



Stock connectivity patterns and indications of sub-stock component structuring of cod in the Sound in the western Baltic Sea

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ABSTRACT

Sustainable management of fish stocks requires knowledge of stock structure and connectivity between spawning and feeding habitats. Cod in the Sound in the western Baltic Sea are an example of a stock component with complex connectivity patterns. Currently cod in this area are managed as part of the western Baltic cod stock, while several studies suggest potential connectivity with the neighbouring stock in Kattegat. Here we assess the degree of ecological connectivity of cod in the Sound with the neighbouring areas using historical tagging data from 1957 to 1987, and contemporary growth data from trawl surveys collected between 2007 and 2021. Furthermore, data from cod tagged outside of the Sound between 1960 and 2018 and recaptured in the Sound was used to examine immigration from outside areas. The ecological connectivity between the Sound and Kattegat appeared to be considerable, primarily during the spawning season. Furthermore, cod tagged in the northern Sound were most likely to be recaptured in Kattegat while cod tagged in the southern part of the Sound were mainly recaptured in the Sound. Only 40 out of 16,789 tagged cod released outside of the Sound were eventually recaptured inside the Sound. Overall, these results highlight the need for further examination into the current stock structure of cod in the western Baltic and adjacent areas.

1. Introduction

A fish stock is defined as a homogenous group of a fish species with similar biological features, such as growth, maturity, and mortality (Hilborn and Walters, 1992), and stock affiliation is based on spatio-temporal patterns in spawning. Stock identification is vital to effective fisheries management, hence stock structure and connectivity between adjacent areas should be documented to underpin efficient management (Begg and Waldman, 1999). In the Baltic Sea and adjacent waters, the Atlantic cod (*Gadus morhua*) is managed as three separate stocks divided by the subdivisions (SDs) used by the International Council for the Exploration of the Sea (ICES): The Kattegat stock (SD 21), the western Baltic stock (SD 22–24), and the eastern Baltic stock (SD 24–32). These divisions were defined based on the best available knowledge at the time of definitions, and subsequent studies have confirmed that the stock divisions, at least to some extent, are consistent with observed patterns of natal homing (Svedäng et al., 2007).

One of these stocks, the western Baltic cod stock, is divided among three different areas: the Belt Seas (SD 22), the Sound (SD 23), and the Arkona Basin (SD 24) (Fig. 1). Cod in these areas are noted to be different from the eastern Baltic cod stock (see Hüsey, 2011 and references therein). The Arkona Basin is additionally known as a mixing ground between the eastern and western Baltic cod stocks (e.g., see Aro, 1989, Hemmer-Hansen et al., 2019, Weist et al., 2019). This has previously caused issues for management, as the ratio between the two stocks in the Arkona Basin has changed over time due to a spill-over of cod from the eastern Baltic cod stock (Eero et al., 2014), making it difficult to estimate the stock assessment parameters and reliable reference points. However, today this high degree of stock mixing is accounted for in stock assessment by the use of otolith shape analyses to separate the two stocks in this mixing zone (ICES, 2022, 2019; Schade et al., 2019).

Stock mixing has also been reported in the Kattegat stock where a North Sea component is transported in as juveniles or larvae and return to the North Sea upon reaching maturity around age 4 (Hemmer-Hansen

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et al., 2020; Hüsey et al., 2022). This annual removal of a large fraction of the cod in Kattegat caused an unrealistically high estimation of total mortality in the stock assessment. Furthermore, recruitment was artificially inflated due to the high influx of juveniles from the North Sea. These issues have recently been accounted for in stock assessments (ICES, 2021), but again illustrate the importance of studying stocks' connectivity between areas.

While cod in the Sound are formally considered as part of the western Baltic cod stock, connectivity between cod in the Sound and Kattegat has previously been reported (e.g., see Aro, 1989, Bagge et al., 1994, Svedäng et al., 2010). Connectivity between Kattegat and the Sound has been noted during the spawning season (Svedäng et al., 2010; Vitale et al., 2008), likely because the full extent of spawning grounds stretches from the central Sound into the southern Kattegat (Hüsey, 2011). The prevailing question is to what extent cod on the spawning grounds in southern Kattegat have moved in from the Sound and/or if cod from Kattegat display feeding migrations to the Sound; for example to feed during fall on herring to prepare for spawning (Aro, 1989; van Deurs et al., 2016), which constitute a lipid rich diet (van Deurs et al., 2022, 2016). If connectivity is high, then it may be more reasonable to manage the Sound with the Kattegat stock. In comparison, movement from the southern and central Baltic Sea into the Sound appears unlikely as cod move into or through the Belt Seas to enter Kattegat (Bagge, 1969; Berner, 1974, 1971a, 1971b) which may challenge the notion to continue to manage the Sound with the rest of the western Baltic cod stock. In addition, it is possible that two separate populations exist in the Sound due to differences in timing of spawning in the northern and southern parts based on reports from fishermen (Olesen, unpubl.). In particular, differences in hydrography and topography may act as potential natural separators for a population in the deeper and more saline water in the north, and one in the shallower and fresher water in the south. Thus, to assess the degree of isolation of the Sound cod and to determine its stock identity, it is imperative to assess the degree of connectivity between the Sound and adjacent areas.

The overall aim of this study is to assess whether cod in the Sound are

affiliated with the rest of the western Baltic cod, mix with the Kattegat stock, or constitute a local population of relatively resident cod. Furthermore, we consider a potential population divide in the Sound based on the prevailing geographic salinity gradient to investigate if the differences in hydrography and topography may drive differences in subpopulations based on a salinity division. We approach this by examining the extent and direction of historical movement patterns using conventional tagging data from across four decades and assessing seasonal movements between the Sound and Kattegat. Additionally, we compare contemporary growth patterns across the western Baltic cod stock components and the Kattegat stock to provide support for the hypothesis that the historical population connectivity patterns observed from tagging data prevail to date. This analysis is based on the assumption that growth patterns of strongly connected populations will be similar, while differences in growth suggest geographically separated populations.

2. Methods

2.1. Tagging data

2.1.1. Releases in the Sound

Data for the Sound tagging projects were digitized from hand-written hard copy records of Danish and Swedish tagging projects and were combined with the Baltic cod tagging database (Lundgreen et al., 2022; Mion et al., 2022, 2020). However, the full Baltic database was not utilized for this study but only releases in the Sound ($n = 797$). The database included spatial and temporal information of individual fish, such as release and recapture locations and time, days at liberty (DAL), and biological information such as release total length (mm) and weight (g). Biological information was only occasionally recorded on recapture. No information on age was available, and information on depth intervals at recapture was only available for a small subset. Cod with DAL < 15 were excluded to allow resumption of normal behaviour following tagging (van der Kooij et al., 2007), and recaptures with no information

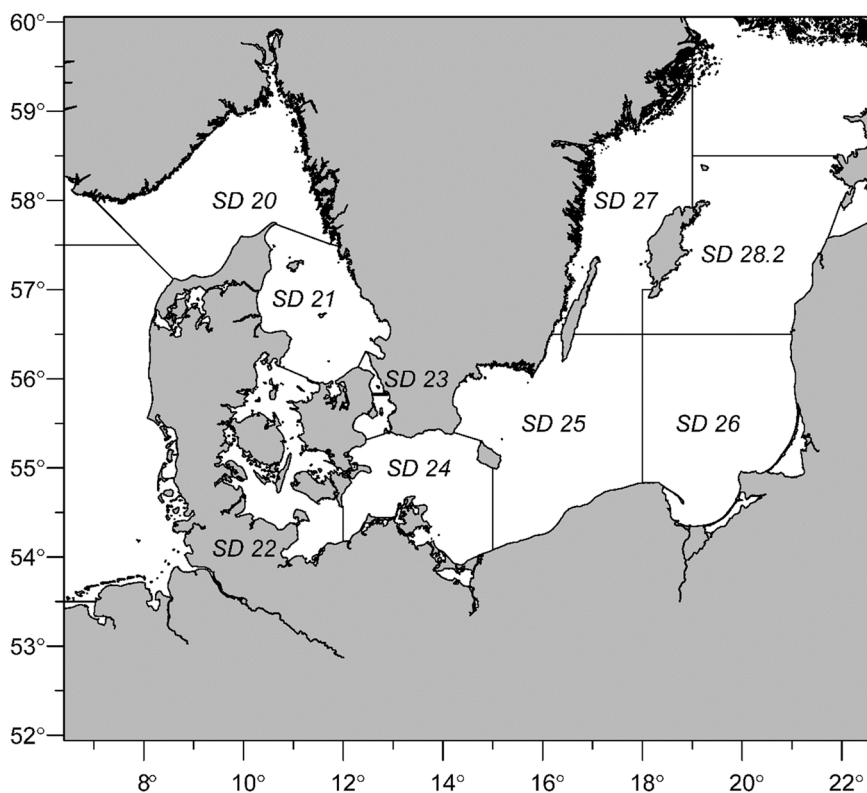


Fig. 1. The Baltic Sea and relevant ICES subdivisions (SDs). SD 20: Skagerrak, SD 21: Kattegat, SD 22: The Belt Sea, SD 23: The Sound, SD 24: The Arkona Basin, SD 25: The Bornholm Sea, SD 26: the south-eastern Baltic Sea, SD 27: The Western Gotland Basin, SD 28.2: The Gotland Sea. Note the black horizontal line in SD 23 which indicates the geographical divide between the two areas based on the salinity division. For depth layers, see Jakobsson et al. (2019) for the Baltic Sea and Funk et al. (2021) for a higher resolution of the western Baltic Sea.

on release or recapture position or DAL were excluded. Cod with recapture positions on land were similarly removed. Following data screening, 215 recaptures were excluded from the analyses ($n = 582$). Cod were released between 1957 and 1987 in the Sound and recaptured between 1957 and 1989. Tag types used were mainly Lea or t-bar tags (Mion et al., 2020). Release numbers for the tagging projects were not available. See the supplementary material where fishing mortality is used to give an indication of survival.

2.1.2. Releases outside the Sound

A subset of the Baltic cod tagging database (Lundgreen et al., 2022; Mion et al., 2022, 2020) of cod released in other SDs but recaptured in the Sound ($n = 44$; $n = 40$ after data screening as above) was used to evaluate the degree of immigration from other areas. This database included tagging data from Danish, Swedish, German, and Polish tagging projects (Lundgreen et al., 2022; Mion et al., 2022, 2020). The same release and recapture information was available as in the Sound tagging database. Cod were released between 1960 and 2018 in Kattegat (SD 21), the Belt Sea (SD 22), the Arkona Basin (SD 24), the Bornholm Sea (SD 25), the south-eastern Baltic Sea (SD 26), and the Gotland Sea (SD 28.2), and recaptured between 1961 and 2020. Overall, the cod were released and recaptured in all quarters throughout the years. The tag types used were also primarily Lea or t-bar tags. See Fig. 1 and figure text for SD denotations and location names. Similarly, release numbers for the tagging projects were not available.

2.2. Estimating transition probabilities

To assess the connectivity of cod released in the Sound with the adjacent areas, a transition matrix was used. A transition matrix is a square matrix that describes the probability of transitioning between different states in a Markov chain. Thus, movement can be described by a Markov process where the probability of moving to a new state is only dependent on the current state, with states in our study representing neighbouring areas, such as the northern and southern Sound. In the case of cod moving between areas, a transition matrix then shows the probability of staying in an area or moving to neighbouring areas within one time step of one week. When applied to the tagging data, the transition matrix shows the most probable area transition patterns based on all data and indicates overall connectivity. We applied this approach to two cases: 1) an overall transition matrix with the Sound divided into northern and southern areas connected to Kattegat and the southern Baltic, respectively, with no seasonal aspect (i.e., no division into spawning and feeding seasons), and 2) two seasonal transition matrices for only the Sound and Kattegat as it was not possible to include the southern Baltic due to a lack of sufficient seasonal data coverage. For the seasonal matrix, it was not possible to divide the Sound due to estimation issues. In addition, to reduce potential bias in the seasonal matrix, the southern releases in the Sound were excluded. Both cases only utilised data for cod released in the Sound and thus we assume that area transitions are only representative of the Sound stock component for analysis purposes. In addition, it should be noted that recapture probability is dependent on spatio-temporal variations in fishing effort which was not accounted for. The potential implications of spatial variations in fishing effort are considered in the discussion.

As the transition matrix assumes that movement is possible between the areas within the chosen time step, it is necessary to choose a time step where area transitions are possible. Additionally, we chose a time step where it is unlikely for the cod to be able to skip areas in one time step, e.g., within the time step, an individual cod in the Sound is able to move to a neighbouring area, such as Kattegat, but not to an area further away, such as the Belt Sea. The definition of a suitable time step was based on observed swimming speeds in resident cod (Løkkeborg and Fernö, 1999). The smallest area, the southern Sound, is approx. 30 km long, and if cod are assumed to be active for around 10 h per day with a mean swim speed of $20\text{--}30\text{ cm s}^{-1}$ (Fernö et al., 2011; Løkkeborg and

Fernö, 1999), it would take approx. 3–4 days for a cod to move from the northern part to the southern part of the Sound. As a lot of time is also spent foraging, the time step was set to one week for modelling purposes for both cases, as it is unlikely for the cod to be able to skip an area in one time step for a week.

To create a grid for the overall transition matrix, the relevant areas were divided into the following groups: Kattegat-Skagerrak (SD 20, 21), the northern Sound (SD 23 N), the southern Sound (SD 23 S), and the southern Baltic (SD 24–27). It was not possible to separate the groups further as this would cause estimation issues by having too little data per group. The Sound was divided horizontally at latitude 55.83 in order to coincide with the salinity gradient (Bendtsen et al., 2007; Momigliano et al., 2018). Recaptures in SD 22 were ignored for the analyses of movement due to the focus on whether cod move north and south of the Sound, and due to low recaptures in SD 22 ($n = 4$). Additionally, this area does not seem to have a high connectivity to the Sound (Bagge, 1969; Berner, 1974, 1971a, 1971b). Note that Skagerrak was combined with Kattegat due to low recaptures ($n = 2$), and henceforth Kattegat-Skagerrak is referred to as Kattegat. Due to the small size of the subset of recaptures from outside the Sound, it was excluded from the transition matrix analyses.

Maximum likelihood optimization was done to estimate the transition probabilities that would maximize the likelihood of observing the dataset. This means that different test values would be tried until the most likely values that would result in the observed dataset were found. To do this, a transition matrix, P_θ , was set up for each individual fish. Based on the test values, the probabilities of moving between areas for each individual fish were estimated by first calculating the probability of moving between the release and recapture area within the days at liberty, which were converted to weeks (t). This was done by raising the power of the transition matrix to the weeks at liberty (P_θ^t), where the transition matrix would then represent the possibilities of moving between each area at each individual time step. The transition matrix is then multiplied by itself for each individual time step and the final multiplication then represents the final transition probabilities between the areas based on t . This was done for each individual recapture.

Finally, the negative log likelihood for each individual fish was calculated and summed to get the overall most likely transition probabilities for the entire dataset based on all recaptures:

$$L(\theta) = - \sum_i \log(P_\theta^t)_{k,j}$$

where P_θ^t indicates a transition matrix for one fish raised to the power of the weekly time step t , k the index of the release area, and j the index of the recapture area in the transition matrix. The negative log likelihood was then optimized until the most likely test values were found to get the most likely probabilities for the observed movement patterns in the dataset and estimate the overall transition matrix.

For the seasonally resolved analyses, the transition matrices were constructed similarly as above, although the seasonal aspect required an additional time component. Peak spawning occurs between January–February and was chosen as the spawning season in this study as most spawning activity occurs during these months (Vitale et al., 2005). Two transition matrices were compiled: a spawning season transition matrix (January–February) and a feeding season transition matrix (March–December). When calculating the probability of a cod moving between areas within the weeks at liberty, the season at each time step was registered. In the case of a cod being out during more than two seasons, the probabilities during the spawning season were used to estimate the spawning seasonal transition matrix while the probabilities during the feeding season were used to estimate the feeding seasonal transition matrix. As such, when calculating the likelihood for each fish, instead of raising P_θ to the power of t , at each time step P_θ was multiplied by either the spawning or feeding seasonal matrix depending on the current season for the time step. As with the overall transition matrix, this was

done for each individual recapture and summed to get the overall most probable area transitions within the two seasons.

Additionally, the geodesic distance between the release and recapture locations was calculated to determine the presence of cyclical patterns, as has been observed previously in North Sea cod (Righton et al., 2007). Only Sound cod released during peak spawning were considered to determine whether they return following spawning migrations (n = 73).

2.3. Growth

Available data on individual length-at-age in the ICES Database of Trawl Surveys (DATRAS) from Baltic International Trawl Surveys (BITS) and North Sea International Bottom Trawl Surveys (NS-IBTS) was utilized for the growth analyses for the western Baltic cod stocks. This included data on length (cm), age, and sampling area. For the growth analyses, data from the Sound (n = 2052), Kattegat (n = 3533), the Belt Seas (n = 6352), and the Arkona Basin (n = 9443) was used following data screening which included removal of outliers based on unrealistic length and age combinations. Data from Q1 between 2007 and 2021 was selected to show contemporary patterns and to coincide with the peak spawning season in the Sound.

To test for growth differences between the four SDs, a global model assuming no differences in growth was first set up using the von Bertalanffy growth function:

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where L_t is the length-at-age t , L_∞ the asymptotic length, K the growth coefficient, t the age of the fish, and t_0 the theoretical size at age 0. This model used length-at-age data for all four SDs combined and estimated four parameters, including the standard deviation (L_∞ , K , t_0 , σ) using maximum likelihood optimization.

Subsequently, another model was created that estimated SD-specific parameters:

$$L_t = L_{\infty SD} (1 - e^{-K_{SD}(t-t_{0SD})})$$

This resulted in 16 SD-specific parameters ($L_{\infty SD}$, K_{SD} , t_{0SD} , σ_{SD}), and the parameters were estimated similarly as above.

A likelihood ratio test was then used to compare the two models to test which model fit the data best by testing whether the ratio between the likelihoods was significantly different from zero. If growth were similar across SDs, the global model would describe the data better than the second model. Alternatively, if growth were different between the SDs, the second model would describe the data better than the global model.

Finally, to specifically address the connectivity between the Sound and the surrounding SDs (Kattegat, the Belt Seas, the Arkona Basin), the analyses were repeated with the Sound and each SD separately.

It should be noted that potential mixing between the stock components in the respective SDs was not accounted for and may have introduced bias to the data used to construct the growth curves. This is elaborated upon further in the discussion.

All analyses were done in R version 4.0.2 (R Core Team 2020). The package *beanplot* (Kampstra, 2008) was used to create the beanplot, and *sp* (Pebesma and Bivand 2005), *rgeos* (Bivand and Rundel 2020), and *rgdal* (Bivand et al., 2020) were used to create the maps.

Table 1

Release and recapture months for cod released in the Sound between 1957 and 1987 and recaptured between 1957 and 1989 (n = 582), and cod released outside the Sound between 1960 and 2018 but recaptured within the Sound between 1961 and 2020 (n = 40).

Area	Jan Q1	Feb Q1	Mar Q1	Apr Q2	May Q2	Jun Q2	Jul Q3	Aug Q3	Sept Q3	Oct Q4	Nov Q4	Dec Q4
The Sound (Releases)	73	-	5	67	80	10	-	-	-	194	135	18
The Sound (Recaptures)	80	107	79	43	29	27	13	21	27	65	38	53
Outside The Sound (Releases)	11	4	6	1	1	-	-	-	4	4	6	3
Outside The Sound (Recaptures)	3	9	7	2	2	2	3	-	1	1	2	8

3. Results

3.1. Tagging data

3.1.1. Releases in the Sound

Recaptured cod had been released throughout the year aside from Q3, with the majority released in Q4 (n = 347; Table 1). In contrast, cod were mainly recaptured in Q1 (n = 266), but recaptures occurred in all quarters (Table 1). 13% and 87% of recaptures were tagged during the peak spawning and feeding seasons, respectively (n = 73; n = 509). In comparison, 32% and 68% of recaptures were caught during the peak spawning and feeding seasons, respectively (n = 187; n = 395).

Recaptures were mainly from the Sound (SD 23; n = 350) and Kattegat (SD 21; n = 162) with occasional recaptures south of the Sound during both the spawning and feeding seasons (n = 44 in SD 24, n = 18 in SD 25, n = 1 in SD 26 and 27, respectively; Fig. 2). In contrast, recaptures in Skagerrak (SD 20) and the Belt Sea (SD 22) were negligible (n = 2 and 4, respectively). Days at liberty ranged from 18 to 1151 days, and most cod were recaptured within one year (median = 210 days). See the supplementary material for indications of survival based on fishing mortality (Table S1, Figure S1).

3.1.2. Releases outside the Sound

Cod released outside the Sound and recaptured in the Sound consisted of only 0.24% of the full Baltic tagging database excluding the Sound releases (n = 16,789). These releases were from Kattegat (SD 21; n = 11; 1.94% of 567 recaptures originating from Kattegat), the Belt Sea (SD 22; n = 1; 0.04% of 2341 recaptures originating from the Belt Sea), the Arkona Basin (SD 24; n = 20; 1.49% of 1345 recaptures originating from the Arkona Basin), Bornholm Sea (SD 25; n = 6; 0.19% of 3174 recaptures originating from the Bornholm Sea), the south-eastern Baltic Sea (SD 26; n = 1; 0.09% of 1147 recaptures originating from the south-eastern Baltic Sea), and the Gotland Sea (SD 28.2; n = 1; 0.09% of 1132 recaptures originating from the Gotland Sea; Fig. 3). This suggests the connectivity between the Sound and the Baltic is limited. Recaptures were generally medium sized when released, and sizes ranged from 247 to 638 mm (median = 462.5 mm). In contrast, recapture sizes ranged from 310 to 980 mm (median = 505 mm). Cod were recaptured evenly throughout the year with no apparent pattern. All cod released in Kattegat were released in January on the edge to the Belt Seas.

3.2. Estimated transition probabilities

Most cod were released in the northern part of the Sound (north: n = 524; south: n = 54). The recapture map showed that cod released south of the salinity divide were mainly recaptured in the northern Sound and slightly less in the Baltic (n = 5 (SD 21), n = 30 (SD 23), n = 8 (SD 24), n = 10 (SD 25), n = 1 (SD 27; Fig. 2). In contrast, cod released north of the salinity division were mainly recaptured in the Sound and southern Kattegat (n = 2 (SD 20), n = 157 (SD 21), n = 320 (SD 23), n = 36 (SD 24), n = 8 (SD 25), n = 1 (SD 26); Fig. 2). Days between release and recapture ranged from 18 to 1151 days for the northern component (median = 224.5 days), and 21–951 days for the southern component (median = 95 days).

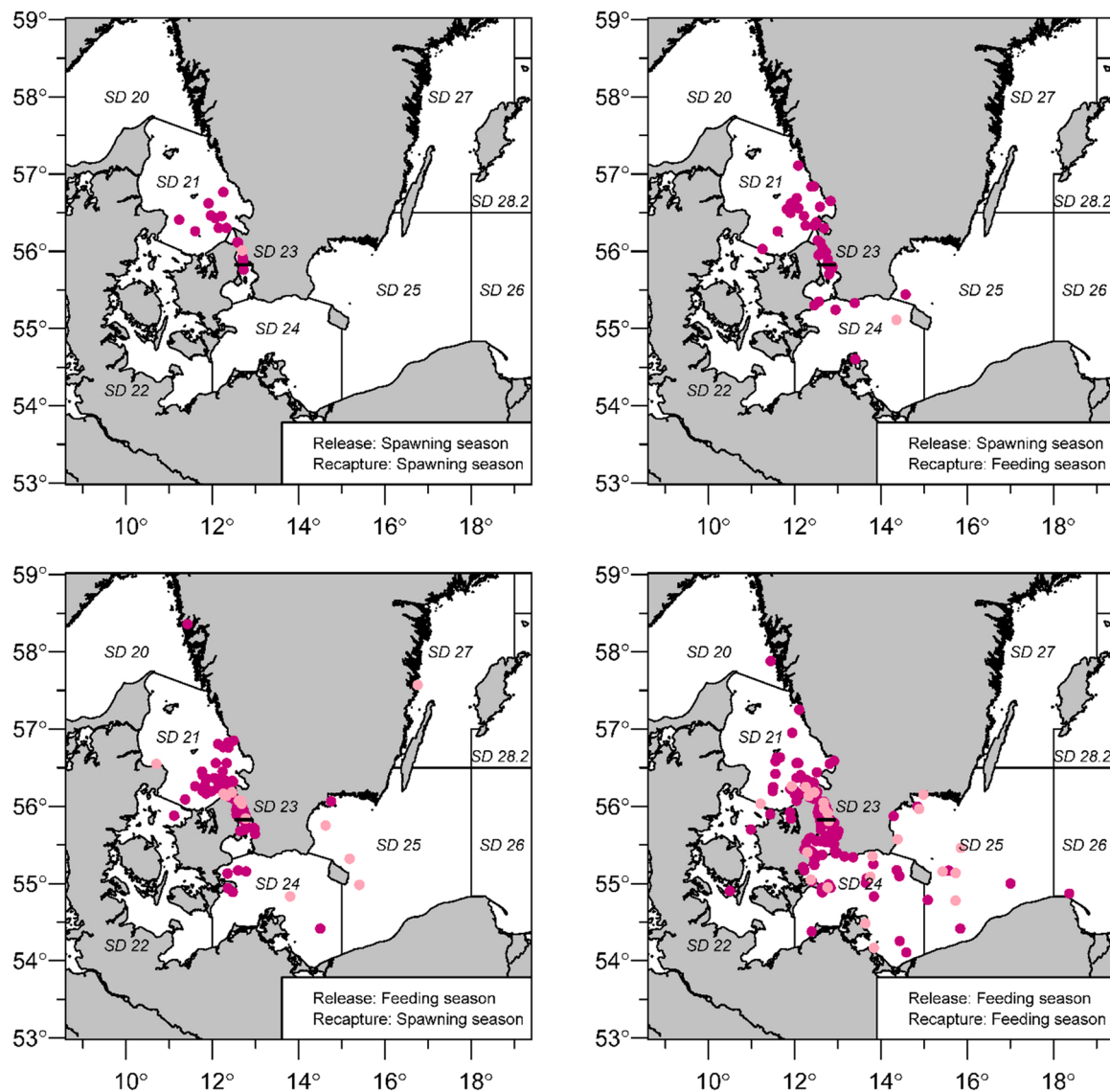


Fig. 2. Recapture positions of cod divided into a northern and a southern component depending on their release position in the Sound and separated by release and recapture times (spawning (January-February) or feeding season (March-December)). The black horizontal line indicates the geographical divide between the two areas. The division was based on topographic features in combination with the salinity gradient prevailing in the Sound (Bendtsen et al., 2007). Dark pink = released north of the divide. Bright pink = released south of the divide. Top left = released and recaptured within the spawning season ($n = 29$). Top right = released within the spawning season and recaptured within the feeding season ($n = 158$). Bottom left = released and recaptured within the feeding season ($n = 351$). Bottom right = released within the feeding season and recaptured within the spawning season ($n = 44$). Cod were recaptured in the following areas: SD 20: Skagerrak ($n = 2$), 21: Kattegat ($n = 162$), 22: the Belt Sea ($n = 4$), 23: the Sound ($n = 350$), 24: Arkona Sea ($n = 44$), 25: Bornholm Sea ($n = 18$), 26: the south-eastern Baltic Sea ($n = 1$), 27: the western Gotland Basin ($n = 1$).

3.2.1. The overall transition matrix

The overall transition matrix suggested a divide into potential northern and southern stock components in the Sound (Table 2). Within a random week during the year, an individual cod tagged in the Sound but currently present in Kattegat was just as likely to stay as moving into the northern Sound (52% and 48%, respectively). However, a cod tagged in the Sound and currently present in the northern Sound was most likely to stay with some probability of movement towards Kattegat (66% and 29%, respectively). In comparison, it was very unlikely for the cod to move to the southern Sound (5%).

An individual cod tagged in the Sound and currently present in the southern Sound was more likely to stay (75%), although with small probabilities of movement to the northern Sound or into the Baltic (17% and 8%, respectively). In contrast, a cod tagged in the Sound but currently present in the Baltic showed low probability for moving into the Sound (8%) and a high probability to stay in the Baltic (92%).

3.2.2. The seasonal transition matrices

For the seasonally divided transition matrix, clear seasonal patterns were observed for Kattegat and the Sound (Table 3). In particular, the probability to leave the respective areas was similar for both areas, suggesting frequent movements between the two areas. Within a random week during the spawning season, a cod tagged in the northern Sound but currently present in Kattegat was most likely to stay in the Kattegat (77%), but still with a notable chance of moving into the Sound (23%). These patterns were similar for a cod tagged in and currently present in the Sound which would be more likely to stay (71%) than move to Kattegat (29%).

In comparison, within a random week during the feeding season, residency in each area was much more probable. While a cod tagged in the northern Sound but currently present in Kattegat would be more likely to stay in the Kattegat (82%) than move to the Sound (18%) as in the spawning season, the probability to move to the Sound was lower.

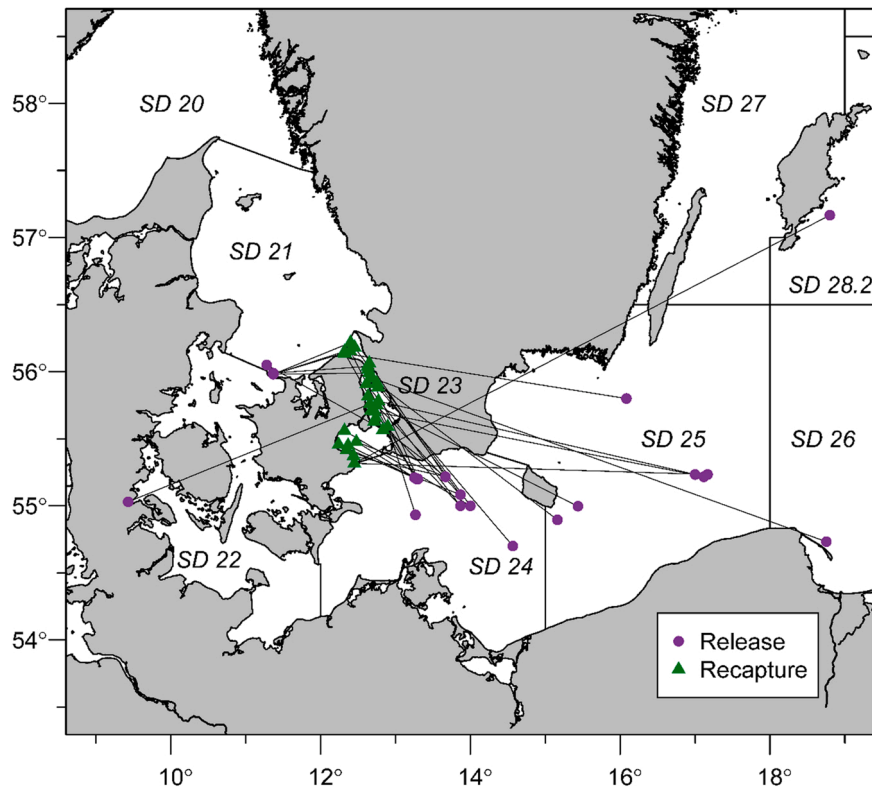


Fig. 3. Recaptures in the Sound released in other areas. Recaptures originated from Kattegat (n = 11), the Belt Sea (n = 1), the Arkona Basin (n = 20), Bornholm Sea (n = 6), the south-eastern Baltic Sea (n = 1), and the Gotland Sea (n = 1).

Table 2

Overall transition matrix based on a salinity divide in the Sound showing the most likely area transitions. The table shows the probability of a cod tagged in the Sound moving from the current area (row) to a neighbouring area (column) within a random week during the year. Values in parentheses indicate confidence intervals for the estimated transition probabilities. Note that the diagonal values lack confidence intervals as they are not estimated but calculated by subtracting the estimated values from 1. The table is only based on releases in the Sound and gives an overall indication of connectivity.

	Kattegat	Northern Sound	Southern Sound	Southern Baltic
Kattegat	0.52	0.48 (0.15, 0.83)		
Northern Sound	0.29 (0.11, 0.61)	0.66	0.05 (0.04, 0.15)	
Southern Sound		0.17 (0.09, 0.33)	0.75	0.08 (0.05, 0.18)
Southern Baltic			0.08 (0.04, 0.16)	0.92

Table 3

Seasonal transition matrices between Kattegat and the Sound during peak spawning (January-February) and feeding season (March-December) showing the most likely area transitions. The table shows the probability of a cod tagged in the northern Sound moving from the current area (row) to a neighbouring area (column) within a random week during either the spawning or feeding season. Values in parentheses indicate confidence intervals for the estimated transition probabilities. The table is only based on northern releases in the Sound and gives an overall indication of connectivity. Southern releases in the Sound were excluded to reduce potential bias.

Season	Kattegat	The Sound
Spawning season		
Kattegat	0.77	0.23 (0.12, 0.39)
The Sound	0.29 (0.18, 0.43)	0.71
Feeding season		
Kattegat	0.82	0.18 (0.11, 0.28)
The Sound	0.04 (0.02, 0.08)	0.96

This was similar in the Sound where a cod originally tagged in the northern Sound was even more likely to stay than leave (96% vs. 4%) compared to the spawning season.

Overall, these results suggest the existence of a population component in the northern Sound with frequent movements to and from

Kattegat, predominantly in the spawning season. Additionally, there appears to be a relatively resident component in the southern Sound with some movement to the northern Sound. Furthermore, cod in the Baltic appear to be relatively isolated from the Sound populations, with some connection to the southern Sound. The analyses of distances between release and recapture locations did not reveal any clear cyclical pattern related to spawning migrations (Figure S2).

3.3. Length distributions in cod in the Sound and growth across populations

The length distributions were similar between released cod from the tagging projects and cod collected in contemporary surveys (tagging: median = 44 cm, range = 18–110 cm; survey: median = 46 cm, range = 12–121 cm; Figure S3). This indicates that the population length distribution was well represented by the tagged individuals (Figure S3).

The von Bertalanffy growth curves showed higher growth rates in Kattegat and the Sound while the Belt Sea and Arkona Sea were characterized by lower sizes-at-age, although the estimates were generally characterized by high standard deviations (Fig. 4, S4–5; see Table 4 for the parameter estimations). Consequently, the likelihood ratio test also showed that the model with SD-specific parameters was significantly

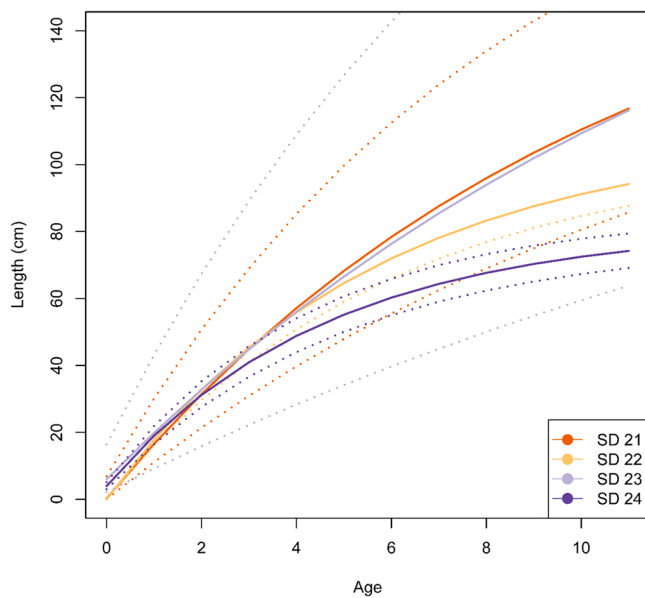


Fig. 4. Von Bertalanffy growth curves for Kattegat and each SD in the western Baltic stock (SD 21, 22–24). The parameters for each growth curve were estimated from individual length-at-age data from Baltic International Trawl Surveys (BITS) and North Sea International Bottom Trawl Surveys (NS-IBTS) by using maximum likelihood estimation. Dotted lines show standard deviations. Note that the upper limit for SD 22 is not shown due to estimation issues. See Table 4 for parameter estimations and confidence intervals.

superior to the global model assuming non-SD-specific parameters (deviance = 2266, df = 12, p = 0), further supporting that growth is not equal across the four areas although potential stock mixing was not accounted for. Similarly, for the individual comparisons with the Sound, the likelihood ratio tests showed that there was a significant difference in growth between the Sound and the other SDs, indicating a certain degree of separation (Kattegat-Sound: deviance = 131, df = 4, p = 0; Belt Seas-Sound: deviance = 76, df = 4, p = ~0; Arkona Basin-Sound: deviance = 692, df = 4, p = 0).

4. Discussion

The main objective of this study was to assess whether cod in the Sound is indeed a stock component of the western Baltic cod stock, or alternatively, whether it can be considered an isolated stock component, or is connected to the Kattegat stock. Furthermore, we aimed to clarify the complex ecological connectivity patterns within the Sound, including any seasonal movements between the Sound and Kattegat. To do this, we compiled historical tagging data which has been previously used in individual studies (e.g., see Berner, 1967, 1981, Otterlind, 1985, Aro, 1989, Bagge and Thurow, 1994). Overall, our results indicated a relatively high degree of movement between Kattegat and the Sound, whereas movement between the Sound and the Baltic appeared to be less pronounced. The seasonally divided transition matrix suggested that connectivity between Kattegat and the Sound was greatest during the spawning season, supporting the notion of a continuous stretch of

spawning area transecting the border between the Sound and Kattegat. Furthermore, our results based on the transition matrices suggested some degree of disconnection between the southern and northern part of the Sound, as the exchange of cod across the salinity divide used to split the Sound into a northern and southern area was less than the exchange across the Kattegat-Sound border. Thus, our results suggest that the Sound stock may belong to the Kattegat stock as they primarily mix during the spawning season.

4.1. The connectivity between the Sound and the Baltic

In earlier studies, the level of connectivity between the Sound and the remainder of the Baltic has not been clearly resolved. One study utilizing genetic analyses reported a clear genetic differentiation between cod in the Sound and the Arkona Basin (Nielsen et al., 2003), but no differentiation between the Sound and the Belt Sea. However, differences between the Sound and the Belt Sea were found in another study (Moth-Poulsen, 1982). In comparison, our study suggests relatively low connectivity between the Sound and the remainder of the Baltic, and the same patterns emerge from previous tagging studies which generally relied on recapture maps and mapping trajectories (Aro, 1989; Bagge and Thurow, 1994; Berner, 1981, 1967; Otterlind, 1985; Svedäng et al., 2010). Indeed, it is more likely that movement from the Baltic to Kattegat occurs through the Belt Seas instead of the Sound (Bagge, 1969; Berner, 1974, 1971a, 1971b), which may explain the low recaptures from the Belt Sea as shown by the historical tagging data in this study. Some level of isolation between the Sound and the remainder of the western Baltic is also supported by differences in growth, as shown in the present study (data from 2017 to 2021) as well as in Svedäng & Hornborg (2017) where data from 1991 to 2016 was utilized. However, it should be emphasized that the Arkona Basin is a mixing area where the relatively slow growing eastern Baltic cod can be found, which complicates comparisons of growth in this area (McQueen et al., 2020), and presumably results in an underestimation of growth. In addition, potential mixing between Kattegat and the North Sea cod might have also affected the growth curves (Hüssy et al., 2022).

4.2. The connectivity between the Sound and Kattegat

The connectivity between the Sound and Kattegat is well documented in the literature and is greatly related to spawning migrations (e.g., see Aro, 1989, Bagge et al., 1994, Svedäng et al., 2010). Similar patterns appear from our results where we used a more advanced analytical approach, and it is apparent that there is some mixing between cod in the Sound and cod in Kattegat. However, the spatial-temporal extent of this mixing appears to be largely confined to the northern part of the Sound and the south-eastern Kattegat, in particular during the spawning season. In contrast, movement between the two areas appears slightly more limited during the feeding season which suggests separate feeding grounds. Similarly, we found differences in growth between the Kattegat and the Sound populations. This would suggest separate stocks, although the uncertainty was relatively high, most likely due to the combination of several age groups. In addition, differences in size distributions caused by fishing gear variability between the areas could potentially have affected the growth

Table 4

Estimates of von Bertalanffy growth parameters for all data combined, and Kattegat, the Belt Sea, the Sound, and Arkona Basin. Values in parentheses indicate confidence intervals for the estimate. * = missing standard deviations due to poor estimate. See Figure S4–5 for growth curves.

Area	L_{∞} (cm)	K	t_0	σ
All data	119.85 (114.24, 125.74)	0.14 (0.13, 0.15)	0.18 (0.16, 0.20)	0.24 (0.236, 0.241)
Kattegat	179.53 (150.60, 214.02)	0.10 (0.08, 0.12)	0.02 (0, 0.28)	0.20 (0.19, 0.20)
Belt Seas	109.71 (104.30, 115.41)	0.18 (0.17, 0.19)	$1e^{-09}$ *	0.20 (0.20, 0.21)
The Sound	212.35 (155.20, 290.55)	0.07 (0.05, 0.10)	0.41 (0.30, 0.56)	0.19 (0.18, 0.20)
Arkona Basin	81.32 (77.31, 85.53)	0.22 (0.20, 0.23)	0.23 (0.20, 0.26)	0.27 (0.26, 0.27)

distributions. Furthermore, potential stock mixing, such as between the Sound and Kattegat as suggested by the tagging data in this study, complicate analyses of growth as it is unclear if the samples from the respective SDs solely consisted of individuals from these areas. As such, the presented growth curves need to be interpreted with some caution.

4.3. Connectivity and genetics

In contrast, the overall lack of genetic differentiation between Kattegat and the Sound would suggest a singular stock. Several previous genetic analyses have relied on microsatellites (e.g., see Nielsen et al., 2003, Svedäng et al., 2010a) but it is possible that microsatellites may not be sensitive enough to detect differences. This is exemplified by single nucleotide polymorphism (SNPs) which have shown a clear genetic differentiation between adults from the North Sea, and the Kattegat/Sound grouped (Svedäng et al., 2019). In contrast, no genetic differences have been found when using microsatellites (Nielsen et al., 2003). Berg et al. (2015) categorized SNPs as either neutral or outlier, with neutral indicating loci not under selection and outlier indicating physically unlinked SNPs, and found no genetic differentiation between Kattegat and the Sound using the full and neutral datasets, while analyses of the outliers showed some genetic differentiation between the two stocks. As such, it is possible that the two groups may be in the process of diverging; however, more dedicated studies are required to determine this.

4.4. Indications of northern and southern Sound components

The spatially resolved movement patterns from the transition matrices suggested a division of cod in the Sound into a northern and southern component based on a salinity and topographic divide. The salinity division revealed relatively well-defined geographic patterns in movements, where the north and south appeared to be separate components. Due to the importance of spawning migrations for stock structuring, these spatially distinct patterns within the Sound may be due to natal homing (Svedäng et al., 2007). This may be due to the northern component potentially spawning in the northern part of the Sound and southern part of Kattegat, and the southern component in the central/southern part of the Sound which coincides with the location of known spawning grounds (Hüssy, 2011). However, it is possible that the salinity divide is not an adequate division. While the eastern and western Baltic cod stocks are adapted to brackish water, it has been shown that both eastern and western Baltic cod are adapted to different salinity levels (Kijewska et al., 2016) but these salinity differences are much greater than in the Sound (e.g., see Bendtsen et al., 2007). This may indicate that the salinity gradient in the Sound is not sharp enough to drive a potential population division and that the observed patterns merely coincide with the salinity divide. Furthermore, seasonal inflows are likely to change the strength and position of the salinity gradient, suggesting further study if the salinity divide is suitable. In addition, the sample size for the southern population was relatively small ($n = 54$) in comparison to the northern population and may not have fully captured the patterns of a potential southern component, as the transition matrix suggested relatively isolated components while the tagging map showed movement from the south into the northern Sound. However, otolith microchemistry analyses have shown a similar structuring based on a slightly different division of the Sound where activity appears to be high in the northern Sound and southern Kattegat with a separate component in the central and southern Sound (Svedäng et al., 2010), and it is possible that differences in topography instead of salinity may drive the observed differences in this study. We suggest further studies are undertaken to study potential sub-population structuring in the Sound utilizing genetic tools.

Overall, the combination of the results of the present study and previous studies utilizing analyses on otoliths (Svedäng et al., 2010), tagging (Aro, 1989; Bagge and Thurow, 1994; Otterlind, 1985; Svedäng

et al., 2010), and genetics (Berg et al., 2015; Moth-Poulsen, 1982; Nielsen et al., 2003) suggests high complexity within the stock component structuring and connectivity in Sound cod. However, it should be noted that interpretation of the historic recapture-data and the resulting connectivity matrix is made difficult because of the lack of information about release numbers and spatial variation of fishing effort during this period, including the high fishing pressure. This is exemplified by high fishing effort in the south of Kattegat which may explain the high number of recaptures in this area, and thus it is likely that the true movement patterns were not captured as this study relied on recapture data. Additionally, the transition matrix approach relies greatly on the quality and quantity of the data available. As such, the transition matrix gives the most probable area transitions based on all the data, but it also assumes that all cod in the database are Sound cod which may not be the case. As stock affiliation depends on where the cod spawn, it is possible that Kattegat cod or southern Baltic cod have been included in the analyses. As an example, this could explain the high probability to remain in the southern Baltic as suggested by the transition matrix as these cod may have originated in the southern Baltic. In addition, the transition matrix relies on recapture patterns, and so high fishing pressure and spatio-temporal variations in fishing effort will undoubtedly affect the results. It is thus unclear if Sound cod actually move further north and south of the Sound than the tagging results suggest but are likely to be caught due to the high risk of being caught near the edges of the Sound. In light of this, it is important to view the transition matrices as indications of overall movement tendencies which should be studied further using genetic tools.

5. Conclusion

Our results suggest the Sound stock component is to some degree connected with the Kattegat cod stock primarily during the spawning season but is relatively isolated from the remaining western Baltic cod stock components. The analyses utilizing the historical data suggest high complexity in structure within the Sound cod stock component with a relatively resident southern component, and a northern component with frequent movements into Kattegat. These results may have implications for future stock assessments, and we suggest future studies focus on the connection between Kattegat, the Baltic, and the Sound using genetics in addition to tagging.

Supplementary material

The following supplementary material is available at Fish Res online: methodology and results of the fishing mortality analyses, including a table on fishing mortality in the western Baltic cod stock (1970–1987) and Kattegat cod stock (1971–1987) and a figure on relative Danish fisheries effort between 1987 and 1990. Furthermore, the supplementary material includes a figure showing the distance travelled for cod tagged in the Sound released in the spawning season, a bean plot showing length distributions for cod in the Sound, and two figures showing von Bertalanffy growth curves for all SDs and each SD separately.

Credit authorship contribution statement

K.H., M.M., S.H., M.C., and U.K. participated in the TABACOD project which produced the Baltic tagging database for the analyses. R.B.C.L. contributed to the tagging database and carried out the data analyses. A.N. assisted in the data analyses, and M.v.D. produced the figure showing the spatial effort. R.B.C.L. and K.H. drafted the manuscript. H.J.O. and M.v.D. assisted in conceptualizing the manuscript. All authors commented on the manuscript and gave final approval for publication.

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.

Data availability

Data will be made available on request.

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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.2023.106617](https://doi.org/10.1016/j.fishres.2023.106617).

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