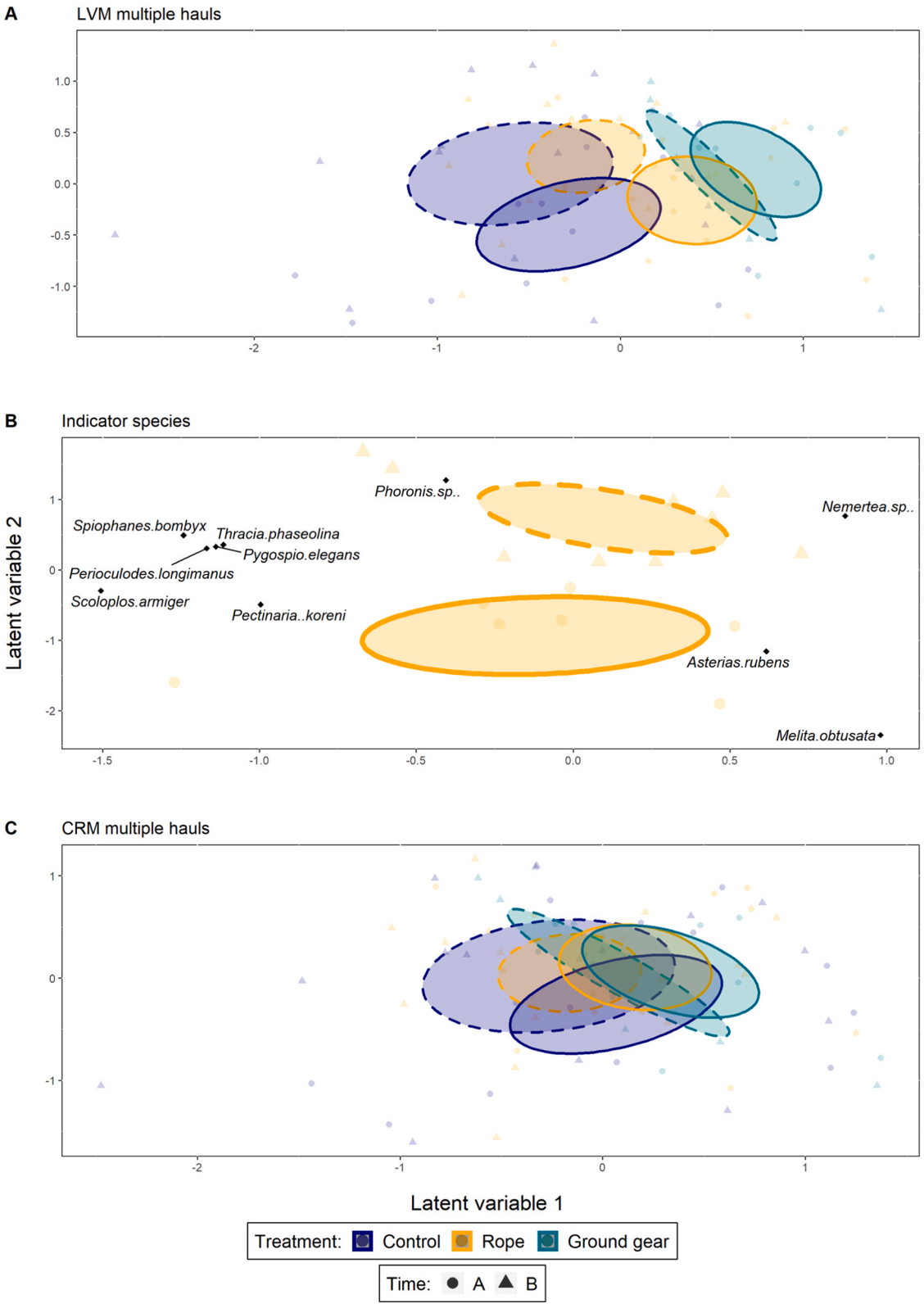

Fig. 4. The multivariate regression analysis showing (A) the unconstrained ordination of the Latent Variable Model (LVM) for the full community - multiple haul site, (B) the unconstrained ordination of the LVM showing the 10 species that contributed most to differences between clusters, (C) the residual ordination of the Correlated Response Model for the full community at the multiple haul site with the BACI interaction included in the model and. Time: A (after) solid ellipses, B (before) dashed ellipses.

4.2. Effect of the Danish seine ground gear

The heavier ground gear was assumed *a-priori* to result in greater benthic impact as it exerts a greater mechanical force on the seabed than the ropes. Counter to our expectations, benthic macrofauna were not reduced in the ground gear area. Instead, there was a positive trend in some community indicators (density and biomass) after both single and multiple hauls of the seine. Increases in benthic density and biomass are known to occur after fishing events due to immigration of scavenging species (Kaiser and Spencer, 1994; Ramsay et al., 1997; Groenewold, Fonds, 2000). Although this was supported by an observed increase in scavenger density after both the single (35 %) and multiple (22 %) hauls (Supplement Table 3), there was high uncertainty associated with the mean values and credible intervals, suggesting weak statistical support for this explanation. In addition, we deliberately waited 72 h after fishing to sample the benthos, which is recommended to allow potential scavengers to disperse after the event (Groenewold and Fonds, 2000).

A possible explanation may lie in potential heterogeneity of the control sites, relative to the gear areas. Samples from the ground gear area were characterised by low macrofaunal density prior to the experiment. After fishing, density was higher in the ground gear area relative to the control, as indicated by the CI-Contributions for both single (78 %) and multiple (93 %) hauls. However, as density overall was more similar after fishing (CI-Divergence single: 16 %, multiple: 25 %), the observed decline in the ground gear area was not truly distinct from observations in the control and suggests an alternate aspect driving the observed decline (Chevalier et al., 2019). The greater geographical distance between the ground gear area and control area, relative to the control and rope areas, may explain why it was potentially a less suitable site for comparison. For context, the control sites were placed to the north and south of the treatment areas to reduce effects of a depth gradient across the controls, which would have been introduced by placing the controls in an east/west orientation.

Another explanation related to the 15 cm diameter rockhopper disks used on the ground gear. These components are 4 cm thick and were spaced approximately 8 cm apart. Accordingly, the area of seabed swept within the ground gear site would have been mainly impacted via these disks being dragged through/over the sediment. This could have resulted in as much as 66 % of the sediment being not directly impacted by the gear, due to the large gaps between each disk (Supplementary Figure 8).

4.3. Whole gear depletion rate & overall effect of the Danish seine

Both component-specific biomass effects estimated from the BACI experiment were associated with high uncertainty, and the ground gear effect was positive. Some potential explanations behind these outcomes are provided above, but regardless the somewhat unexpected results for the ground gear impact adds uncertainty to our estimate of a whole-gear depletion rate of 0.068. It should be also noted that the whole gear depletion rates are calculated from the 4 mm fraction of the sampled fauna. This fraction was prioritised in this study due to its potentially high sensitivity to trawling (McLaverty et al., 2020), and due to logistical constraints limiting our ability to estimate the wet weight biomass of a further 120 small fraction samples. Accordingly, the higher sensitivity of the large fauna in this calculation might explain why our estimated whole gear depletion rate of 0.068 is higher than the assumed estimate of 0.009 in Rijnsdorp et al. (2020), and the 0.057 overall otter trawl estimate of Pitcher et al. (2022).

Overall, the effects of a single Danish seine haul resulted in relatively little change to the benthic community. It is likely at low trawling intensities, i.e., a single haul, changes to the benthos from seining are less than that of natural variability. However, the power to detect a fishery effect, particularly at low fishing intensities, is influenced by the number of replicates sampled, and factors such as the degree of variation observed within treatments. Accordingly, when the intensity of seining was higher i.e. three hauls, we were able to detect an effect of the seine rope on the density of *Phoronis* spp. and the tube builder trait. This suggests that there may be a cumulative effect of the gear on the community, whereby the benthic mortality increases with increased fishing frequency, and in our case, became measurable with the experimental sampling effort deployed.

4.4. Implications for management

Given that the state of the seabed in European fishing grounds are some of the most deteriorated worldwide (Pitcher et al., 2022), alternative or low-impact fishing methods should be considered to improve the environmental status of important fishing grounds. More broadly, a key tenet of an ecosystems approach to fisheries management is to minimise the environmental impacts of fishing to the wider ecosystem, whilst maintaining economically feasible fisheries. The results of this study show that single and multiple passes of a Danish seine result in relatively minor impacts to benthic macrofauna communities. This finding may be of relevance to management as beam and otter trawls are deployed in similar grounds to Danish seines, and target similar species e.g. European plaice (*Pleuronectes platessa*), common dab (*Limanda limanda*), cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*).

Accordingly, we suggest that prioritising lighter seines over beam and otter trawls could help to improve the quality of seabed habitats and ecosystems in fishing grounds, particularly where sensitive or functionally important subsurface dwelling species are present. Furthermore, spatial restrictions on bottom-towed fishing gear that reduce the benthic impacts from fishing have led to increased densities of commercially sized target species (Beukers-Stewart et al., 2005), and increased habitat complexity associated with greater densities of juvenile demersal fish and shellfish (Howarth et al., 2015). By extension, the use of Danish seines in intensive trawling grounds that overlap with areas protected for non-benthic nature features e.g. bird and cetacean species, may also benefit from switching to lower benthic impact fishing gears. This may be relevant as commercial bottom trawling takes place over half (~59 %) of European marine protected areas, with trawling intensity often higher in protected areas than outside Dureuil et al., 2018). Overall, the use of alternative fishing gears, particularly those like the Danish seine that have relatively high catch and fuel efficiency (Dinesen et al., 2018; Noack et al., 2019; Bastardie et al., 2022), have the potential to provide a possible mitigation measure for management by reducing impacts to benthic habitats and ecosystem functionality, improving the sustainability of fisheries in commercially important fishing grounds, and better integrating an ecosystem approach to fisheries management.

CRediT authorship contribution statement

McLaverty Ciaran: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Finbarr G. O'Neill:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation. **Thomas Noack:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Grete E. Dinesen:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Katrina Bromhall:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tim J.G. Wilms:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Ole R. Eigaard:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2025.107611.

Data availability

Data will be made available on request.

References

Amoroso, R.O., Pitcher, C.R., Rijnsdorp, A.D., McConnaughey, R.A., Parma, A.M., Suuronen, P., Eigaard, O.R., Bastardie, F., Hintzen, N.T., Althaus, F., Baird, S.J., Black, J., Buhl-Mortensen, L., Campbell, A.B., Catarino, R., Collie, J., Cowan, J.H., Durholtz, D., Engstrom, N., Jennings, S., 2018. Bottom trawl fishing footprints on the world's continental shelves. Proc. Natl. Acad. Sci. 115 (43), E10275–E10282. https://doi.org/10.1073/pnas.1802379115.

Bastardie, F., Hornborg, S., Ziegler, F., Gislason, H., Eigaard, O.R., 2022. Reducing the fuel use intensity of fisheries: through efficient fishing techniques and recovered fish stocks. Front. Mar. Sci. 9. https://doi.org/10.3389/fmars.2022.817335.

Beukers-Stewart, B.D., Vause, B.J., Mosley, M.W.J., Rossetti, H.L., Brand, A.R., 2005. Benefits of closed area protection for a population of scallops. Mar. Ecol. Prog. Ser. 298, 189–204. https://doi.org/10.3354/meps298189.

Bolam, S.G., Coggan, R.C., Eggleton, J., Diesing, M., Stephens, D., 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: a biological trait approach. J. Sea Res. 85, 162–177. https://doi.org/10.1016/j.seares.2013.05.003.

Bolam, S.G., Garcia, C., Eggleton, J., Kenny, A.J., Buhl-Mortensen, L., Gonzalez-Mirelis, G., van Kooten, T., Dinesen, G., Hansen, J., Hiddink, J.G., Sciberras, M., Smith, C., Papadopoulou, N., Gumus, A., Van Hoey, G., Eigaard, O.R., Bastardie, F., Rijnsdorp, A.D., 2017. Differences in biological traits composition of benthic assemblages between unimpacted habitats. Mar. Environ. Res. 126, 1–13. https://doi.org/10.1016/j.marenvres.2017.01.004.

Bromhall, K., Dinesen, G.E., McLaverty, C., Eigaard, O.R., Petersen, J.K., Saurel, C., 2022. Experimental effects of a lightweight mussel dredge on benthic fauna in a eutrophic MPA. J. Shellfish Res. 40 (3), 519–531.

Bürkner, P.C., 2017. brms: an R package for Bayesian Multilevel Models Using Stan. J. Stat. Softw. 80, 1–28. https://doi.org/10.18637/jss.v080.i01.

Callaway, R., 2006. Tube worms promote community change. Mar. Ecol. Prog. Ser. 308, 49–60. https://doi.org/10.3354/meps308049.

Chevalier, M., Russell, J.C., Knape, J., 2019. New measures for evaluation of environmental perturbations using Before-After-Control-Impact analyses. Ecol. Appl. 29, 1–12. https://doi.org/10.1002/eap.1838.

Conner, M.M., Saunders, W.C., Bouwes, N., Jordan, C., 2016. Evaluating impacts using a BACI design, ratios, and a Bayesian approach with a focus on restoration. Environ. Monit. Assess. 188 (10). https://doi.org/10.1007/s10661-016-5526-6.

de Juan, D., Thrush, S., Demestre, M., 2007a. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Mar. Ecol. Prog. Ser. 334, 117–129. https://doi.org/10.3354/meps334117.

DHARM, H.F., 2019. *residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2. 0. 2018* [online].

Dinesen, G.E., Rathje, I.W., Højrup, M., Bastardie, F., Larsen, F., Sørensen, T.K., Hoffmann, E., Eigaard, O.R., 2018. Individual transferable quotas, does one size fit all? Sustainability analysis of an alternative model for quota allocation in a small-scale coastal fishery. Mar. Policy 88, 23–31. https://doi.org/10.1016/j.marpol.2017.10.038.

Dureuil, M., Boerder, K., Burnett, K.A., Froese, R., Worm, B., 2018. Elevated trawling inside protected areas undermines conservation outcomes in a global fishing hot spot. Science 362 (6421), 1403–1407.

Eigaard, O.R., Bastardie, F., Breen, M., Dinesen, G.E., Hintzen, N.T., Laffargue, P., Mortensen, L.O., Nielsen, J.R., Nilsson, H.C., O'Neill, F.G., Polet, H., Reid, D.G., Sala, A., Sköld, M., Smith, C., Sørensen, T.K., Tully, O., Zengin, M., Rijnsdorp, A.D., 2016. Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsv099.

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., Vanelslander, B., Rijnsdorp, A.D., 2017. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES J. Mar. Sci. 74, 847–865. https://doi.org/10.1093/icesjms/fsw194.

Engel, J., Kvitek, R., 1998. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. Conserv. Biol. 12 (6), 1204–1214.

Gelman, A., Jakulin, A., Pittau, M.G. and Su, Y.S., 2008. A weakly informative default prior distribution for logistic and other regression models.

Gislason, H., Bastardie, F., Dinesen, G.E., Egekvist, J., Eigaard, O.R., 2017. Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. Ecol. Indic. 82, 260–270.

Green, R.H., 1979. Sampling design and statistical methods for environmental biologists. John Wiley & Sons.

Groenewold, S., Fonds, M., 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. ICES J. Mar. Sci. 57, 1395–1406. https://doi.org/10.1006/jmsc.2000.0914.

Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Mazor, 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. 114, 8301–8306. https://doi.org/10.1073/pnas.1618858114.

Hiddink, J.G., Kaiser, M.J., Sciberras, M., McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Parma, A.M., Suuronen, P., Rijnsdorp, A.D., Jennings, S., 2020. Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. J. Appl. Ecol. 57, 1199–1209. https://doi.org/10.1111/1365-2664.13617.

Hinz, H., Prieto, V., Kaiser, M.J., 2009. Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecol. Appl. https://doi.org/10.1890/08-0351.1.

Howarth, L.M., Pickup, S.E., Evans, L.E., Cross, T.J., Hawkins, J.P., Roberts, C.M., Stewart, B.D., 2015. Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve. Mar. Environ. Res. 107, 8–23.

Hui, F.K.C., 2016. boral – Bayesian ordination and regression analysis of multivariate abundance data in R. Methods Ecol. Evol. 7, 744–750. https://doi.org/10.1111/2041-210X.12514.

Hui, F.K.C., Taskinen, S., Pledger, S., Foster, S.D., Warton, D.I., 2015. Model-based approaches to unconstrained ordination. Methods Ecol. Evol. 6, 399–411. https://doi.org/10.1111/2041-210X.12236.

Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C.V., 2006. Global analysis of response and recovery of benthic biota to fishing. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps311001.

Kaiser, M.J., Spencer, B.E., 1994. Fish scavenging behaviour in recently trawled areas. Mar. Ecol. Prog. Ser. 112, 41–50. https://doi.org/10.3354/meps112041.

Kaiser, M.J., Spencer, B.E., 1996. The effects of beam-trawl disturbance on infaunal communities in different habitats. J. Anim. Ecol. 348–358.

Kenchington, E.L.R., Gilkinson, K.D., MacIsaac, K.G., Bourbonnais-Boyce, C., Kenchington, T.J., Smith, S.J., Gordon, D.C., 2006. Effects of experimental otter trawling on benthic assemblages on Western Bank, northwest Atlantic Ocean. J. Sea Res. 56, 249–270. https://doi.org/10.1016/j.seares.2006.03.010.

McLaverty, C., Beukhof, E.D., Bromhall, K., Dinesen, G.E., Erichsen, A.C., Eigaard, O.R., 2024. The relative effects of bottom trawling, organic enrichment, and natural environmental factors on coastal seabed communities. Mar. Pollut. Bull. 209. https://doi.org/10.1016/j.marpolbul.2024.117169.

McLaverty, C., Dinesen, G., Gislason, H., Brooks, M., Eigaard, O., 2021. Biological traits of benthic macrofauna show sizebased differences in response to bottom trawling intensity. Mar. Ecol. Prog. Ser. 671, 1–19. https://doi.org/10.3354/meps13790.

McLaverty, C., Eigaard, O.R., Gislason, H., Bastardie, F., Brooks, M.E., Jonsson, P., Lehmann, A., Dinesen, G.E., 2020. Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. Ecol. Indic. 110, 105811. https://doi.org/10.1016/j.ecolind.2019.105811.

Noack, T., Frandsen, R.P., Wieland, K., Krag, L.A., Berg, F., Madsen, N., 2017. Fishing profiles of Danish seiners and bottom trawlers in relation to current EU management regulations. Fish. Manag. Ecol. 24, 436–445. https://doi.org/10.1111/fme.12244.

Noack, T., Savina, E., Karlsen, J.D., 2020. Survival of undersized plaice (Pleuronectes platessa) discarded in the bottom otter trawl and Danish seine mixed fisheries in Skagerrak. Mar. Policy 115, 103852. https://doi.org/10.1016/j.marpol.2020.103852.

Noack, T., Stepputtis, D., Madsen, N., Wieland, K., Haase, S., Krag, L.A., 2019. Gear performance and catch process of a commercial Danish anchor seine. Fish. Res. 211, 204–211. https://doi.org/10.1016/j.fishres.2018.11.012.

Norling, K., Rosenberg, R., Hulth, S., Grémare, A., Bonsdorff, E., 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem

functions in marine sediment. Mar. Ecol. Prog. Ser. 332, 11–23. https://doi.org/10.3354/meps332011.
O'Neill, F.G., Ivanović, A., 2016. The physical impact of towed demersal fishing gears on soft sediments. ICES J. Mar. Sci. 73, i5 i14.
O'Neill, F.G., Noack, T., 2021. The geometry and dynamics of Danish anchor seine ropes on the seabed. ICES J. Mar. Sci. 78, 125–133. https://doi.org/10.1093/icesjms/fsaa198.
O'Neill, F.G., Robertson, M., Summerbell, K., Breen, M., Robinson, L.A., 2013. The mobilisation of sediment and benthic infauna by scallop dredges. Mar. Environ. Res. 90, 104–112.
Pitcher, C.R., Hiddink, J.G., Jennings, S., Collie, J., Parma, A.M., Amoroso, R., Mazor, T., Sciberras, M., McConnaughey, R.A., Rijnsdorp, A.D., Kaiser, M.J., Suuronen, P., Hilborn, R., 2022. Trawl impacts on the relative status of biotic communities of seabed sedimentary habitats in 24 regions worldwide. Proc. Natl. Acad. Sci. 119. https://doi.org/10.1073/pnas.2109449119.
R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL ⟨https://www.R-project.org/⟩.
Ramsay, K., Kaiser, M.J., Moore, P.G., Hughes, R.N., 1997. Consumption of fisheries discards by benthic scavengers: utilization of energy subsidies in different marine habitats. J. Anim. Ecol. 66, 884. https://doi.org/10.2307/6004.
Reiss, H., Greenstreet, S.P.R., Sieben, K., Ehrich, S., Piet, G.J., Quirijns, F., Robinson, L., Wolff, W.J., Kröncke, I., 2009. Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. Mar. Ecol. Prog. Ser. 394, 201–213. https://doi.org/10.3354/meps08243.
Rickwood, M., Kerry, C., Eigaard, O.R., Sala, A., McLaverty, C., Roberts, C.M., Godley, B. J., Metcalfe, K., 2025. Regional variation in active bottom-contacting gear footprints. Fish Fish. 26 (3), 488–503.
Rijnsdorp, A.D., Hiddink, J.G., van Denderen, P.D., Hintzen, N.T., Eigaard, O.R., Valanko, S., Bastardie, F., Bolam, S.G., Boulcott, P., Egekvist, J., Garcia, C., van Hoey, G., Jonsson, P., Laffargue, P., Nielsen, J.R., Piet, G.J., Sköld, M., van Kooten, T., 2020. Different bottom trawl fisheries have a differential impact on the status of the North Sea seafloor habitats. ICES J. Mar. Sci. 77 (5), 1772–1786. https://doi.org/10.1093/icesjms/fsaa050.
Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J., Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hillborn, R., Collie, J.S., Pitcher, C.R., Amoroso, R.O., Parma, A.M., Suuronen, P., Kaiser, M.J., 2018. Response of benthic fauna to experimental bottom fishing: a global meta-analysis. Fish Fish 19, 698–715. https://doi.org/10.1111/faf.12283.
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. https://doi.org/10.3354/meps12434.
Suuronen, P., Chopin, F., Glass, C., Løkkeborg, S., Matsushita, Y., Queirolo, D., Rihan, D., 2012. Low impact and fuel efficient fishing-Looking beyond the horizon, 120 Fish. Res. 119, 135–146. https://doi.org/10.1016/j.fishres.2011.12.009.
Tillin, H.M., Hiddink, J.G., Jennings, S., Kaiser, M.J., 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318, 284–286. https://doi.org/10.3354/meps318031.
Underwood, A.J., 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J. Exp. Mar. Biol. Ecol. 161, 145–178. https://doi.org/10.1016/0022-0981(92)90094-Q.
Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. 27, 1413–1432. https://doi.org/10.1007/s11222-016-9696-4.
Walsh, S.J., & Winger, P.D. (2011). Bottom Seining in Canada, 1948-2010: Its Development, Fisheries and Ecosystem Impacts. Fisheries and Marine Institute Canadian Technical Report of Fisheries and Aquatic Sciences No. 2922. *Canadian Technical Report of Fisheries and Aquatic Sciences*, (2922), XI +147.
Watanabe, S., 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. J. Mach. Learn. Res. 11, 3571–3594.