

ARTICLE

Coastal and Marine Ecology

Spatial capture–recapture reveals resource use and declining skipper numbers in Baltic Sea salmon trolling fisheries

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Abstract

Many populations of Atlantic salmon (*Salmo salar*) native to the Baltic Sea are endangered. A significant group targeting salmon in this region is the recreational trolling fishery. Due to frequent changes in fisheries regulations and conditions, both salmon conservation and fishers are affected. This study aims to enhance our understanding of the spatial extent and population dynamics of salmon trolling boat skippers in the Baltic Sea by estimating their population size and resource use. The study uses participation lists of skippers from recreational fishing tournaments and automatic identification system (AIS) data to track their movements. These lists are formatted as encounter histories for spatial capture–recapture models, while AIS data are integrated as telemetry data to estimate resource selection. The results reveal a 51% decrease in the number of skippers from two time periods: years 2014–2020 and 2021–2023, with the count dropping from 5343 individuals (95% CI = 4622–6178) to 2604 individuals (95% CI = 2273–2983). The decline may be attributed in part to heavy regulations imposed on recreational salmon fisheries in 2022. Furthermore, the resource selection analysis indicates that these skippers target various species outside the Baltic Sea, such as Atlantic Bluefin tuna (*Thunnus thynnus*) in Skagerrak, and endangered Atlantic salmon stocks elsewhere, such as in Lake Vänern. The results of this study suggest that regulations and changes in the Baltic Sea salmon trolling fishery may have broader impacts on seemingly unrelated species and ecosystems.

KEYWORDS

Atlantic salmon, Baltic Sea, fish conservation, fisheries management, recreational fisheries, spatial ecology

INTRODUCTION

Effective fisheries management requires understanding how fishing activity is distributed across space and how

the fishery changes over time. The Atlantic salmon (*Salmo salar*) is a crucial species in both recreational and commercial fisheries, as well as in aquaculture. However, many salmon populations are in decline, endangered, or

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extinct due to habitat loss and other anthropogenic pressures (Kesler et al., 2011; Klemetsen et al., 2003). In the Baltic Sea, the primary driver of declining salmon numbers is the loss of riverine habitats, with hydropower development contributing significantly to population extinctions (HELCOM, 2011). Salmon in the Baltic Sea are confined to its basins and do not extend through the Danish Straits (Kallio-Nyberg & Ikonen, 1992). The region hosts at least 43 self-reproducing populations native to distinct river systems, so-called wild salmon, although many populations are maintained through brood stocking programs due to habitat loss (HELCOM, 2011). These stocked salmon, often marked by adipose fin removal, enable selective fishing pressure between farmed and wild fish (HELCOM, 2011). Adult salmon mix in southern and southwestern Baltic feeding grounds before returning to their natal rivers to spawn, while younger fish remain closer to home (Jacobson et al., 2020; Palm et al., 2008; Whitlock et al., 2018). Because small and large populations mix, this complicates efforts to protect vulnerable populations, such as the small population in Estonia's Purtse River, alongside larger populations in Kalix and Torne/Tornio rivers in Sweden and Finland (Kärgerberg et al., 2019; Kesler et al., 2011; Miettinen et al., 2021).

To safeguard small and vulnerable populations, a series of restrictions have been implemented in the open sea. Within recreational sea fisheries, salmon landings come predominantly from trolling fisheries (Hartill et al., 2020; ICES, 2021). Therefore, when regulating the marine salmon fishery of the Baltic Sea, trolling has been a key focus. Baltic Sea salmon stocks native to specific rivers may cross national borders while at sea. Prior to 2022, the Baltic Sea salmon trolling fishery was governed by a mix of international, national, and regional harvest policies, and there was no EU-wide recreational salmon retention rule (Council of the European Union, 2020). Recent restrictions aim to streamline policies and protect vulnerable populations, notably Council Regulations for 2022–2025 (Council of the European Union, 2021, 2022, 2023, 2024). The regulatory framework is complex and varies by year and jurisdiction; here, only the aspects most relevant to the present analyses are summarized. These regulations prohibit wild salmon landings in recreational fisheries in Baltic Sea ICES subdivisions 22–31 while allowing limited retention of marked (farmed) salmon in recreational fisheries, typically up to one adipose-fin-clipped salmon per person and day (and, from 2023 onwards, requiring that fishing for salmon stops after the first retained salmon). From 2022 onwards, there were fewer regional disparities and more restrictive harvest regulations due to EU legislation. However, some geographic and jurisdictional differences remain, including national regulations in northern areas,

where fishing restrictions differ by latitude and by year. For example, within the EU coastal derogation area (May 1–August 31, within 4 nautical miles of the baselines; north of 59°30' N in 2022, 2023 and 2025, and in ICES subdivision 31 in 2024), Swedish national regulations (Havs- och vattenmyndigheten, 2025, FIFS 2004:36, 5 kap. 1 §) require that only farmed salmon may be retained in recreational trolling and landed whole, and the EU regulation's coastal derogation provision does not state a daily numerical bag limit (Council of the European Union, 2021, 2022, 2023, 2024). These new and stringent regulations may influence the trolling fleet. Hence, estimating the number of active skippers can help quantify trolling-fleet dynamics and assess the effects of regulatory change, key questions this study aims to address.

Two major salmon fishing tournaments, the Trolling Master Bornholm and the Trollingträff Åland, provide annual participation lists of skippers. These lists, combined with capture–recapture modeling, enable population size estimation. Capture–recapture models were initially developed to monitor animal populations through marking and recapture (Otis et al., 1978) and have since been extended to human populations using lists of individuals instead of physical captures (Chao et al., 2001). Capture–recapture models estimate population size by predicting the number unobserved individuals based on the number of observed individuals and their detection probability. While the first primitive detection models assumed homogeneous detection probabilities across all dimensions (Otis et al., 1978), current models are developed to handle real-world heterogeneity such as individual behavior, temporal variation, and spatial factors (Royle et al., 2018; Royle, Chandler, Sollmann, & Gardner, 2013). For example, behavioral covariates account for how previous detection affects subsequent detection probabilities: a positive effect means individuals previously detected are more likely to be detected again than those not yet detected, whereas a negative effect means the opposite (Chap. 7 in Royle, Chandler, Sollmann, & Gardner, 2013). The covariate essentially captures a change in behavior after the first detection. For example, ursid populations studied with baited traps often show positive behavioral effects because animals are attracted to bait and learn the trap locations (Molina et al., 2017; Sun et al., 2017). In the corresponding encounter histories, an animal may go undetected for many sampling occasions, but once detected, it tends to be re-detected more frequently. This is directly relevant to the trolling fleet and tournament participation: skippers who have never participated may be less inclined to register than those with prior participation. Ignoring a positive behavioral response can bias

estimates by overestimating the detection probability of never-detected individuals and, in turn, underestimating population size; the converse holds for a negative response (Borchers & Efford, 2008; Chap. 7 in Royle, Chandler, Sollmann, & Gardner, 2013). Thus, incorporating behavioral covariates corrects for this detection heterogeneity and improves accuracy of the population size estimate.

Spatial capture–recapture (SCR) models build on traditional capture–recapture methods by incorporating spatial information to model movements, habitat use, and resource selection (Fuller et al., 2016; Royle, Chandler, Sun, & Fuller, 2013). A key advantage of SCR is its ability to explicitly link population size to geographic area, enabling density estimation while accounting for spatial biases in detection (Efford, 2004). Detection probabilities in SCR are modeled as a function of the distance between an individual's home range center and a detection device, improving accuracy compared to non-spatial models. SCR also uses spatial recaptures to estimate individual home range centers and movement parameters, which are formally linked to the model's detection probability function and to the population's spatial extent (Efford, 2004; Sutherland et al., 2019). Telemetry data—such as automatic identification system (AIS) positions from trolling boats—can enhance SCR models by providing high-resolution information on individual movements. Telemetry may reduce the need for extensive spatial trapping and operates at a finer spatial scale than trapping alone (Linden et al., 2018; Royle, Chandler, Sun, & Fuller, 2013). Telemetered individuals are assumed to behave similarly to the rest of the population (Linden et al., 2018). This assumption also applies to skippers, even though AIS transponders are operated by skippers and carried by vessels rather than by the animals themselves as in many ecological telemetry studies. In wildlife telemetry, tagged individuals can be a non-representative subset of the population when tag burden and handling alter animals' behavior and even affect their survival (Brownscombe et al., 2019), and collared animals are sometimes captured in particular parts of the population range where capture is feasible, which can limit sample size and spatial representativeness (Chandler et al., 2022). Integrating telemetry into SCR improves estimates of movement and space use and allows fitting a resource selection function (RSF) within the SCR framework (Linden et al., 2018). The RSF describes the relative importance of habitats within the state space; in this study, “habitats” correspond to different fishing grounds.

This study combines participation lists (SCR data) with AIS telemetry data to estimate the number of trolling boat skippers from 2014 to 2023 and assess changes in response to recent regulations. By modeling skipper movements and resource selection, the study identifies fishing grounds'

relative importance and explores how restrictions might shift skipper activity. Such shifts could impact populations beyond those targeted by the regulations, underscoring the need for spatially informed management strategies.

METHODS

Adherence to the general data protection regulation (GDPR)

Personal data were collected with as little information about the participants as possible. The tournament participation lists used in this study are public and were available from the organizers' webpages. The Trolling Master Bornholm (TMB) is broadcast on the regional Danish television channel TV2/Bornholm, and the Trollingträff Åland (TTÅ) takes place at Käringsund Resort & Conference on the island of Eckerö in the Åland archipelago. Although the personal information provided to organizers is publicly accessible, registering for a tournament does not in itself constitute consent for research use. Processing was carried out by the Swedish University of Agricultural Sciences (SLU), as data controller, in the performance of a task carried out in the public interest (GDPR Article 6(1)(e)), with safeguards consistent with research processing under Article 89(1). In line with GDPR Article 11, once study-specific IDs were created, the study did not maintain or acquire additional information for the purpose of identifying individuals beyond what was necessary for the analyses. Therefore, all data presented in the manuscript and all data made available for download were pseudonymized through data minimization and removal of direct identifiers. Individual notice was not provided because the number of participants is large (>1000) and the publicly available lists do not provide complete contact information, making individual outreach impracticable and potentially a disproportionate effort (GDPR Article 14(5)(b)), with safeguards consistent with research processing under Article 89(1). AIS data were used only to quantify movements; where linkage to tournament records was possible, the same pseudonymization and data-minimization safeguards were applied. GDPR considerations were discussed with the Swedish University of Agricultural Sciences' data protection support.

Data collection: Creating a data frame of individual encounter histories based on tournament data

The southwestern and western parts of the Baltic Sea are where the majority of salmon feed (Jacobson et al., 2020;

Kallio-Nyberg & Ikonen, 1992). When the salmon return from their feeding grounds to their great northern rivers, they mainly use the western and central parts of the Baltic Sea as their main migration route (Jones et al., 2022; Siira et al., 2009). Consequently, popular trolling areas include off the Danish island of Bornholm, which is situated in the center of the salmon's southern feeding ground. Another important area is between the Swedish mainland and the Åland archipelago (Finland), which salmon pass when migrating north. At these locations, two major salmon trolling tournaments take place. The TMB has been held annually since 2005 but has been on hiatus since 2024; TV 2/Bornholm cites very low salmon catches and tightened salmon angling rules, and the event will only return if fishing conditions improve. The TTÅ is still ongoing annually. TMB was the largest tournament in the Baltic Sea and has during the study period attracted 210–420 teams annually (each team reporting one skipper). TTÅ is smaller and has attracted between 38 and 90 teams annually. The main reason for including these tournaments is that data are plentiful and well documented. Between these two tournaments it was possible to gather far greater sample sizes than typically required to run SCR models (see [Results](#)). Heuristic minimum sample sizes are 10–20 unique individuals (Otis et al., 1978), >20 recaptures (Efford et al., 2009; Palmero et al., 2023), and >5 spatial recaptures (Efford & Boulanger, 2019). Therefore, including other smaller tournaments was not deemed necessary, and information on skipper movements was plentiful from the AIS data, and hence, parameter estimation was not strictly dependent on additional SCR sampling.

Encounter histories, that is, lists of participants from the trolling tournament TMB, were sourced from the web, and lists from TTÅ were obtained upon request after contacting the tournament organizers. The trolling tournaments are held annually, and data were collected for the years 2014–2023. During the COVID-19 pandemic, the TMB tournament was canceled in 2020 and 2021, while TTÅ still had participant lists for those years. For the years 2014–2017, no data were included from TTÅ. Occasions (i.e., year–tournament combinations) that lack data are noted in the model's trap-operation file to avoid confounding no data as no detections (Sutherland et al., 2019). The TMB tournament takes place at the end of April each year, and the TTÅ begins in early June, making it possible to participate in both tournaments in a single year. The encounter data were stratified into two sessions to account for changes in the population size of trolling boats between strata, with the years 2014–2020 comprising one stratum and 2021–2023, the other. Initially the data were intended to be symmetrical and include two strata of 3 years each (2018–2020

and 2021–2023), but as more data allow fitting more complex models allowing estimation of parameters for heterogeneous detection probability (see two sections below), additional years were included. Because the AIS data were not available before 2019 (see next section below) and the importance of estimating a recent skipper population size, data were divided into strata of 7 and 3 years. By including strata-specific covariates for density and detection probability, these estimates can be calculated independently for each stratum, that is, 2014–2020 and 2021–2023. Within each stratum (but not between strata), the skipper population is assumed to be closed, that is, no birth, immigration, death, and emigration.

For the participation lists from TMB, information included the team name, the skipper's first and last name, the skipper's residence (hometown and country), and the tournament year. Similarly, for the TTÅ, the lists comprised the team name, the skipper's first and last name, the skipper's residence (not hometown but country), and the tournament year. None of this personal data is displayed in the following results or in the attached data of the study. To create unique identifiers for encounter histories, the skippers' names were utilized. Using this information, it was possible to create highly credible unique identifiers for the skippers. However, because there is no conclusive way to identify individuals without a personal identification number, these data contain some degree of measurement error. Although this is the case in nearly all real-world field data (Kéry & Royle, 2021), it is to some extent more apparent in this dataset. These data are mostly prone to false-positive errors arising from participants writing their names differently from tournament to tournament. In contrast, false negatives are less likely but may occur if two different skippers share the same name and cannot be distinguished using auxiliary information.

To create the encounter-history data frame (individual \times tournament \times year) needed to fit the SCR models, all yearly tournament data were stacked row-wise with columns for skipper name, tournament, year, team name, country, and hometown (if available). In other words, the participation records correspond to individual detections (i), the tournament to the geographic location of the trap (j), and the year to the occasion (k) the individuals were detected. This three-dimensional dataset (ijk) is the core of the SCR encounter probability model (Royle et al., 2018). In total, there were 2753 entries with skipper names from TMB and 394 from TTÅ. Names were occasionally inconsistently formatted across tournaments, with variations including the inclusion or omission of middle names, different orders of first and last names, misspellings, or differing abbreviations. In these

instances, the skipper's hometown, team name, tournament year, and country were used to identify discrepancies. If these combinations suggested that it was the same or a different skipper, the skipper's name was edited to ensure consistency or discrepancy across years and tournaments. To detect these formatting issues, several steps were taken. The first was to transform all names to lowercase letters. Then, a character distance matrix was created using the `stringdistmatrix` function in the `stringdist` R package (van der Loo, 2014) to calculate the Levenshtein distance matrix. A distance of 0 indicates that names are identical, and a distance of 1 indicates that one character is different, and so on. Names with one-letter differences were corrected. Second, all special characters and non-English letters (e.g., ü, å, ä, ö, ø) were replaced with English letters (u, a, a, o, o), and all double and triple spaces were replaced with a single space. This was followed by splitting the name strings at every single space and then concatenating the first and last names, creating a new variable omitting middle names. Thereafter, the Levenshtein distance matrix was repeated, and names with differences of up to three letters were scrutinized and corrected. The next step was to check for and correct identical matches between first names and last names, which indicates if participants reversed their order when signing up for the tournaments. This was followed by using the "nchar" function to count the number of characters in the names to detect the use of initials.

Skippers can only participate once per tournament and year. Hence, by looking for duplicated entries of the same name, distinct individuals with the same name could be detected and corrected. A further check was to split the data frame by team name and browse through the skipper names of every team. This detected a few skippers who had used last and middle names interchangeably and used nicknames. As a final check that the encounter data were correct, the number of occurrences of a unique name per year was checked to determine whether it was 1 or 2, depending on the availability of data from one or two tournaments. The maximum possible occurrences were 1 in 2014, 2015, 2016, and 2017, as only TMB data were sourced, and 2 in 2018, 2019, 2022, and 2023, when both TMB and TTÅ data were available. In 2020 and 2021, the COVID-19 pandemic led to the cancellation of TMB, leaving only TTÅ, which meant a maximum of 1 occurrence was possible in those years. Consequently, there could be a total of 8 occurrences in TMB and 6 in TTÅ across all years, and these totals were confirmed. There were in total 74 direct name corrections, and 15 global string corrections (e.g., diacritics, punctuation, and hyphens). The raw participation lists contained 1174 unique skipper records (including aliases/misspellings); after cleaning, 1093 unique

skippers remained, indicating that most edits removed false-positive duplicates.

AIS data: Used as telemetry data in the SCR model

AIS data were obtained from Sjöfartsverket (the Swedish Maritime Administration). The data included the position of maritime traffic for every day in 2019 and 2022 for the whole of Sweden and neighboring countries. AIS transponders are mandatory for ships with a gross tonnage of 300 or more, and virtually all trolling boats fall below this threshold. When installed on non-mandatory vessels, these AIS transponders are typically class-B transponders, which are designed for smaller vessels and have lower transmission power and functionality compared to the class-A transponders used on larger, mandatory vessels. This means that only vessels belonging to skippers who chose to install a transponder can be found in this dataset. Additionally, data were only transmitted if the skipper chose to use the transponder, as the skipper can choose when to switch the system on or off. AIS transponders are governed by international regulations set by the International Maritime Organization (IMO), and more information can be found on the organization's webpage.

To extract telemetry fixes from the raw AIS data, data were first filtered to select class B transponders and then to retain pleasure crafts and fishing vessels. The AIS data included information about the ship name, position (latitude/longitude), country, time and date, and a maritime mobile service identity (MMSI) that is unique for the vessel. In the AIS data, the ship names were concatenated with the respective country and matched against the tournament data where the team names were concatenated with the respective country. Hence, ship names in the AIS data often matched with team names in tournaments. This resulted in 116 and 187 exact matches, respectively, for the years 2019 and 2022, where there was only one unique vessel with this name and country according to the MMSI. These ships were retained from the data. Vessels used by multiple skippers (7 in 2019; 4 in 2022) were removed. Conversely, when a single skipper used two vessels (2 skippers in 2019; 6 in 2022), the AIS tracks were merged by skipper because the capture–recapture analysis is indexed by skipper, not vessel.

The AIS telemetry fixes were incorporated in the SCR models to estimate resource selection and the movement parameter σ (see section below). AIS positions are recorded at irregular intervals, but often every few seconds. Telemetry fixes in SCR are assumed to be independent observations of the position of the individual.

Although complete independence is unlikely in any telemetry data (Chandler et al., 2022; Royle, Chandler, Sollmann, & Gardner, 2013), a way to reduce dependence is to thin the observations. As a first step, this was achieved by creating hourly fixes by calculating the mean position within every hour per skipper. Next, skippers with <50 observations were removed, resulting in 24 and 139 remaining skippers. For skippers with >50 observations, 50 fixes per skipper were sampled at random to be used as telemetry fixes in the RSF implemented by the oSCR package (Sutherland et al., 2019). Although not strictly required by the model, this standardization of 50 fixes per skipper ensures that no single skipper dominates the estimation of movement and space-use parameters. Sampling was done using a fixed random number generator so that results would be identical each time the code was executed. The 2019 and 2022 telemetry data were matched with the tournament detections of 2014–2020 and 2021–2023, respectively; this resulted in 23 and 111 individuals in each telemetry data frame.

Density estimation and creating the state space and resource selection data frame

SCR models have a hierarchical structure that combines two key components: an observation model that describes the detection process of individuals at specific spatial locations, and a latent ecological process model that estimates the spatial distribution, movement, and abundance of the population (Sutherland et al., 2019). The standard SCR model was used to estimate detection probability. This model assumes that the detections of individuals are random Bernoulli events, $y_{ijk} \sim \text{Bernoulli}(p_{ijk})$. Further, the model assumes that detection decreases with Euclidean distance from the individual's home range center s_i to the trap location x_j (Efford, 2004). In this study, the effective trap locations are the locations of the trolling tournaments, and the home range centers are latent variables to be estimated. The decreasing detection probability is described by the “half normal” model as $p_{ijk} = p_0 \exp\left[-\text{distance}(x_j, s_i)^2/2\sigma^2\right]$, where i is the individual, j is the trap location, and k is the sampling occasion. p_0 is the intercept, which corresponds to the capture probability of an individual at the center of its home range, that is, where the distance between the trap and the home range center is zero, $\text{distance}(x_j, s_i)^2 = 0$, (Efford, 2004). Sigma (σ) is the movement parameter of the half normal detection function and describes the decay rate of the detection probability with increasing distance.

Because different subpopulations may have different detection probabilities (Borchers & Efford, 2008), the detection model included four covariates to accommodate this. A behavioral response estimates whether individuals previously detected have a different detection probability. This is important to include if there is a group of highly devoted tournament skippers that have a greater detection probability than the baseline consisting of skippers that have not yet participated in a tournament. A session covariate that stratifies the population and allows for different detection probabilities per time period, 2014–2020 and 2021–2023. A binary covariate, allowing skippers residing in Denmark to have a different detection probability than skippers residing in other countries. The rationale for this was the large number of skippers with Danish residence in the data, and the short distance from Denmark to the most popular fishing grounds. Finally, an area covariate was included to estimate differences in detection probability depending on a set of predetermined areas that are believed to be important for trolling anglers, described further below. Using a complementary log–log link (Chap. 5 in Royle, Chandler, Sollmann, & Gardner, 2013), the detection probability (p_{ijks}) is modeled as:

$$\text{cloglog}(p_{ijks}) = \log\left\{-\log(1-p_{ijks})\right\} = \eta_{ijks} - \frac{d(x_j, s_i)^2}{2\sigma^2}, \quad (1)$$

with linear predictor

$$\eta_{ijks} = \alpha_0 + \alpha_2 \text{behavior}_{ik} + \alpha_3 \text{session}_s + \alpha_4 \text{country of residence}_i + \alpha_5 \text{area}_j.$$

Here, $d(x_j, s_i)^2$ is the distance between detector (trap) location x_j and individual activity center s_i ; where $\alpha_0, \dots, \alpha_5$ are parameters to be estimated, and the distance effect corresponds to $\alpha_1 = 1/2\sigma^2$ under this parameterization.

The same binary country of residence covariate was included for the σ model allowing for different movement parameters for Danish and non-Danish residents. The sigma model can be expressed as:

$$\log(\sigma_i) = \delta_0 + \delta_1 \text{country of residence}_i. \quad (2)$$

The state space \mathbf{S} was discretized into a regular grid with 50×50 km cells. Grid spacing was chosen to be sufficiently fine relative to the movement scale (σ) so that numerical integration over \mathbf{S} is accurate. For a half-normal encounter model, a common rule of thumb is to use a grid spacing of approximately 0.5σ (Sutherland et al., 2019). Because σ is not known a priori, AIS-based

movement was used as a rough proxy by calculating the mean maximum distance moved (MMDM); MMDM was $\exp(10.7) \text{ m} = 44.4 \text{ km}$ for 2019, and $\exp(11.6) \text{ m} = 109.1 \text{ km}$ for 2022, supporting a 50-km spacing. The state space should include the activity centers s_i of the skippers that were detected in the tournaments, and its area is therefore based on the distance moved by the individuals of the population (Sutherland et al., 2019). The state-space buffer was defined as the area extending 400 km from the two tournament locations which corresponds to about $3-4\sigma$. At this distance, detection probability is essentially zero and is therefore used as the state-space border. Home ranges were assumed to be uniformly distributed across the state-space pixels g , but their expected density was allowed to differ between sessions accommodated by stratifying the skipper population per time period 2014–2020 and 2021–2023:

$$\log(E(D_s)) = \beta_0 + \beta_{\text{session}_s}. \quad (3)$$

Pixel-specific frequencies from the telemetry data were used to model multinomial probabilities of space use $m_{ig} \sim \text{Multinomial}(R_i, \pi_{ig})$, where R_i is the number of telemetry fixes for individual i in pixel g , and π_{ig} is the relative probability of use for individual i in pixel g (Linden et al., 2018; Royle, Chandler, Sun, & Fuller, 2013), such that

$$\pi_{ig} = \frac{\exp\left(-\alpha_{1i}d(x_g, s_i)^2 + \alpha_6 \text{areaBornholm}_g + \dots + \alpha_7 \text{areaRemaining area}_g\right)}{\sum_g \exp\left(-\alpha_{1i}d(x_g, s_i)^2 + \alpha_6 \text{areaBornholm}_g + \dots + \alpha_7 \text{areaRemaining area}_g\right)}. \quad (4)$$

Here, only two of the total six areas are shown to simplify the equation above. The resource selection covariate was created by calculating the distance from the state-space pixels to five distinct points representing five areas that are popular among trolling anglers: Bornholm, Danish Straits, Vänern and Vättern, Skagerrak, and Åland. If the distance was $\leq 100 \text{ km}$, the state-space pixel was assigned the area factor. The remaining pixels that are $> 100 \text{ km}$ from these five points were assigned simply as the factor level “remaining area.”

By integrating the joint likelihood function of telemetry data and spatial trap captures in the SCR model, the spatial resolution of the movements of individuals can be estimated both by trap detections and telemetry fixes (Linden et al., 2018; Royle, Chandler, Sollmann, & Gardner, 2013; Royle, Chandler, Sun, & Fuller, 2013).

Telemetry data also allow for estimating resource selection, by modeling pixel-specific relative probability of use, which reveals if certain pixels of the state space are more important than others for the skipper population (Linden et al., 2018). Pixels with higher estimated detection indicate greater relative importance for the population’s resource use. Linden et al. (2018) modified the integrated SCR–RSF likelihood (Royle, Chandler, Sun, & Fuller, 2013) to accommodate the lack of independence between data sources, when individuals in the SCR data are also available in the telemetry data. This dependence can be specified in the R package oSCR (Sutherland et al., 2019), which implements likelihood-based SCR models and was used to fit the SCR–RSF models described above. Together with null models and including all covariate combinations, this resulted in 64 candidate models. Models were ranked by Akaike information criterion (AIC) to select the best one.

Sensitivity of SCR–RSF results to telemetry sampling

The data used in the SCR–RSF models consist of two components: telemetry (AIS) data and SCR data. The telemetry data inform two key parts of the model: (i) the spatial movement scale (σ), and (ii) the relative use of dif-

ferent pixels in the landscape, that is, resource selection at the population level. In principle, SCR data alone can estimate both σ and resource selection from SCRs (Linden et al., 2018; Royle, Chandler, Sun, & Fuller, 2013). However, when trap coverage is limited or uneven, SCR-only estimates can become sensitive to sampling design and effort (Sun et al., 2014), and telemetry can strongly improve precision (Royle, Chandler, Sun, & Fuller, 2013).

In this study, SCR data were only available from two focal areas (Bornholm and Åland). Outside these areas, information on space use comes entirely from telemetry. To assess how sensitive model results were to the specific telemetry sample, a set of alternative sampling schemes was created. These systematically reduced either (1) the number of fixes per skipper or (2) the number of skippers

contributing telemetry, while keeping the SCR data unchanged (Table 1). For each scheme, 20 replicate datasets were generated by random resampling, and each replicate was fitted to the same top-ranking SCR–RSF model. A model with no telemetry was also fitted. Parameter estimates were compared across schemes and against the top model reported in *Results*. Together, this allows evaluation of which parameters are robust to telemetry and skipper sampling.

RESULTS

Fifty hourly fixes per skipper from AIS positions were randomly sampled from 23 skippers in 2019 and 111 skippers in 2022 (Figure 1) and were included in the SCR–RSF models. These “AIS-skippers” were identified in the AIS data for that focal year (2019 or 2022) and were also present in the tournament data for the corresponding session (2014–2020 for 2019, and 2021–2023 for 2022). A total of 1093 Baltic Sea salmon trolling boat skippers were detected in tournament lists from 2014 to 2023. From 2014–2020, 937 unique skippers were detected with 580 individuals redetected and 40 individuals with spatial redetections

(i.e., registered to both tournaments), while from 2021 to 2023, 458 unique skippers were detected with 243 individuals redetected and 15 spatial redetections (Table 2). In Bornholm, Denmark, most skippers were Danish residents, with Swedes being the second most common residency (Figure 2a). In Åland, Finland, most skippers were Finnish residents, followed by Swedes as the second most common residency (Figure 2b). Across both tournaments, Danish residency was the most common, followed by Swedish (Figure 2c).

The top model received overwhelming support based on AIC ranking, with $\Delta\text{AIC} = 42.3$ (Table 3). This model included area, behavior, session, and country of residence as covariates for the detection model, while the density model included session, and the sigma model included country of residence. Predictions from the top model indicated a much lower density of Baltic Sea salmon trolling boat skippers in 2021–2023 compared to 2014–2020, with estimates of 2604 (95% CI: 2273–2983) and 5343 (4622–6178), respectively (Table 3). This corresponds to a 51% decrease between sessions. The population extent is illustrated in Figure 1 and Figure 3a.

Detection probability was influenced by all four included covariates: area, behavior, session, and residency (Table 4). Third-order resource selection (within-home-range space use) was highest around the island of Bornholm in the Baltic Sea and the lowest in the area designated as “remaining area,” that is, the part of the state space not designated as a trolling area (Figure 3). The behavioral response showed that skippers who had previously participated were more likely to be detected than those who had not yet participated (Figure 4a). The inclusion of a session covariate revealed that the detection probability was greater during 2021–2023 than during 2014–2020 (Figure 4b). Danish residents had a lower detection probability than residents of other countries (Figure 4c). The movement model sigma showed that skippers residing in Denmark moved over shorter distances (Figure 4d) and had smaller home ranges than skippers from other countries (Figure 4e).

Across sampling schemes, parameter estimates were much more robust to reducing and resampling telemetry fixes while holding skippers constant than to reducing and resampling skippers while holding fixes per skipper constant (Figure 5a–m). Specifically, randomly sampling skippers produced much greater variation in parameter estimates, indicating that skippers are heterogeneous in where they fish and how far they travel. The key benefit of including telemetry is improved estimation of the movement parameter σ and resource selection (Chandler et al., 2022; Linden et al., 2018; Royle, Chandler, Sun, & Fuller, 2013). Accordingly, reducing the number of telemetry fixes and/or skippers inflated the σ intercept (Figure 5e), with a corresponding decrease in the density

TABLE 1 Overview of telemetry sampling schemes.

Sampling scheme	No. fixes per skipper	No. skippers	No. sampled datasets
Top model	50	134	1
1/1 fixes, 1/1 skippers	50	134	20
1/2 fixes, 1/1 skippers	25	134	20
1/10 fixes, 1/1 skippers	5	134	20
1/1 fixes, 1/2 skippers	50	66	20
1/1 fixes, 1/10 skippers	50	13	20
No telemetry	1 (SCR-only model)

Note: Schemes used to evaluate the sensitivity of estimates from the integrated spatial capture–recapture (SCR)–resource selection function (RSF) model to telemetry sampling. Each scheme varies the number of automatic identification system (AIS) fixes per skipper and/or the number of skippers contributing telemetry. For each scheme, 20 replicate datasets were generated and the top-ranking model structure (see *Results*) was fitted to each replicate. The top model and the no-telemetry model with only SCR data were also included as comparisons. For schemes with 134 skippers, the skipper set was fixed (not randomly sampled) because 134 is the maximum available in the data. In the 50-fix scheme, two skippers had only 50 fixes available and therefore could not be resampled. Across all skippers, the median number of available hourly AIS fixes was 178 (maximum 7091), and 36 of the 134 skippers had fewer than 100 fixes to sample from.

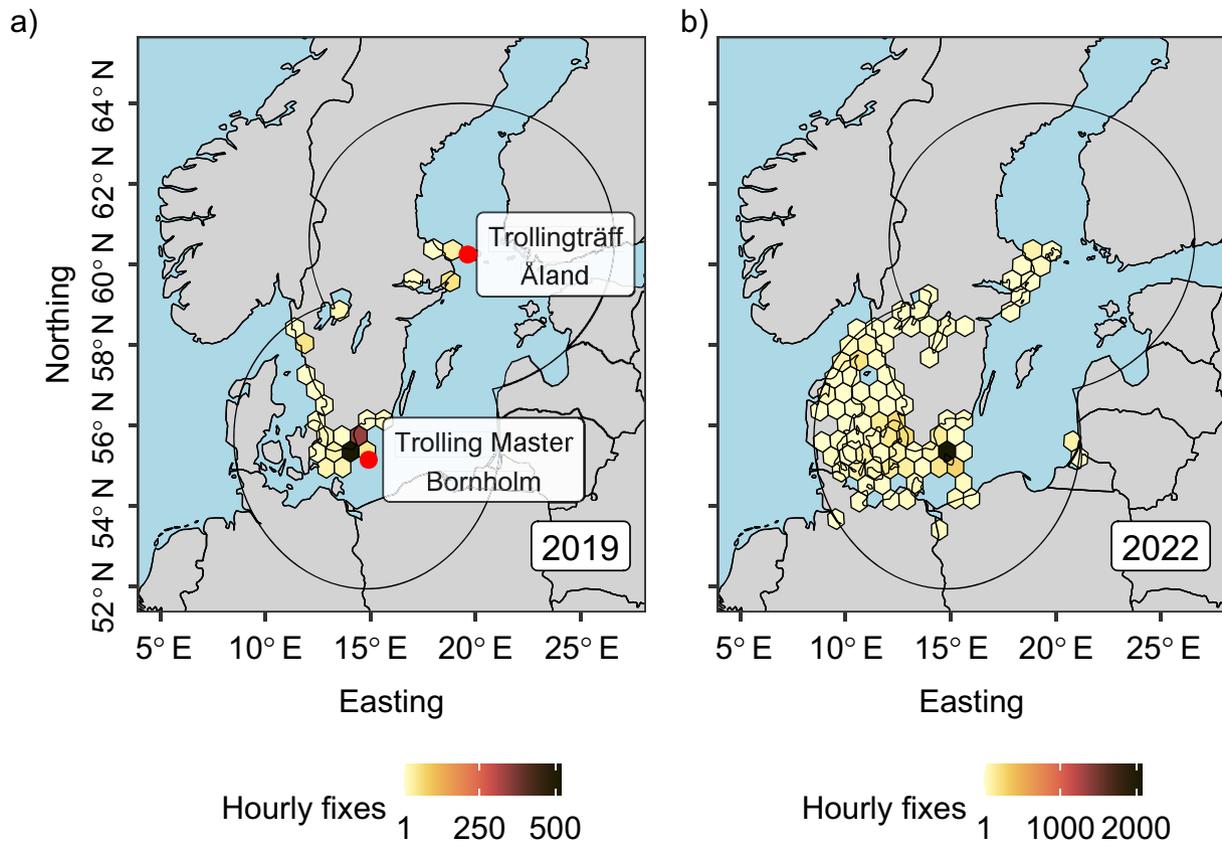


FIGURE 1 The hourly average positions (telemetry fixes) of trolling boat skippers based on automatic identification system (AIS) data. (a) The positions of 23 skippers for the year 2019; (b) the positions of 111 skippers for the year 2022, with each skipper represented by 50 randomly sampled fixes. These AIS telemetry data were incorporated in the resource selection function (RSF) component of the integrated spatial capture–recapture (SCR) model; all skippers shown had both AIS fixes and tournament detections. In panel (a), the locations of the two tournaments, Trolling Master Bornholm and Trollingträff Åland, are indicated. Notably, in 2019 and 2022, 45% and 37% of the total number of fixes, respectively, fall within the grid cell with the highest number of fixes, situated near the island of Bornholm. The circular area extending from the tournament locations represents the extent of the state space (the area over which population density is estimated). Telemetry fixes outside this extent were removed from the SCR–RSF analyses.

TABLE 2 Summary of skipper detection frequencies in tournaments.

Tournaments	Years	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Both	2014–2023	388	230	143	109	66	67	40	40	3	4	2	0	1	0
Both	2014–2020	357	200	140	84	63	82	7	4	0
Both	2021–2023	215	205	32	5	1
Bornholm	2014–2023	342	207	123	101	62	60	38	36
Bornholm	2014–2020	329	183	123	82	62	87
Bornholm	2021–2023	171	179
Åland	2014–2023	81	40	26	14	9	9
Åland	2014–2020	63	30	18
Åland	2021–2023	57	38	28

Note: This table presents the frequencies of the number of detections per skipper in both the Trolling Master Bornholm and the Trollingträff Åland, as well as in each tournament separately. The Years' column shows 2014–2023 corresponding to both sessions 1 and 2 in the models, where 2014–2020 is designated as session 1, and 2021–2023 is session 2. Trolling Master Bornholm was closed due to the COVID-19 pandemic in 2020 and 2021, resulting in no skippers being detected during those years. Additionally, there are no data from Trollingträff Åland for the years 2014–2017. For each tournament–year combination (row), the maximum number of possible detections is indicated by a number in columns 1–14, in contrast to a “...”. Note that in most rows, the number of skippers that participated at least twice is greater than the number that only participated once.

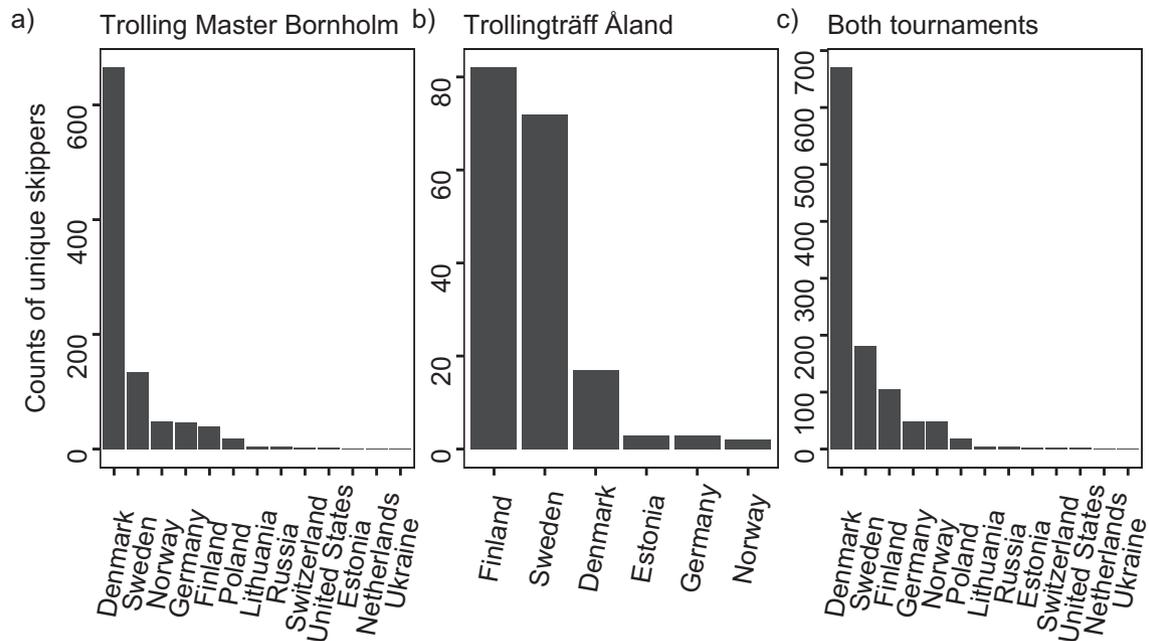


FIGURE 2 Unique participants by country of residence in (a) Trolling Master Bornholm (Denmark), (b) Trollingträff Åland (Finland), and (c) both tournaments, spanning the years 2014–2023. In the spatial capture–recapture analyses, country of residence was collapsed into two groups: Denmark and all other countries of residence (outside Denmark).

intercept (Figure 5l), because skippers are spread over a larger area when σ increases. Note that σ in the top model versus the no-telemetry model is, on the natural (back-transformed) scale, nearly halved: $\exp(11.27)$ m = 78.7 km versus $\exp(11.95)$ m = 155.5 km. Additionally, the resource-selection coefficients for the Danish Straits, Skagerrak, Vänern–Vättern, and “Remaining area” became highly variable when skippers were reduced and resampled (Figure 5g–j). As expected, these four areas cannot be estimated at all without telemetry because the SCR data contain no information there, whereas Bornholm (reference area included in the detection intercept; Figure 5a) and Åland (Figure 5k) can still be estimated without telemetry. Comparing the top model to the scheme with the same number of fixes (50) and skippers (134), most parameter estimates were robust; the exception was the Danish Straits (Figure 5g), which had a very small effect size and, in some random draws of telemetry fixes, switched sign. Furthermore, the session effect—lower skipper density (Figure 5m) and higher detection probability (Figure 5b) in 2021–2023 relative to 2014–2020—was present in all sampling schemes; the positive behavioral covariate showed the same consistency (Figure 5d).

DISCUSSION

A key result from this study is a significant decline of approximately 51% in the number of Atlantic salmon

trolling skippers in the Baltic Sea from the years 2014–2020 to 2021–2023. Because the two periods differ in length (7 vs. 3 years), both time frames were estimated with independent detection probabilities. The years 2021–2023 had, as expected, fewer detections, but more importantly, a greater detection probability. In a SCR framework, this combination leads to a lower estimated population size of skippers. Thus, in recent years, mainly the most devoted skippers, which are fewer in number, remain in the trolling fishery, and their fishing effort may still be considerable although this cannot be quantified from the present data. The decline of skippers is likely due to an increased regulation of the salmon trolling fishery, which no longer allows the harvest of wild salmon in the Baltic Proper (and Bothnian Sea in 2024), and in most cases, only permits one farmed salmon to be harvested per person per day (Council of the European Union, 2020, 2021), where north of latitude 59°30' N is the exception (north of 63°30' N in 2024). These changing regulations likely reduced angler satisfaction, and together with changes in the global economy in 2022, with rising fuel prices and inflation, this may have affected the population negatively. Notably, TMB was paused in 2024 (and did not run in 2025), and the organizers at TV 2/Bornholm cited tightened salmon angling rules and very low catch prospects around Bornholm; the event will only return if fishing conditions improve. Furthermore, TTÅ only had 17 teams participating in 2024 and 35 teams in 2025 in

TABLE 3 Model selection analysis for population estimates of Baltic Sea salmon trolling boat skippers.

Density	Detection	\mathcal{L}	np	AIC	Δ AIC	AIC ω	AIC ω +	$\hat{N}1$	$\hat{N}2$
$D(\text{session})$	$p(\text{area} + \text{session} + \text{country of residence} + \text{b})$	19,005.64	14	38,039.28	0	1	1	5343 (4622–6178)	2604 (2273–2983)
$D(\text{session})$	$p(\text{area} + \text{country of residence} + \text{b})$	19,027.79	13	38,081.57	42.3	0	1	5095 (4570–5680)	3411 (2985–3898)
$D(\text{session})$	$p(\text{area} + \text{session} + \text{country of residence})$	19,043.67	13	38,113.35	74.07	0	1	4549 (4152–4985)	2187 (1955–2446)
$D(1)$	$p(\text{area} + \text{country of residence} + \text{b})$	19,052.7	12	38,129.4	90.13	0	1	4615 (4250–5011)	4615 (4250–5011)
$D(1)$	$p(\text{area} + \text{session} + \text{country of residence} + \text{b})$	19,052.68	13	38,131.36	92.08	0	1	4606 (4242–5000)	4606 (4242–5000)
$D(\text{session})$	$p(\text{area} + \text{country of residence})$	19,065.76	12	38,155.52	116.25	0	1	4339 (3971–4742)	2758 (2463–3089)
$D(\text{session})$	$p(\text{area} + \text{session} + \text{b})$	19,066.08	13	38,158.16	118.89	0	1	5032 (4473–5659)	1992 (1509–2629)
$D(1)$	$p(\text{area} + \text{country of residence})$	19,098.57	11	38,219.13	179.85	0	1	3750 (3587–3922)	3750 (3587–3922)
$D(1)$	$p(\text{area} + \text{session} + \text{country of residence})$	19,098.62	12	38,221.24	181.96	0	1	3731 (3441–4045)	3731 (3441–4045)
$D(\text{session})$	$p(\text{area} + \text{session})$	19,109.4	12	38,242.79	203.51	0	1	4167 (3513–4941)	1653 (1432–1908)

Note: This table presents the model selection results for the top 10 models out of 64. The Density column shows the covariate structure for the density model (D), where session represents the two time periods (2014–2020 and 2021–2023). The Detection column shows the covariate structure for the detection probability model (p), including the resource-selection covariate area, the time-period covariate session, the behavioral covariate (b) (testing whether prior tournament participation affects subsequent participation), and residency (Denmark vs. all other countries). The sigma component is not shown in the table, as all models in the top 10 included the same country of residence covariate. A value of “1” indicates an intercept-only specification for that model component. \mathcal{L} represents the model log likelihood, np denotes the number of parameters, AIC shows the Akaike information criterion (AIC) used for ranking the models, Δ AIC displays the AIC ranking with the lowest AIC model on top, AIC ω represents the model weights based on AIC, and AIC ω + indicates the cumulative model weight. The columns $N1$ and $N2$ provide the estimates and 95% CIs of the population size of Baltic Sea salmon trolling boat skippers from each model for the two respective sessions.

contrast to the average of 66 teams participating in the years 2018–2023.

Further, to maintain and support fisheries, an average of 4.4 million salmon smolts were released into the Baltic Sea from hatcheries between 2018 and 2022 (ICES, 2023). However, due to COVID restrictions at the hatcheries, out of the 4.6 million released smolts in 2021, only 1.9 million were fin-clipped, compared to the annual average of 3.3 million (ICES, 2023). Because fin-clipping indicates that the salmon is farmed and can be harvested, the number of harvestable salmon in the Baltic Sea is likely to decrease in the coming years. A gradual decrease of fin-clipped salmon is anticipated in 2023 as this cohort will have spent one winter at sea and begins to be targeted by trolling anglers (see fig. 2 in Karlsson & Karlström, 1994). Stronger effects of this cohort are expected in 2024 and 2025. A reduction in the number of fin-clipped salmon released into the Baltic Sea is likely to further increase angler dissatisfaction. As a result, the reduced availability of harvestable salmon is

likely to lead to a decline in participation in this fishery in general, and in trolling tournaments in particular (Birdsong et al., 2021).

Resource selection was estimated for each pixel of the state space by integrating the trolling boats' AIS data as telemetry fixes to the SCR model. Pixels with greater estimated detection probability are more important as resources for the skippers (Linden et al., 2018; Royle, Chandler, Sun, & Fuller, 2013), suggesting that Bornholm is the most intensively used area for this population. This is an expected finding as the TMB attracted hundreds of anglers yearly, and the AIS data showed that more than 30% of all trolling boat fixes fall near the island of Bornholm. The next most important area is the Danish Straits, a highly populated region near major cities. In contrast to Bornholm, most of this area is not used for trolling for salmon, so other species are in focus here, such as sea-run brown trout (*Salmo trutta*), which are common nearshore along these islands (Kristensen et al., 2019; Thorstad et al., 2016). The third most

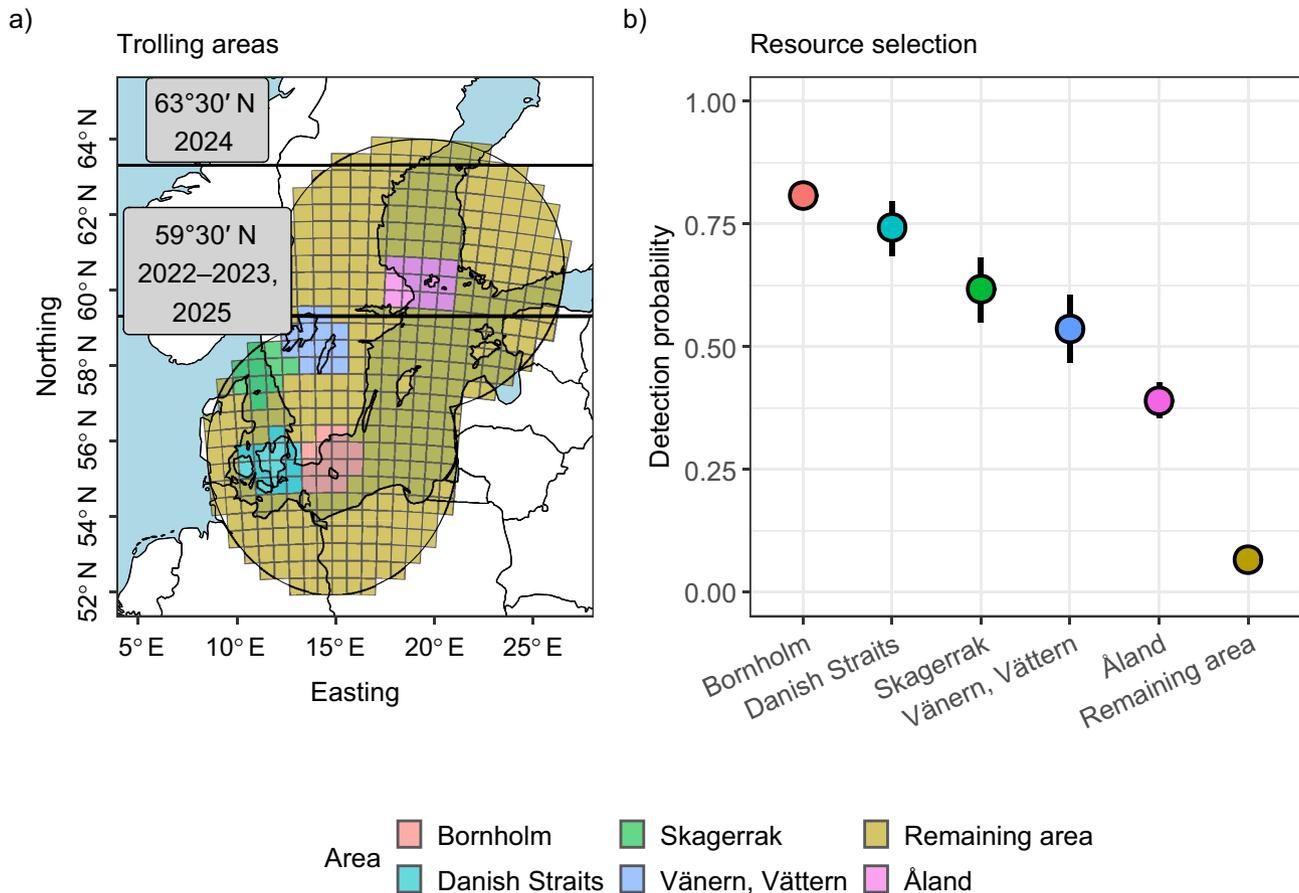


FIGURE 3 (a) The six areas within the resource selection dataset. Five areas—Bornholm, Danish Straits, Skagerrak, Vänern and Vättern, and Åland—are well-known trolling areas for recreational fishing. The “Remaining area” essentially denotes the region not designated as a trolling area; however, recreational trolling may still occur here. The area around the tournament locations shows the extent of the state space (grid cell size 50×50 km), that is, the area over which population is estimated. The lines labeled $59^{\circ}30' N$ (2022, 2023, 2025) and $63^{\circ}30' N$ (2024) indicate the year-specific latitudinal boundary used in salmon fishing regulations. North of the line, there are no harvest restrictions on farmed salmon between May 1 and August 31, within 4 nautical miles from the baselines, although wild salmon must still be released. South of the line, all wild salmon has to be released and only one farmed fish is allowed to be kept per person and day. (b) The detection probability predictions from the top model (based on Akaike information criterion ranking), where areas are color-coded and plotted on the x-axis. Higher predicted detection probability reflects greater relative use of the area by trolling anglers. Error bars represent the 95% CIs. For each area, estimates were calculated at a distance of zero from trap to home range center, that is, $\text{distance}(x_j, s_i)^2 = 0$, and averaged across the remaining predictors (i.e., partial predictions; Fox & Weisberg, 2018).

important area was Skagerrak, where focus is also on species other than salmon, such as Atlantic bluefin tuna (*Thunnus thynnus*). In Skagerrak, recreational anglers have been involved in research projects to capture and tag individuals with electronic pop-up satellite archival tags (Aarestrup et al., 2022; Birnie-Gauvin et al., 2020). The Bluefin tuna migrate to Skagerrak and Kattegat from their spawning grounds in the Gulf of Mexico and Mediterranean Sea (Aarestrup et al., 2022) where they have recently shown signs of recovery due to conservation efforts (Aarestrup et al., 2022; ICCAT, 2006). The trolling areas of least importance were the Swedish Great Lakes, Vänern and Vättern, which host a popular salmon trolling fishery (Andersson et al., 2020), and the area off

the Åland archipelago in the Northern Baltic Proper. The remaining area of the state space (study area) had comparatively very low importance for trolling skippers.

The results from the resource selection analysis show that areas outside of the Baltic Sea and species other than salmon are also important for this population of skippers. This means that these skippers establish a link between different populations of fish. For example, the same population of skippers targets a wild population of Baltic salmon native to the Purtse River in Estonia (Kesler et al., 2011) and a landlocked wild population of salmon in the Gullspång River, native to Lake Vänern in Sweden (Piccolo et al., 2012). This indicates that restrictions on one stock may have unforeseen cascading effects

TABLE 4 Parameter estimates and statistics for the top model.

Parameter	MLE	SE	<i>z</i>	<i>p</i>
Detection, intercept	0.318	0.122	2.605	0.009
Detection, country of residence: all other	1.382	0.05	27.498	<0.001
Detection, session: 2021–2023	0.684	0.119	5.733	<0.001
Detection, behavior	0.521	0.089	5.885	<0.001
Sigma, intercept	11.273	0.01	1121.819	<0.001
Sigma, country of residence: all other	0.427	0.017	24.632	<0.001
Area: Danish Straits	−0.412	0.144	−2.864	0.004
Area: Remaining area	−4.51	0.134	−33.64	<0.001
Area: Skagerrak	−1.067	0.141	−7.585	<0.001
Area: Vänern Vättern	−1.447	0.142	−10.185	<0.001
Area: Åland	−2.126	0.093	−22.876	<0.001
Density, intercept	2.63	0.071	37.247	<0.001
Density, session: 2021–2023	−0.719	0.073	−9.889	<0.001

Note: This table presents the maximum likelihood estimates (MLE), SE, *z* values, and *p* values of the top model, as selected by the Akaike information criterion rankings (refer to Table 3). The detection parameter is modeled on the complementary log–log link scale. The detection intercept includes the reference levels: Danish residents, the session 2014–2020, the behavior group with zero previous detections, and the Bornholm area. The country of residence parameter indicates that individuals with a residency other than Danish have a greater detection probability. The session parameter shows that detection probability was greater during 2021–2023 than during 2014–2020. The behavioral effect indicates that previously detected individuals had higher detection probability than those with no previous detections. All other areas had lower predicted detection probabilities than the reference area (Bornholm); higher values indicate greater relative importance for trolling skippers. The movement parameter sigma is modeled on the log scale; Danish residents (reference level) had smaller home ranges than non-Danish residents, as indicated by the residency effect on sigma. Finally, the log-scale density parameter shows lower skipper abundance in 2021–2023 relative to 2014–2020.

on another if skippers shift areas depending on regulations. This is important for fisheries managers because restrictions should not be more stringent than necessary, as this likely intensifies fishing in other areas. Furthermore, the relaxed regulations in the Northern Baltic Sea likely have little effect on the northern salmon populations as this area is relatively unimportant for trolling skippers and these populations are relatively viable. Instead, the regulations may relieve sensitive southern populations in more attractive areas from high fishing pressure. This finding agrees well with the recently implemented area-specific restrictions.

The model results showed that trolling boat skippers are a heterogeneous group in terms of tournament participation. Skippers who had previously participated in a tournament showed a higher detection probability than those who had not yet participated, indicating a group of highly dedicated skippers that participate more frequently. This pattern corresponds to trap-happiness (a positive behavioral response) in capture–recapture models, where individuals are more likely to be detected after a previous detection (Chap. 7 in Royle, Chandler, Sollmann, & Gardner, 2013). In datasets where trap-happy effects are present, the null model overestimates baseline detection probability because individuals who are never observed have lower detection probabilities than those with previous detections.

Consequently, if this parameter is excluded, the skipper population size will be underestimated. Although there were fewer skippers during 2021–2023, they were more likely to participate in tournaments, consistent with a decline in occasional participants and a remaining core of frequent participants. This persistent repeat participation of some individuals may reflect that tournament participation is a motivating and positive experience for many skippers, although it could also arise from stable differences among skippers in their propensity to participate; thus, more than one mechanism may contribute to the estimated behavioral effect (Borchers & Efford, 2008; see also Karlsson et al., 2025).

The binary detection covariate country of residence estimated that skippers residing in Denmark had a lower detection probability than skippers residing in other countries, which may be due to their proximity to the TMB, allowing for more spontaneous participation. Thus, Danish residents may participate just occasionally. Whereas skippers residing in other countries, who must travel farther, may have a greater devotion to participate in tournaments and, therefore, a higher detection probability. This theory is further supported by the movement scale parameter sigma. Danish residents traveled much shorter distances than those from other countries, which could be caused by their proximity to important fishing

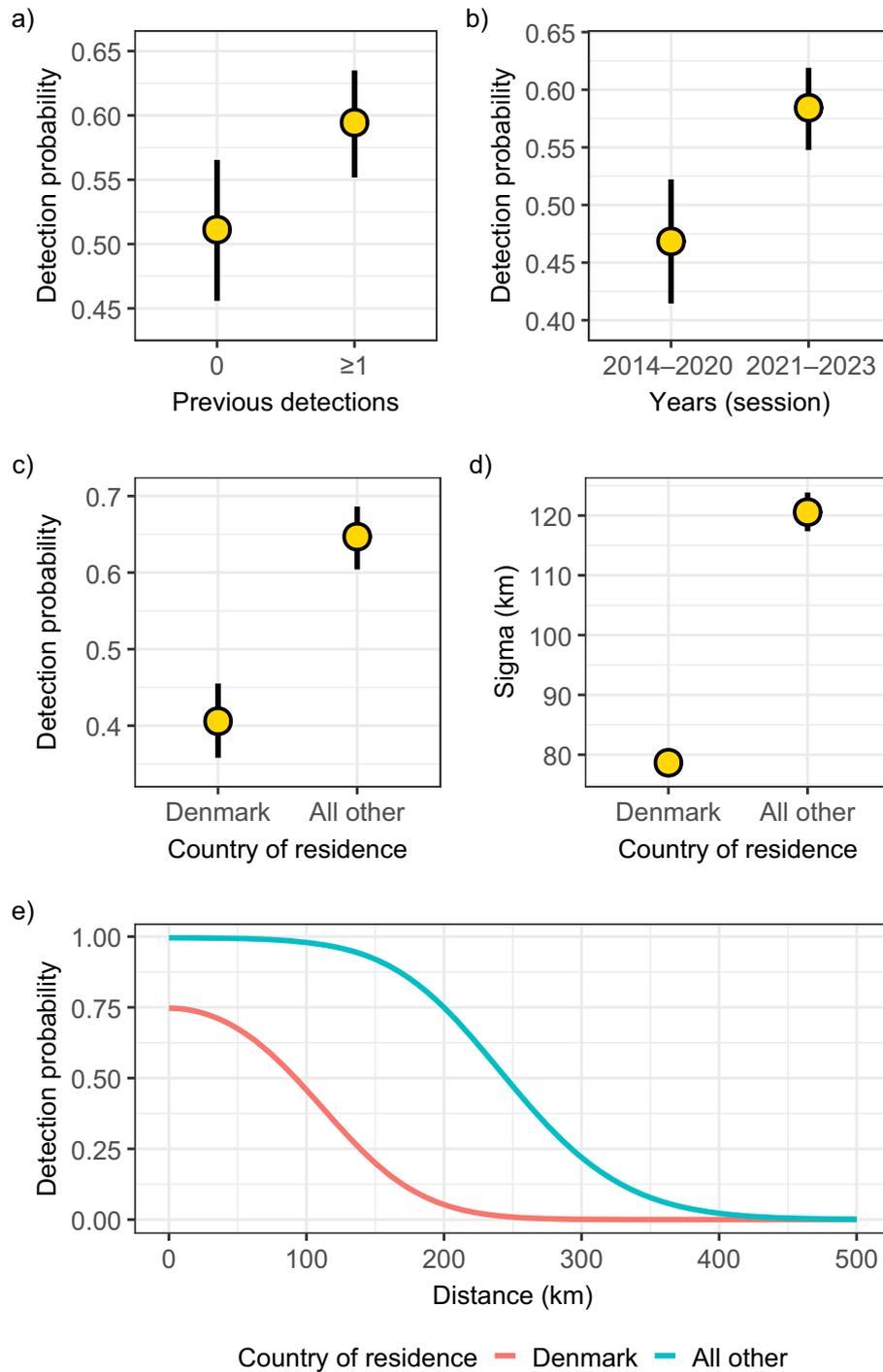


FIGURE 4 Predictions from the top-ranked model (based on Akaike information criterion ranking) for (a–c) detection probability and (d–e) movement. (a) Predicted detection probability by behavioral state (no prior detection vs. ≥ 1 prior detection). (b) Predicted detection probability by session, showing higher detectability in recent years. (c) Predicted detection probability by residency group (Denmark vs. all other countries). (d) Predicted movement parameter sigma by residency group. (e) Detection probability across the home range for each residency group calculated by combining the detection intercept and sigma under the half-normal detection function described in *Methods*, using estimates from the top model. Error bars in panels (a)–(d) represent the 95% CIs. In panels (a)–(d), estimates are calculated at a distance of zero from the trap to the home range center, that is, distance $(x_j, s_i)^2 = 0$, and averaged across areas and the remaining predictors (i.e., partial predictions; Fox & Weisberg, 2018).

grounds in general, and to the TMB specifically. A skipper living in Denmark has a home range radius of approximately 250 km, compared to 450 km for skippers

residing in other countries. Thanks to the numerous AIS detections, the movement parameter of skippers could be estimated with great precision, with a ratio between

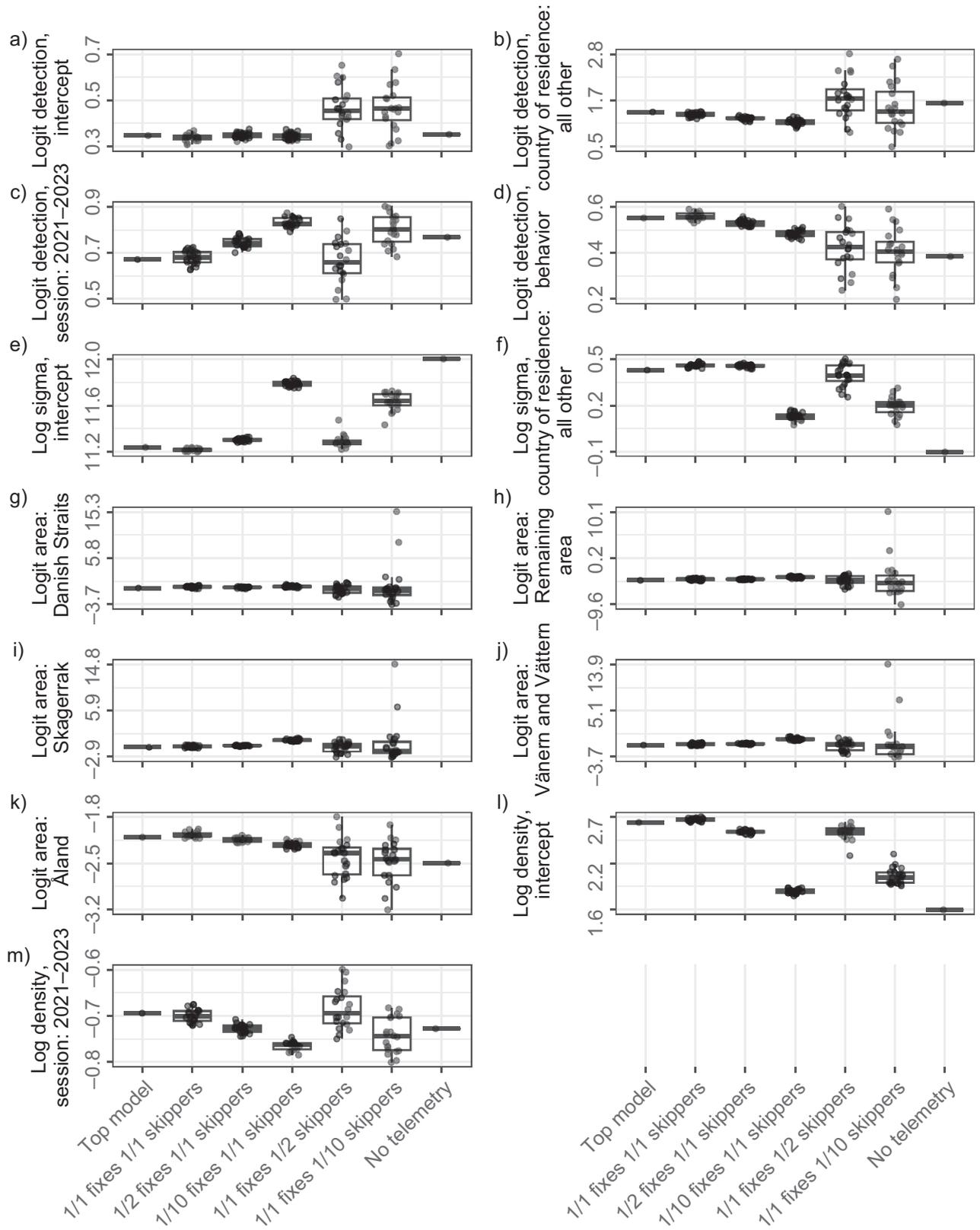


FIGURE 5 Legend on next page.

estimate and standard error (z value) of approximately 1122 for the sigma intercept.

Robustness to telemetry sampling and key assumptions

The sensitivity of the integrated SCR–RSF results to telemetry data was evaluated with 20 resamples per scheme. Holding the set of skippers fixed and thinning AIS fixes per skipper (50 → 25 → 5) yielded very similar parameter estimates, indicating that fix frequency is not driving inference. In contrast, randomly reducing the number of skippers while holding fixes per skipper constant (134 → 66 → 13 at 50 fixes each) produced much larger variance in σ and in regional space-use coefficients, consistent with distinct spatial strategies across skippers and with some regions being informed by few individuals. Three key findings were stable across all schemes: (1) density in 2021–2023 was markedly lower than in 2014–2020 and skipper detectability higher, (2) resource-use parameters persisted where Bornholm scored high and Åland low, and (3) detectability increased after a skipper’s first tournament participation (behavioral effect, trap-happiness). To avoid overweighting a few intensively tracked skippers, the main analysis standardized telemetry to 50 fixes per skipper. The two-session split reflects clear regulatory contrasts taking place during the second session (2021–2023) and is modeled via session-specific detection and density. Together, these checks suggest that the principal conclusions (population decline and core areas Bornholm and Åland) are robust, whereas fine-scale patterns in fringe regions (e.g., Danish Straits, Skagerrak, Vänern–Vättern) should be interpreted cautiously. Note, however, that area coefficients are expressed relative to Bornholm (the reference level); re-parameterizing the model with, for example, Åland as the reference would change the numerical contrasts (e.g., enlarge the reference level–Danish Straits difference), so including these fishing grounds remains informative even though their effect sizes are small under the current parameterization.

The SCR component estimates a latent population while accommodating detection heterogeneity (behavior, country of residence, session, and area). When the chance that any one skipper appears at a given occasion is small, many skippers will never be detected over a finite set of tournament occasions; the models estimate how likely it is to be seen at least once, and therefore how many all-zero skippers are implied. The population size N is estimated as $\hat{N} = n + \hat{n}_0$, where n is the number of observed skippers and \hat{n}_0 is the estimated number never observed skippers in the population (Chap. 6 in Royle, Chandler, Sollmann, & Gardner, 2013). The key point is that \hat{n}_0 is not assumed; it is inferred from the full distribution of encounter histories (e.g., 001, 101, and 111). As detectability varies by session, behavior, area, and country of residence, abundance is scaled accordingly. It is not assumed that detected and undetected skippers share a single constant detectability. Detection heterogeneity is modeled explicitly with covariates in the SCR component. Thus, undetected skippers are governed by the same parametric detection model as detected skippers, with differences arising through these covariates. The behavioral formulation follows standard SCR practice and is estimated by the individual encounter histories leading up to the first detection and the ones after the first detection, for example, 001011 gives 001 versus 011 with detections being more frequent after the first detection in this example. This allows undetected and detected skippers to have separate detection probabilities (Borchers & Efford, 2008; Chaps. 6 and 7 in Royle, Chandler, Sollmann, & Gardner, 2013).

Telemetry (AIS) does not add additional skippers to the SCR data; it stabilizes the spatial part of the detection model (movement scale and resource use), so detectability is modeled consistently across space. The sensitivity analysis showed that thinning fixes per skipper had little effect on parameters, whereas thinning the number of skippers increased variance in movement and regional space use but left several main results unchanged: density was lower in 2021–2023 while detectability was higher, the behavioral response was positive, and Bornholm/

FIGURE 5 (a–m) Parameter estimates under alternative telemetry resampling schemes, holding either the number of fixes per skipper or the number of skippers constant. The leftmost column shows estimates from the top model (50 fixes per skipper and 134 skippers); the rightmost column shows estimates from a model without telemetry. The five middle columns show results from models fitted with 20 random resamples of the telemetry data: Points are individual maximum likelihood estimates, and boxplots show their median and interquartile range (25th–75th percentiles); whiskers extend to the most extreme values within $1.5 \times$ interquartile range of the hinges. “1/1, 1/2, 1/10 fixes” correspond to 50, 25, and 5 fixes per skipper, respectively; “1/1, 1/2, and 1/10 skippers” correspond to 134, 66, and 13 skippers, respectively. All models included the same parameters, session-specific density; detection probability depending on session, country of residence, behavior, and area; and the movement parameter depending on the country of residence. Area effects for Danish Straits, “remaining area,” Skagerrak, and Vänern–Vättern are not estimable in the no-telemetry model because they are informed by telemetry (automatic identification system) data.

Åland remained core areas. In fact, these results were persistent even when completely removing the telemetry data. Together, these results indicate that the participation histories do contain enough information to infer the number of non-participating skippers and that the conclusions are robust to reasonable choices about telemetry effort.

Conclusions, limitations, and future directions

The SCR framework includes models that can estimate many variables necessary for describing human populations. Both skipper behavior and their movements are incorporated in the detection probability function, resulting in more realistic estimates of population density and extent. Naturally, not every aspect of the skipper population can be included in the models, and assumptions about the population must be understood in part through the included covariates. Overly complex models, which include too many assumptions about the population, are often data-deficient, do not generalize well, and are more likely to incorporate less significant parameters that may not be relevant over time (Chap. 4 in Royle, Chandler, Sollmann, & Gardner, 2013).

A limitation of this type of study is the sensitive nature of working with personal data, which may affect the future scalability of modeling tournament participation as encounter histories. Furthermore, for this study in particular, the low spatial resolution relying on only two tournament locations was mitigated by integrating AIS data, which allowed for estimating resource selection and movements. However, only two sampling locations do not allow estimating variation in density, which is currently assumed to be uniformly distributed across the state space, although most likely skipper density is higher near populated areas and important fishing grounds. A heterogeneous density model would chiefly redistribute skipper home-range centers according to a state-space covariate and would not necessarily change the estimated total population size (Chap. 11 in Royle, Chandler, Sollmann, & Gardner, 2013).

In a fishery that heavily restricts harvest but still allows the catching of salmon, estimating catch-and-release mortality becomes increasingly important (Thorstad et al., 2003). Currently, there are no published studies on catch-and-release survival of salmon in the Baltic Sea trolling fishery, though many studies address survival in rivers (Keefe et al., 2022; Van Leeuwen et al., 2021; Van Leeuwen et al., 2023). Survival at sea is an important future topic to better quantify the effects of recreational fishing on Baltic salmon populations.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and script to perform the models (Karlsson, 2026) are available from Zenodo: <https://doi.org/10.5281/zenodo.18221487>.

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