Geographical Information Management and Applications

"Moving back in"

Assessing habitat suitability and space use for re-introduced Thornback Ray in the Western Scheld and Belgian Exclusive Economic Zone

Final thesis report

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Abstract

The Thornback ray (Raja clavata) has virtually disappeared in the Dutch coastal areas since 1958. In an attempt to repopulate Raja clavata and other species in the Dutch coastal area the Dutch World Wildlife Fund (WNF), Blue Linked, Stichting de Noordzee, the Dutch Shark Society and the Dutch Anglers Association (Sportvisserij Nederland) set up a program named ‘Sharks and rays back in the North Sea’. As part of the program, thornback rays were artificially reared and released into the Eastern Scheldt and Western Scheldt areas. Some rays within this program got tagged and their location was monitored using an acoustic telemetric system. This paper uses data on 79 tagged rays that were released back into the Western Scheldt to model the spatial behaviour of these Raja clavata within the Western Scheldt and Belgian Exclusive Economic Zone. Of a total dataset of 79 juvenile rays, twenty were found to have sufficient data to represent natural resident behaviour inside of the study area through a weighted residency index (I_{WR}). For these animals, the dynamic Brownian Bridge Movement Model (Kranstauber et al., 2012) was applied in order to estimate occurrence distributions. The outputs of the model were then used to compute .95 and .50 utilisation distributions (UD) showing spatial behaviour of the animals throughout the study period. The research concludes that overall, the Western Scheldt and Belgian Exclusive Economic Zone can be considered a suitable habitat for juvenile Raja clavata as the re-introduced rays showed residential behaviour. Especially the areas in the Western Scheldt between Vlissingen and Terneuzen and west of Terneuzen were intensively utilized by the animals, as well as the harbour of Zeebrugge at the Belgian coast. Male and female rays showed different utilisation distributions, with females showing more resting behaviour in the Western Scheldt and males showing more active behaviour moving out of the estuary. In winter the animals tended to stay within the estuary, as in summer they show more active movement behaviour towards the outer estuary and Belgian coastline. The study also highly recommends future research on the spatial relationship between Raja clavata presence and their five biggest predicting abiotic factors: water temperature, bathymetry, salinity, bottom shear stress and sediment type. Furthermore, the outcomes of this research can be used to design more detailed strategies in order to protect, maintain and potentially expand the population of Raja clavata in the Western Scheldt and surrounding areas.

Contents

1 Introduction and background

1.1 Introduction

Historically speaking, the near local extinction of large skates (Rajidae) is arguably the most significant consequence of fishing activities in the North Sea (Walker & Hislop 1998; Rogers et al., 1999). Comparably, populations of smaller skate species like the Thornback ray (Raja clavata) suffered the same consequences. Whereas in the start of the 20th century the Thornback ray was still widely abundant in the whole of the greater North Sea area (Poos et al., 2023), the stock of Thornback rays has declined from then onwards (Poos et al., 2023; ICES, 2017; Wiegand et al., 2011). As of 2014, the Thornback Skate was assessed as “Near Threatened” for the IUCN Red List of Threatened Species in Europe (Fabrizio, 2014). Thornback rays are mostly by-catch in fishing activities targeted at other fish species (Ellis et al., 2008; Walker & Hislop, 1998). As a result of the population decline in the 20th century, the distribution area of most ray species in the North Sea reduced (Poos et al., 2023). Over the past decades, the distribution of the thornback ray has confined mainly to the Thames Estuary and its surrounding area of the South-West part of the North Sea (Poos et al., 2023; Jongbloed et al., 2017; Wiegand et al., 2011; Walker & Heesen, 1996). In recent years, the presence of Raja clavata has been considered stable and even increasing in the hotspot of the Thames Estuary and its surroundings (Jongbloed et al., 2017).

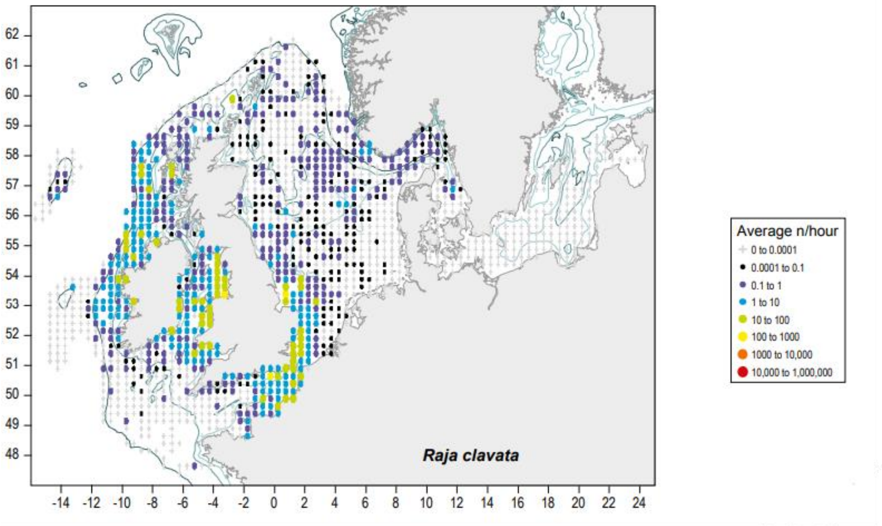


Figure 1: Catchment (survey) data of Raja clavata in the broader North Sea area between 1977 and 2013 (Heessen et al. 2015)

In the Dutch coastal area however, the Thornback ray has virtually disappeared in 1958 (Walker & Heesen, 1996), except for a limited number of observations in the Eastern Scheldt and Voordelta regions (Jongbloed et al., 2017). In an attempt to repopulate Raja clavata and other species in the Dutch coastal area the Dutch World Wildlife Fund (WNF), Blue Linked, Stichting de Noordzee, the Dutch Shark Society and the Dutch Anglers Association (Sportvisserij Nederland) set up a program named ‘Sharks and rays back in the North Sea’. As part of the program, thornback rays were artificially reared and released into the Eastern Scheldt and Western Scheldt areas. Some rays within this program got tagged and their location was monitored using an acoustic telemetric system. This paper will use data on 79 tagged rays that were released back into the Western Scheldt. The acoustic telemetric system is situated in the Western Scheldt and Belgian Exclusive Economic Zone (figure 2) and consists of stationary receivers placed on buoys that detect presence of the Thornback ray through encoded acoustic signals transmitted by the tags attached to the Thornback rays. This method is applied on a wide scale to track the movement and behaviour of aquatic animals (Matley et al., 2022).

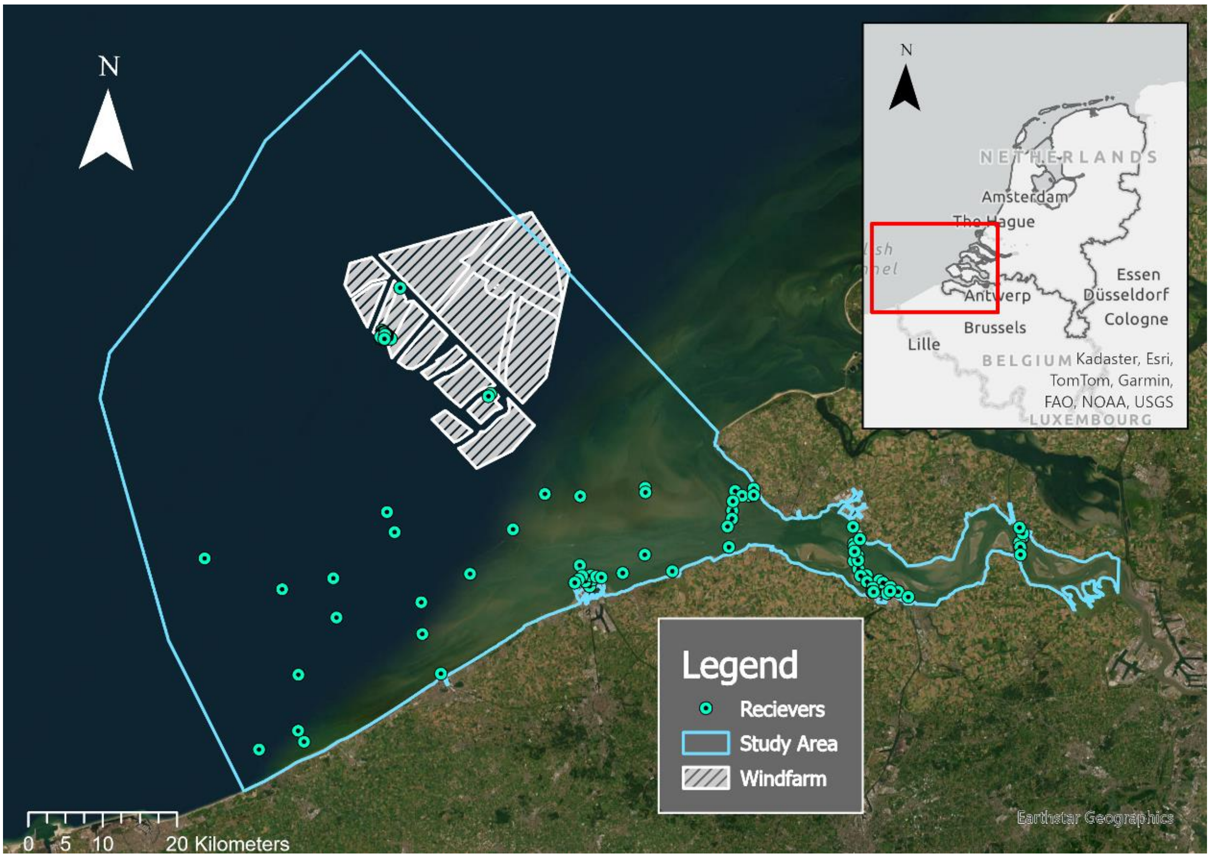


Figure 2: Study area with the positions of recievers, release locations and windfarm Borssele

Prior to their reintroduction in the Western Scheldt in 2018, Winter & Jongbloed (2018) assessed the suitability of the Western Scheldt estuary as a habitat for Raja Clavata. This research concluded that the western part of the Western Scheldt is a suitable habitat for the species, with expected migration behaviour to for instance the Thames coastal area in winter due to low water temperature (Winter & Jongbloed, 2018). These conclusions on the habitat suitability of the Western Scheldt area were based on a literature review by Jongbloed et al. in 2017. In this literature review, multiple studies on Raja Clavata ecology were considered in order to generate a general overview of habitat preferences. This study focussed mainly on abiotic factors, as biotic factors have not yet been specifically researched in relation to habitat suitability for Raja Clavata (Jongbloed et al., 2017). Jongbloed et al. (2017) found from literature that the most important abiotic factors to predict habitat suitability for Raja clavata are depth, bottom shear stress, salinity, water temperature and sediment type.

Jongbloed et al. (2017) explicitly exclude possible effects of human interference in their analysis. However, the Dutch coastal area is subject to quite some human interference. Especially the Western Scheldt, being an important portal between the ports of Vlissingen and Antwerpen. In highly urbanised estuary's such as the Western Scheldt, regular displacement by boat traffic potentially has a negative impact on fish population (Becker et al., 2013). Another example of human interference in the Dutch North Sea area is the offshore windfarm of Borssele (figure 2). Derduwen et al. (2012) suggest that windmill parks can function as a refugium for demersal fish.

1.2 Research need

The most apparent research need the project in the Western Scheldt aims to fulfil is to assess the suitability of the Western Scheldt and Belgian Exclusive Economic Zone as a habitat for the reintroduced rays. Literature review to assess this suitability has been done (Jongbloed et al., 2018) and the project data has been analysed to distinguish spatial-temporal patterns (Essink, 2023). However, these analyses have been of exploratory nature, leaving room for more specific use of methods in order to model space use of Raja clavata more accurately. Obtaining a more detailed overview of the spatial behaviour of Raja clavata can serve multiple purposes. Firstly, it would add to the underlying ambition of the project by WWF and Sportvisserij, answering the question of whether (certain parts) of the researched area can be used by the species as a habitat. Comparisons between area use in certain seasons of the year or between animal sex can help to understand the dynamic processes of Raja clavata behaviour. Second of all, knowing specific locations in which Raja clavata reside can contribute to establishing more effective conservation methods.
Limited telemetric studies have been performed on Raja clavata specifically. An example is a study by Papadopoulo et al. (2023), which did consider abiotic and biotic factors, but had a limited sample size of n=14 animals. Another property of the project in the Western Scheldt is the fact that the rays were artificially reared instead of caught, tagged, and released. This reintroduction component in combination with more extensive telemetric data make this project unique in it’s potential to fulfil the above-mentioned research needs.

1.3 Research Objectives and questions

The general objective of this research is to explore the space use and habitat suitability for Raja clavata in the Western Scheldt and Belgian Exclusive Economic Zone. In order to pursue this objective, it is of utmost importance to gain a deeper understanding of the time and space distribution of Raja clavata in the Western Scheldt and Belgian Exclusive Economic Zone. Hence, the following research questions were established:

Main research question:

To what extent do (parts of) the Western Scheldt and Belgian Exclusive Economic Zone serve as a suitable habitat for reintroduced Raja clavata?

Sub questions:

1. *How is the occurrence of reintroduced Raja clavata distributed in the Western Scheld and Belgian Exclusive Economic Zone?*
2. *How does the spatial distribution of reintroduced Raja clavata differ between male and female animals?*
3. *How does the spatial distribution of reintroduced Raja clavata differ between the summer and winter periods?*

2 Literature review

2.1 Raja clavata ecological background

Ecological characteristics:
The Thornback ray, Raja clavata (Linnaeus 1758) is a species of Rajidae that is found in the Atlantic coastal waters of Europe and western Africa, from South Africa to the southwestern Indian Ocean and the Mediterranean and Black Seas. Raja clavata is a benthic species, meaning it spends a significant amount of time partially embedded within seafloor sediment (Jongbloed et al., 2017). The maximum length derived by studies in the southern North Sea is 118 cm, whereas the length at 50% maturity is estimated at 77 cm for males and 68 cm for females. The size in disc width (DW) for mature animals lies approximately between 45-54 cm for males and 38-48 cm for females (Fitzmaurice, 1974; Capapé, 1976; Nottage & Perkins, 1983). Raja clavata have a relatively low reproduction rate, low fertility, and high maturity age. Male thornback rays mature at approximately 5.3 years, whereas female thornback rays take 7 years to reach maturity (Kadri & al., 2014). The minimum reproduction age has been reported at five years (Ryland & Ajayi, 1984), with a gestation period varying between 4 and 6 months (Jongbloed et al., 2017; Ellis & Shackley 1995). Eggs are laid in a wide-ranging breeding season from February to September, with a peak in May and June (Holden, 1975). Several studies on the fecundity of Raja clavata have been performed, with resulting estimations ranging from a minimum of 48 to a maximum of 167 eggs per year (Jongbloed, 2017; Ellis & Shackley, 1995; Ryland & Ajayi, 1984; Capapé 1976; Holden, 1975). Due to their low reproduction rate, low fertility and high maturity age, Raja clavata are a species highly susceptible to mortality increase caused by for instance fishing activities (Jongbloed et al., 2017).

Species Name	Raja clavata	Linnaeus, 1758
Geographic Distribution	Atlantic coastal waters of Europe and western Africa, South Africa to the southwestern Indian Ocean, Mediterranean, and Black Seas	Ellis et al., 2016
Maximum Length	Males: 98 cm; Females: 118 cm	Walker, 1998
Length at 50% Maturity	Males: 77 cm; Females: 68 cm	Walker, 1998
Disc Width (DW) at maturity	Males: 45-54 cm; Females: 38-48 cm	Fitzmaurice, 1974; Capapé, 1976; Nottage & Perkins, 1983
Maturity Age	Males: 5.3 years; Females: 7 years	Kadri & al., 2014
Minimum Reproduction Age	5 years	Ryland & Ajayi, 1984
Gestation Period	4-6 months	Jongbloed et al., 2017; Ellis & Shackley, 1995
Breeding Season	February to September, peak in May and June	Holden, 1975
Fecundity	48 - 167 eggs per year	Jongbloed, 2017; Ellis & Shackley, 1995; Ryland & Ajayi, 1984; Capapé, 1976; Holden, 1975

Table 1: Ecological characteristics for Raja clavata

Migration and movement:
Several studies have been conducted on the spatial and temporal distribution of Raja clavata within the North Sea (Walker 1997; Hunter et al., 2005; Chevolot et al., 2006; Humphries et al., 2016). These studies used conventional tagging methods or tagging with data storage tags (DST). These studies imply seasonal migration, with most rays retaining a position within a few tenths of kilometres from their tagging locations (Walker et al., 1997; Hunter et al., 2005). Some rays do however travel bigger distances, mostly up to 130 kilometres with exceptions travelling even further (Jongbloed et al., 2017). This offshore migration to relatively deep water (30m) takes place in the winter months whereas in the summer months rays tend to return to inshore, shallow water (10m). This seasonal migration is mainly attributed to the trend for Raja clavata to return to important habitats for reproduction and laying eggs in the summer months (Heessen et al., 2015). Based on these studies, Winter & Jongbloed (2018) predict migration behaviour to wintering areas in the southern North Sea (Winter & Jongbloed, 2018).

2.2 Habitat preferences

Abiotic factors:
Prior to assessing the habitat suitability off the Western Scheldt, Jongbloed et al. (2017) performed a similar analysis for the Eastern Scheldt and Voordelta. In order to estimate habitat suitability, Jongbloed et al. (2017) established the most influential abiotic factors and their preference values for Raja Clavata. A literature review was performed on various studies that modelled abiotic preferences of Raja clavata in similar habitats in the North Sea, Irish Sea, Keltic Sea and the English Channel. Jongbloed et al. (2017) conclude there are five main factors to predict presence of Raja clavata: depth, bottom shear stress, salinity, water temperature and sediment type. Preference values of Raja Clavata for these five factors as subtracted from literature by Jongbloed et al. (2017) are given in table 2.

Factor	Preference values for Raja Clavata
Depth	Broad range and age-dependent: shallow for juveniles (**< 40 m**), deeper for adults (**< 82 m**). In North Sea season dependent: deeper (**20-35 m**) during fall and winter; shallower (**< 20 m** during spring and summer).
Bottom shear stress	Broad range and age-dependent: weak (juvenile) to intermediate and strong tidal currents (adult) (Martin et al., 2012). **Between 0 and 1.5 N/m2** (Maxwell et al., 2009).
Salinity	Broad range including **32.4 – 34.9 ppt.** Juvenile rays can also utilize habitats with lower salinity.
Water temperature	Higher temperatures between **9.5˚C – 19˚C**. Juveniles prefer higher temperatures than adults.
Sediment type	Broad range: **Silt, fine sand, coarse sand, gravel,** and **pebbles.** Age-dependent: **silt** and **sandy** for juveniles to **gravel** and **pebbles** for adults.

Table 2: Raja Clavata habitat preference values for abiotic factors (Jongbloed et al., 2017)

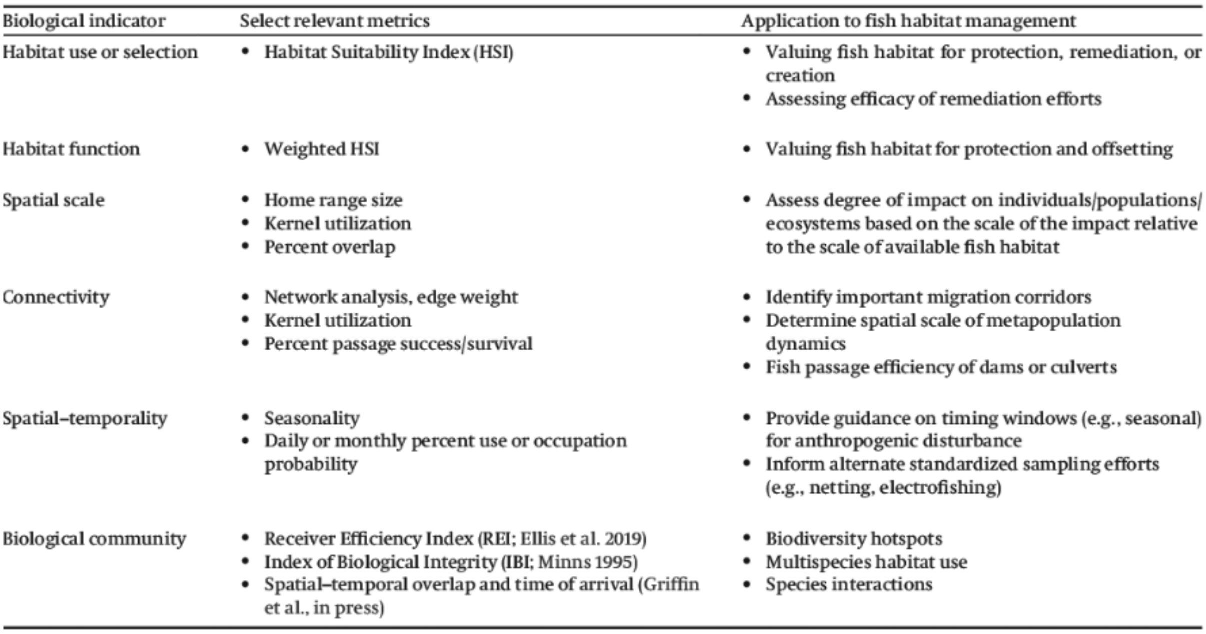
Biotic factors:
Biotic factors also play a key role in habitat suitability for Raja clavata. The main biotic factors for the development of a population of Raja clavata are food supply, competition, predators, parasites, and illnesses. However, there is scarce knowledge on these factors (Jongbloed et al., 2017). Jongbloed et al. (2018) also suggest that biotic factors will most probably not be limiting to habitat use for Raja

clavata in the Western Scheldt and Belgian Exclusive Economic Zone. Therefore, biotic factors will be excluded from all analyses performed in this paper.

Habitat suitability of the Western Scheldt and Belgian Exclusive Economic Zone:
Winter & Jongbloed ultimately assessed the suitability of the Western Scheldt as a habitat for Raja clavata. The western part of the estuary, roughly west of Terneuzen, appears suitable for juvenile thornback rays in terms of water depth, sediment type, and salinity levels (Winter & Jongbloed, 2018). Specifically, the area between Vlissingen and Terneuzen exhibits favourable conditions in terms of bottom shear stress. However, it remains unclear whether juvenile thornback rays could utilize the estuary further eastward of Terneuzen, although evidence from the Thames suggests potential migration deeper into the estuary. Regarding water temperature, winter values are too low, necessitating seasonal migration to nearby overwintering areas. For (sub)adult thornback rays, a range of water depths and bottom shear stresses are suitable. Nonetheless, it remains uncertain if they would venture into lower salinity zones to the east (Winter & Jongbloed, 2018). Similar to juveniles, (sub)adults would likely undertake seasonal migration to overwintering areas due to low winter water temperatures (Winter & Jongbloed, 2018). Biotic factors influencing habitat suitability remain poorly understood. Factors such as the availability of shrimp, a crucial food source for juvenile thornback rays, appear favourable, as does the favourable development of water quality and benthic fauna in the Western Scheldt (Winter & Jongbloed, 2018).

2.3 Acoustic telemetry

Biotelemetry is now a widely used method to study movement, interaction, and behaviour of aquatic animals (Hussey et al, 2015). There are three main technologies used in the field of biotelemetry: acoustic, radio and satellite telemetry (Lennox et al., 2017). Of these three, the use of acoustic telemetry is most widespread (Hussey et al., 2015), mostly due to its relative affordability, usability in both freshwater and marine environments, cross-compatible technology, and versatility (Heupel & Webber, 2012). Especially the study of fish biology has benefited from the technological advancement and widespread application of electronic tagging technology (Hussey et al., 2015). An important development in this process has been the *passive acoustic array*. A passive acoustic telemetry array is composed of three elements: receivers, transmitters and studied individuals (Kraft et al., 2023). Acoustic transmitters (tags) placed on the individual emit a sonic pulse that is detected by a receiver. Individual tags can be coded so that separate IDs for individuals are transmitted. This way individuals can be tracked within a group of animals (Crossin et al., 2017). These tags can also be equipped with sensors transmitting environmental data (e.g. temperature, depth) or physiological data on the individual (e.g. heart rate) (Cooke et al., 2016). In fish telemetry methods specifically, Brownscombe et al. (2022) distinguish four main application categories: habitat suitability, spatial scale and connectivity, spatial-temporal patterns, and biological community (table 3).



Biological indicator	Select relevant metrics	Application to fish habitat management
Habitat use or selection	• Habitat Suitability Index (HSI)	• Valuing fish habitat for protection, remediation, or creation • Assessing efficacy of remediation efforts
Habitat function	• Weighted HSI	• Valuing fish habitat for protection and offsetting
Spatial scale	• Home range size • Kernel utilization • Percent overlap	• Assess degree of impact on individuals/populations/ ecosystems based on the scale of the impact relative to the scale of available fish habitat
Connectivity	• Network analysis, edge weight • Kernel utilization • Percent passage success/survival	• Identify important migration corridors • Determine spatial scale of metapopulation dynamics • Fish passage efficiency of dams or culverts
Spatial–temporality	• Seasonality • Daily or monthly percent use or occupation probability	• Provide guidance on timing windows (e.g., seasonal) for anthropogenic disturbance • Inform alternate standardized sampling efforts (e.g., netting, electrofishing)
Biological community	• Receiver Efficiency Index (REI; Ellis et al. 2019) • Index of Biological Integrity (IBI; Minns 1995) • Spatial–temporal overlap and time of arrival (Griffin et al., in press)	• Biodiversity hotspots • Multispecies habitat use • Species interactions

Table 3 : Applications of telemetry in fish habitat science (Brownscombe et al., 2022)

Despite its strengths, there is also some limitations that should be accounted for when using an acoustic telemetric system. Evidently, detections cannot be recorded in locations that fall outside of the receivers' range. This can bias area use estimations if a tagged animal is present in locations outside of the network. The fate of undetected animals is hard to establish, as it often can be attributed to several factors or processes (Klinard & Matley, 2020). Finally, the detection range of receivers can fluctuate unpredictably in four dimensions due to environmental factors such as environmental noise, water stratification and other environmental factors (Kessel et al., 2014).

2.4 Residence and space use estimation using acoustic telemetry

Movement is a central and complex component of animal life (Nathan et al., 2008). Therefore, movement and space use dynamics are crucial to consider when planning spatial protection and effective management of fish populations (Kraft et al., 2023). The success of for instance aquatic protected areas (APAs), habitat restoration, fish passageways, population estimates, and place-based fisheries management zones all depend on understanding the movement behaviour of the fish species they intend to protect or restore (Brownscombe et al., 2022). In the past, movement analysis would rely primarily on catch-recapture studies. More recently however, animal movement is increasingly being studied by using telemetric systems (Kraft et al., 2023; Brownscombe et al., 2019; Kranstauber et al., 2012). Telemetry is well suited for tracking animal movement, as it can provide long-term monitoring of the spatial scale of fish behaviour. (Brownscombe et al., 2022). The two most common metrics to quantify animal movement within a habitat are residency and space use measurements. Residency refers to the individual's preference for an area over an extended period of time, whereas space use refers to the distribution of animal presence throughout an area within a specific timeframe. Brief departures from the area can occur and are part of resident behaviour. The definition of residency is defined by the specific timeframe defined by the research or researcher (Kraft et al., 2023).

The concept of residency is very closely related to the concept of home ranges. One of the more frequently quoted definitions of home range is one by Burt (1943): *"the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home* *range." […] "The size of the home range may vary with sex, possibly age, and season."* Home range estimation through telemetric studies is commonly done by modelling space use in order to derive how animals occupy space (Kraft et al., 2023). There are two levels of space use often reported: the core- or 50% area (the most frequently visited part of an area), and the home range or 95% area (which represents the definition of home range given by Burt (1943)). Core- and home range estimates are perhaps the most common focus of telemetry studies (Heupel & Webber, 2012). Several methods for estimating home range have been developed over time. Most of these methods can be classified into two main categories: geometric (hull-based) estimators and density distribution (probabilistic) estimators (Kraft et al., 2023).

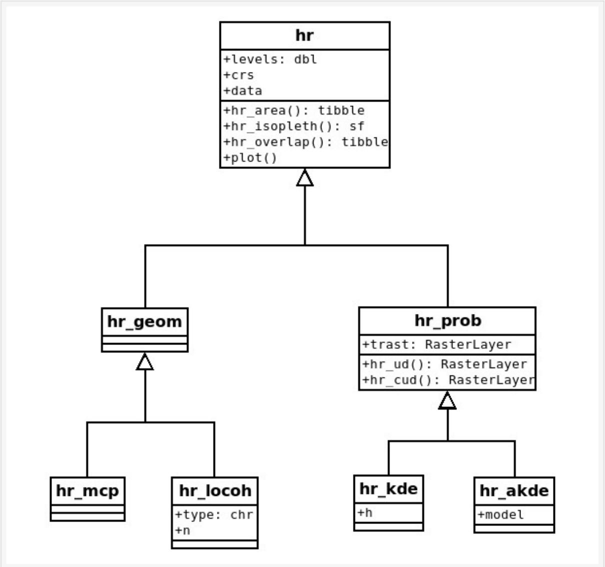
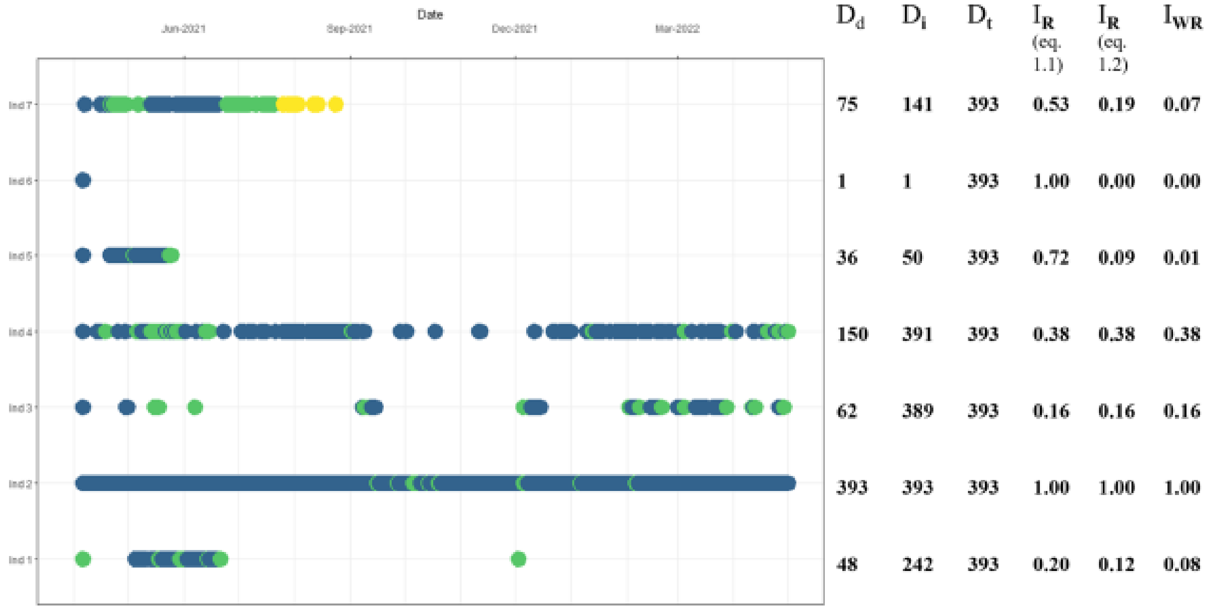


Figure 3: A schematic representation of home range estimators (Signer & Frieberg, 2021)

2.4.1 Residency indexes and abacus plots

Before discussing these two methodological categories and the different methods they encompass, Kraft et al. (2023) mention a few tools for initial exploration of telemetric data. A simple and informative way to get a general overview of animal residency are *abacus or calendar plots*. An abacus plot shows each individual animal's detections spread out over time like a chronogram, with the X-axis displaying time and the Y-axis displaying tagged animals (Figure 4). While not providing any spatial information, abacus plots are highly effective in identifying unusual detection patterns, for example due to fish capture, mortality, or tag loss (Klinard & Matley, 2020).



	D_d	D_i	D_t	I_R (eq. 1.1)	I_R (eq. 1.2)	I_{WR}
Ind 7	75	141	393	0.53	0.19	0.07
Ind 6	1	1	393	1.00	0.00	0.00
Ind 5	36	50	393	0.72	0.09	0.01
Ind 4	150	391	393	0.38	0.38	0.38
Ind 3	62	389	393	0.16	0.16	0.16
Ind 2	393	393	393	1.00	1.00	1.00
Ind 1	48	242	393	0.20	0.12	0.08

Figure 4: Abacus plot showing detection patterns of seven Raja clavata individuals, and their respective indexes (Kraft et al., 2023)

A simple metric to estimate residency within a telemetric system is the *residency index* (I_R). There are two ways to calculate the residency index, either by dividing the total number of days the animal was detected (D_d) by (1) the time in days between the first and last detection (D_i) or (2) the time in days of the study (D_t). The results of these equations can be intepreted from 0 (no residency) to 1 (full residency) (Afonso et al., 2008).

$$I_R = \frac{D_d}{D_i} \qquad (1.1)$$

$$I_R = \frac{D_d}{D_t} \qquad (1.2)$$

Both of these indexes have their implications. Equation 1.1 represents the maximum residency value, and accounts for tag loss, while equation 1.2 gives a minimum residency value which assumes the animal was alive throughout the whole study period (Cochran et al., 2019). Due to their simplicity however, these equations tend to overestimate or generalize residency. Equation 1.1 overestimates residency for short detection intervals (which causes high residency estimations for an animal that has been present only a short period of time). Equation 1.2 can be biased upwards for animals tagged later during the study. Both equations assume absence of detections to be because the animal is out of detection range, without considering other scenarios like death from predation or fishing (Kraft et al., 2023). As these events often result in divergent patterns, they can be assesed

by observing individual detection plots (e.g. a tag at the bottom will be detected constantly at the same reciever) (Green et al., 2021).
A weighted residency index (I_{WR}) can be calculated by weighing equation 1.2 with a second fraction, the period between first and last detections (D_i) divided by D_t. This approach is sometimes preferred over equation 1.1 as it does not overestimate cases of animals with few but consecutive detections and is more robust to periods without detections (Kraft et al., 2023).

$$I_{WR} = \frac{D_d}{D_t} \times \frac{D_i}{D_t} \tag{2}$$

While I_R and I_{WR} give insight into residency, both equations consider that animals consistently reside within the study extent. However, on large temporal scales animals can show natural behaviour tht leads them out of the detection range (e.g. migration patterns). In order to account for these kinds of behaviour, Ohta and Kakuma (2005) calculated residency as the continuous presence without absences longer than 24 hours around recievers, defining these time gaps as migratory behaviour. *Continuous time residence* (CTR) generalised this method. Instead of using 24 hours, it defines a period by applying a statistical procedure to the data, also considering the previous knowledge of researchers (Capello et al., 2017). This period is called the Maximum Blanking Period (MBP) and is described as the maximum time allowed to pass between two detections before assumption of the animal leaving the monitored area. CTR is then defined as the timeframe an animal is detected in which the time between detections is smaller than the MBP (Soria et al., 2009). When the animal re-enters the area, a new CTR timeframe will start. In this way, a CTR is constructed by a series of these timeframes throughout the study period. The MBP is determined by a statistical analysis akin to constructing a survival curve, which reflects the probability of the CTR being interrupted. For this, the data is analysed using incremental [1:N] MBP values in order to obtain multiple CTRs. The optimal MBP is reached when the survival curves stabalize (Kraft et al., 2023).

2.4.2 Geometric (hull-based) estimators

Minimum Convex Polygons:
The most widely known hull-based home range estimor is the *Minimum Convex Polygons* (MCP) method. MCP is amongst the first methods for estimating home range (Mohr et al., 1947), but are still widely used to this day (Signer & Fieberg, 2021; Börger et al., 2006). MCP is a two-dimensional area estimator that is otained by drawaing a polygon aroud the exterior points of animal detections (figure 5a)**.** Due to their simplicity, MCPs are fast to compute and have been widely used for decades (Kraft et al., 2023). Sometimes MPCs are used to estimate the maximum area used by a species (Nilsen et al., 2008). However, despite their use in specific areas and data-poor situations (Pimm et al., 2017), MCPs have been said to be too simple and fails to adequately characterize and predict species distribution (Peterson, 2017). One of the main flaws of MCPs is that the focus on the location outline dismisses internal data points as even use of the area is presumed (Powell, 2000).

Characteristic Hull Polygons (CHP)
A second hull based estimator handling point distribution better is the *Charasteristic Hull Polygons* method (CHP). CHP is a hull construction approximation obtained by creating triangles by Delaunay triangulation of neighbouring points. Home range estimates are then given by discarding the trianges with the largest perimiters, retaining only the 95% smallest triangles (Kraft et al., 2023). CHPs can also have “holes” and disjoint polygons in order to accommodate for distribution of animals avoiding certain areas. CHPs give a better representatipn of point distribution than MCPs, as

they can build non-convex hulls and more complex shapes. They do however perform relatively worse when home ranges have certain shapes (e.g. covex or concave), because of the process of removing triangles (Downs & Horner, 2009). CHPs are less frequently used or studied than MCP's, but can broadly be aquired due to Delaunay triangulation being implemented in many standard GIS software (Downs & Horner, 2009).

Local Convex Hulls (LoCoH)

A third geometric estimator is the *Local Convex Hull method* (LoCoH). Also known as the *k-nearest neighbour convex hull*, the k-LoCoH is an extension of the MCP which estimates space use by constructing local convex hulls around each data point using the k-1 nearest neighbours, acting like small McPs (Kraft et al., 2023). These hulls are than ordered from small to large in order to create 50% or 95% isopleths and utilization distributions (UDS) from the amount of points in each local hull. Selection of the number of nearest neigbours is user-defined and follows the *minimum spurious hole covering* rule. Low k values generate "holes" that dissapear when k increases. These holes can represent restrictions to movements such as cliffs, mountains or water edges. The smallest k-value that produces a convex hull reconstruction with a sape that matches the study area is then selected. LoCoH tends to perform better in boundary areas produced by geographic features than MCP and kernel-based methods (Getz et al., 2007) and are less prone to type I errors (including unused areas into the estimate). However, LoCoHs can take a longer time to compute (Calenge, 2006) and is more prone to type II errors (exclusion of used areas) (Lichti & Swihart, 2011).

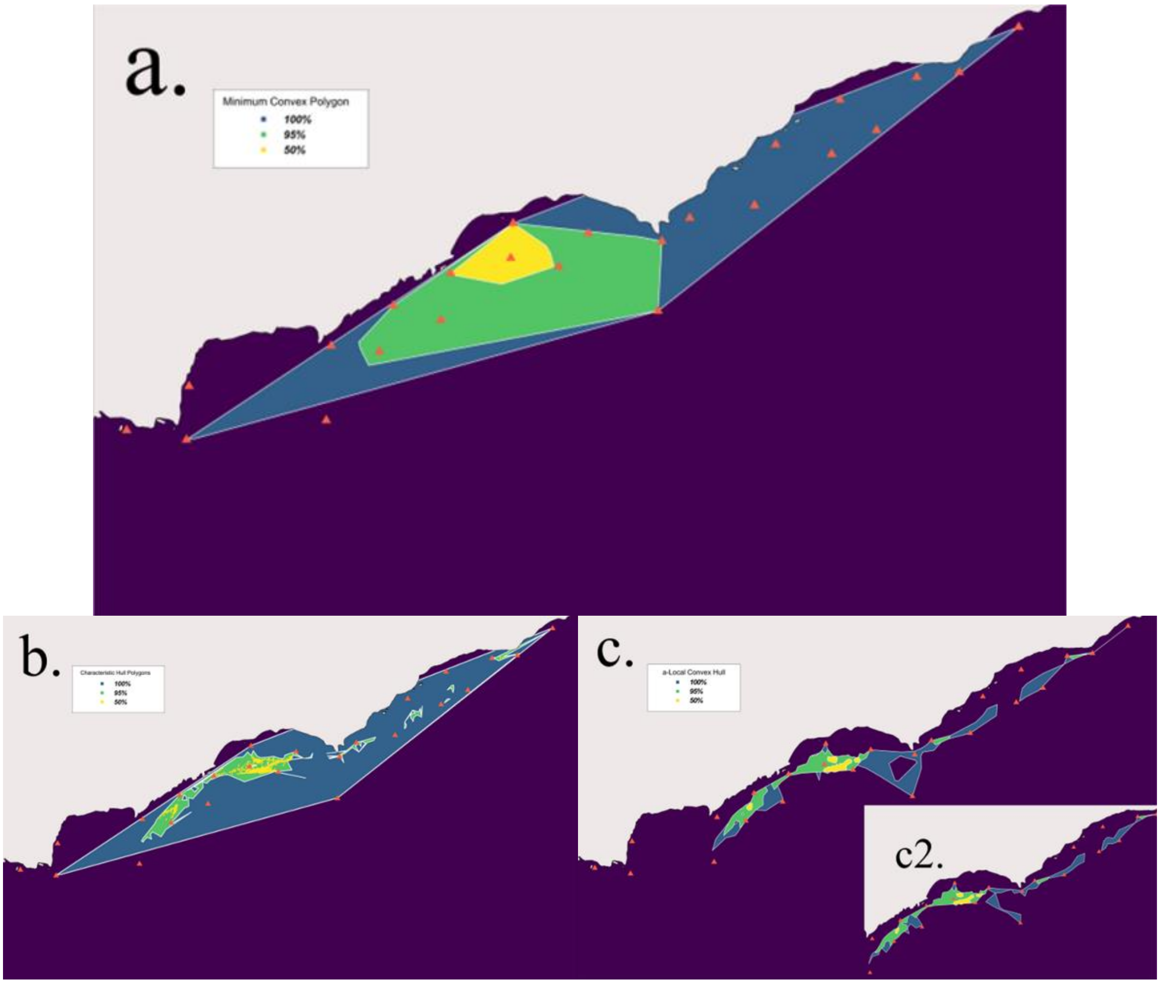


Figure 5: (a) Minimum Convex Polygons, (b) Characteristic Hull Polygond and (c) Local Convex Hull estimators (Kraft et al., 2011)

2.4.3 Density distribution (probabilistic) estimators

Kernel Utilization Distribution (KUD)

One of the best known estimators for estimating animal space use is the *Kernel Utilization Distribution* (KUD) (Laver & Kelly, 2008). There are two core concepts to the KUD method, being the *Utilization Distribution* (UD, figure 6) and *bandwith or smoothing factor* (*h*) (Kraft et al., 2023). The Utilization Distribution is broadly referred to as the use of location data points of an animal to create a two-dimensional relative frequency distribution over time in a specific area (Winkle, 1975). UDs describe space use as a probabilistic model in order to represent the probability of an animals location. This probability is then used to estimate metrics such as home range or core-use area's (Worton, 1989). UDs are directly influenced by the bandwith used in kernel methods. The bandwith refers to the standard deviation of the kernel, hence the extent to which a location influences the home range estimation. The bandwith *value* and *number of bandwiths* are user-defined. A higher bandwith value widens the UD over each data point which allows more distant points to have greater influence, increasing the size of the home range. A higher bandwith also smooths out sampling errors and eliminates small fine scale details. A smaller *h* gives more small scale detail, yet tends to be sensitive to measurement error (Winkle, 1975; Worton, 1989). There are mulptiple ways to determine bandwidth, such as least-square cross-validation, reference bandwidth, ad-hoc choice of *h*, direct plug-in, and solve the-equation (Eidous et al., 2010). The amount of bandwidths can be either fixed (global bandwidth) or variable (local bandwidth). This results in ether a *fixed-kernel analysis* or an *adaptive kernel analysis* (Worton, 1989). The use of fixed or variable *h* has long been debated. However, studies show the value of *h* to be of bigger influence on bias and type I/II errors than the selection of a fixed or variable *h* (Kie, 2013).

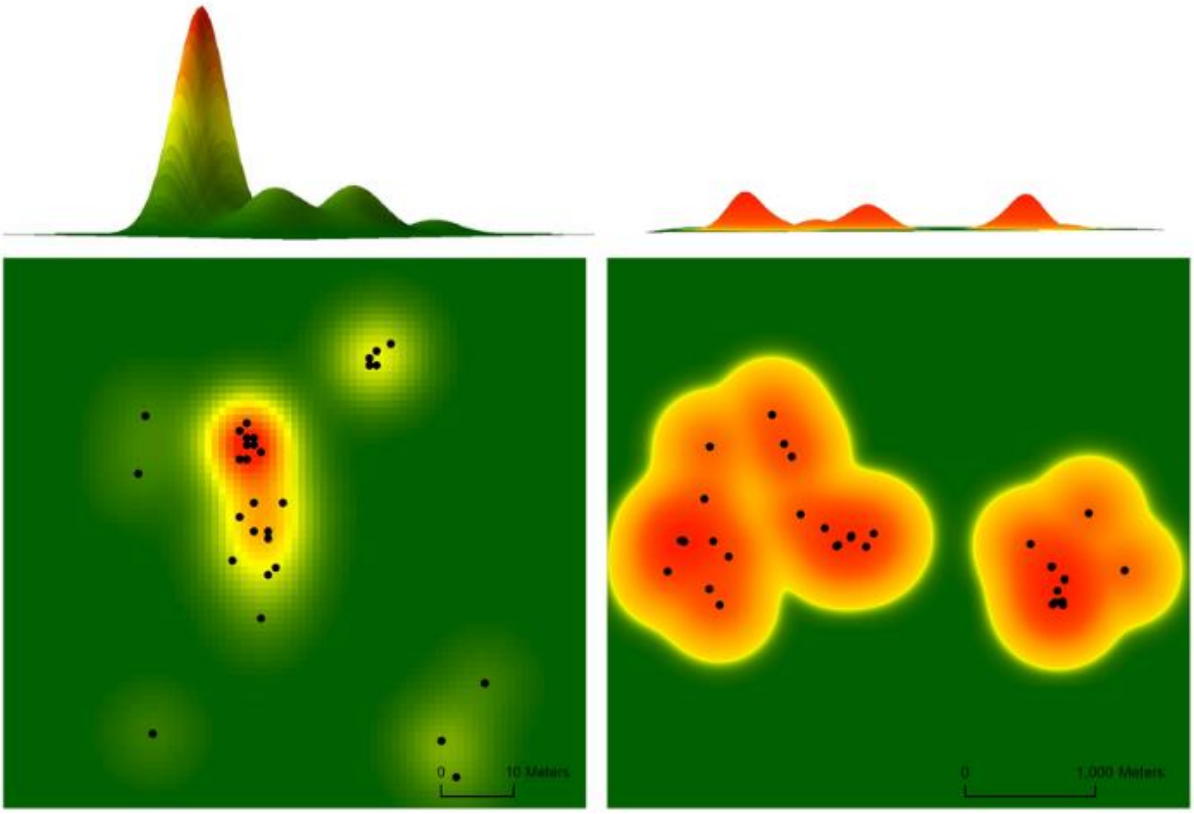


Figure 6: Example utilization distribution (spatial extent) and 95% kernel density estimate (height and coloration), as a metric of space-use intensity (Farnsworth et al., 2015)

Using these two concepts, KUD calculates the area of probability of finding an individual by placing a kernel over each data point. Once parameters are defined and kernels are generated, estimates of density are calculated by averaging the densities of all overlapping kernels (figure 7). Although KUD is a straightforward method well documented in statistical literature, there are several assumption and biases that present challenges to its appliance. For instance, detection locations are assumed to be independent of each other and identically distributed. Movement data on the other hand is inherently autocorrelated, and this is seen as a valuable source of biologically relevant information (Cushman et al., 2005). Not meeting this assumption could result in biased result such as underestimation of home range size (Fleming et al., 2015). Also, kernelas are placed around points in all directions, including areas that are not part of an animals home range (e.g. over impenetrable barriers or narrow trails (Powell, 2000)). Other biases often encountered in KUDs are sample size (Hemson et al., 2005), especially overestimation at low sample sizes (Girard et al., 2002), and point pattern shape (Downs & Horner, 2008).

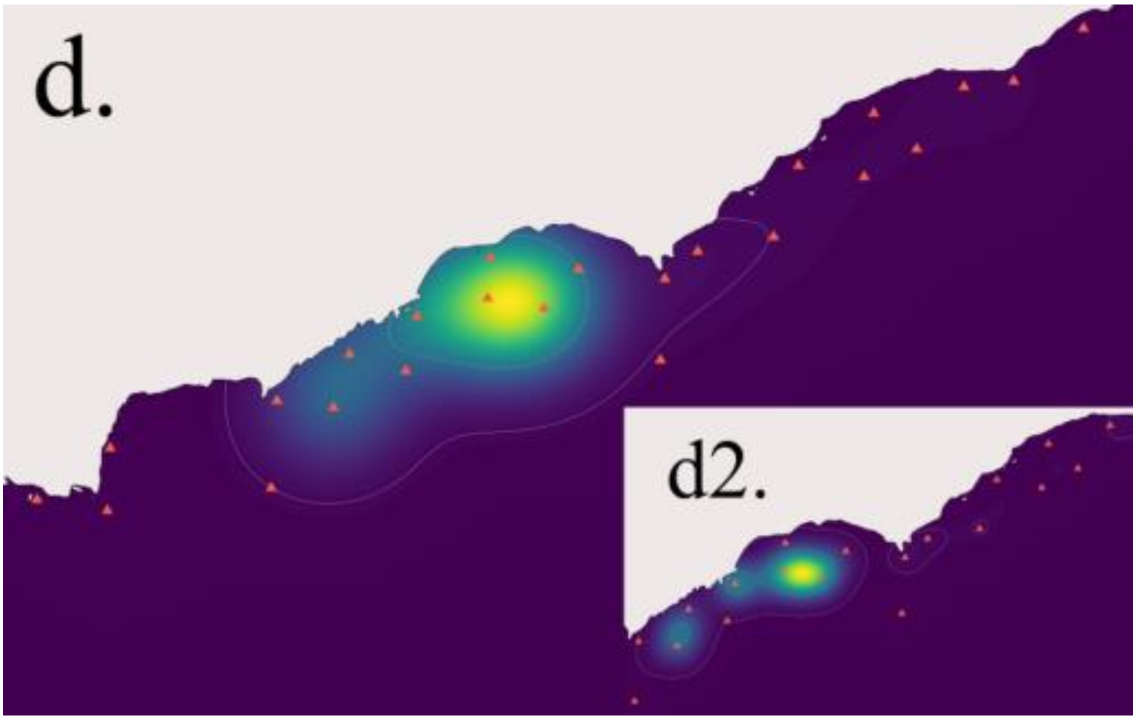


Figure 7: (d, d2): Kernel Utilization Distributions (Kraft et al., 2023)

Autocorrelated Kernel Density Estimation:

Autocorrelated Kernel Density Estimation (AKDE) methods incoorperate autocorrelation into range estimation, tackling the space use underestimation often present in KUD. However, in order to have the same positional information as an uncollerated dataset, autocorrelated data would need to be larger and span for a much longer period. Kraft et al. (2023) mention two enhancements on the AKDE method. The first is the area-corrected AKDE (AKDE$_C$), which adjusts the positive area estimation bias created by the use of the Gaussian reference function in AKDE (Fleming & Calabrese, 2017). The more recent optimally weighted AKDE$_C$ (wAKDE$_C$, Fleming et al., 2018) optimizes estimates by correcting time related sampling biases such as irregularly collected or missing data (Kraft et al., 2023).

State-Space Models (SSM)

State-Space Models (SSM) combine (1) an observational model to statistically describe a sampling procass and (2) a movement model, which describes movement dynamics in space and time. SSM is a useful method to assess different behavioural modes and estimate behavioural states over time (Patterson et al., 2008).

Brownian Bridge Movement Model (BBMM):

Whereas the latter KD methods calculate kernels at (static) point location, there are also probabiity estimation methods that interpret the data as a collection of consecutive points in time. This way one can model a time-structured path (track) of the expected path an animal has traversed. A relatively new but already broadly implemented model that uses this principle is the the *Brownian Bridge Movement Model* (BBMM) by Horne et al. (2007). The BBMM constructs a track following the principles of a conditional random walk between successive locations, dependent on the time and distance between locations and a Brownian motion variance (σ^2_m) related to the animal's mobility (Horne et al., 2007). The random walk from position a to b has a normal distribution. The mean of this normal distribution moves from a to b proportional to the time between a and b. At t=0 the variance equals 0, increases until the midpoint in time, and then decreases again until it equals 0 at t=T. This stochastic process is called a Brownian bridge. This Brownian bridge model estimates the probability of an animal being in area A at a specific time (t) in the interval [0,T]. This probability is then converted to occupation time in order to obtain the fraction of time spent in region A (see Horne et al., 2007). Figure 8 shows a 3D representarion of the probability density calculated by the BBMM from one point to another.

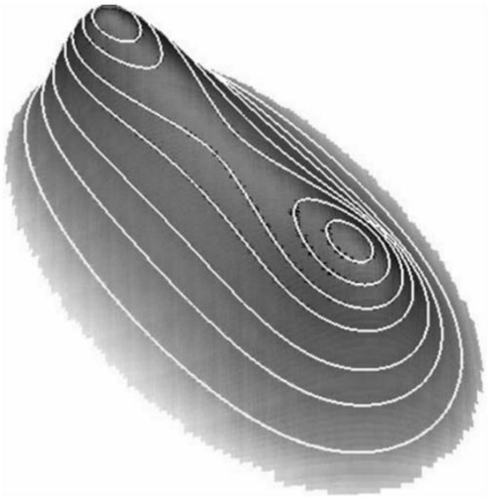


Figure 8: Probability density for the fraction of time spent in different regions, constructed using the Brownian bridge movement model. (Horne et al., 2007).

Horne et al (2007) extend this model to a situation in which animal movement is monitered over an extended period of time. This is simply done by weighting each part of the trajectory as a fraction of the total measuring time.

While time and location parameters are are specified by the input data set, the parameter for Browian motion variance σ^2_m is related to the animals mobility, and needs to be estimated for appropiate model use. An empirical estimate of σ^2_m can be derived from the location data by assuming that the path connecting any two observed locations is a brownian bridge. To make this estimation, we have to assume n is even and compute Brownian bridges over each even observation point: [t_0, t_2], [t_2,t_4], . . ., [t_{n-2}, t_n]. This leaves n/2 independent odd observatiions, which can be put into a likelihood function in order to estimate Brownian motion variance σ^2_m (figure 9).

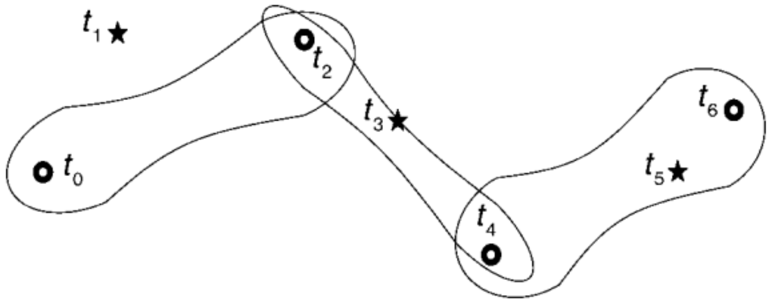


Figure 9: Example of three Brownian bridges connecting even observations at time intervals [t0, t2], [t2, t4], and [t4, t6]. The in between observations at times t1, t3, and t5 are independent observations from these Brownian bridges and can be used to estimate the Brownian motion variance parameter (Horne et al., 2007).

BBMM is considered to provide more biologically meaningful results to KUD as it accounts for autocorrelation and is less sensitive to irregular sampling as it accounts for time difference between locations. The probability distribution of the BBMM spreads in the direction of actual movement instead of every direction as in KUD. This allows for linkage between areas of frequent use, and excludes areas that the animal does not use (Kraft et al., 2023). It has been rapidly adopted in ecological studies because it provides straigt forward results, is based on clear assumptions, can incorperate location errors and applies to a wide range of movements (Kranstauber et al., 2012). Despite its advantages over other density approximation methods, the BBMM's robustness in finding movement paths decreases with higher time intervals between locations. Additionally, the assumption of diffusive movement might not always effectively estimate habitat prefereences, as it can rule out biological information that might be explanatory for changes in movement patterns (Benhamou, 2011).

The biggest limitation to BBMM is the use of one single value for the Brownian motion variance parameter (σ^2_m). This value is based on an average over the whole dataset, so only describes one movement pattern. However, animal movement is composed of a succession of behaviourally distinct movement patterns (Morales et al., 2004). On a smaller scale, almost all animal species break up their day into periods of movement and rest (Boyce et al., 2010). On a broader scale, species change in movement behaviour over the span of a year or even a lifetime, with the most notable example being migration patterns.

Dynamic Brownian Bridge Movement Model (dBBMM)

An adjusted BBMM method by Kranstauber et al. (2012) accounts for this limitation. Instead of assuming σ^2_m to be the same along the whole path, the *dynamic Brownian Bridge* (dBBMM) estimates a σ^2_m for subsections of the trajectory. The process takes subsets of location points to evaluate breakpoints in the Brownian motion variance. This is done by placing a sliding window the size of w locations is placed on a subset of location points, leaving out a margin *m* of locations on both sides of the window which are not taken into account for the estimation. First, a single variance value is calculated for the window, wich then gets split into all possible pairs within the window. Next, a σ^2_m is calculated for each split window. Then Bayesian information criterion values are calculated, and the case with the lowest value gets selected. If a single variance value is favoured, the entire window gets assigned this value. If a behavioural break is favoured, the calculated values for each split are assigned to segments on either side of the break (Kranstauber et al., 2012). Using these variance values, UD's are calculated as in the BBMM. The dBBMM gives more realistic estimations of space used as a flexible σ^2_m is less biased. One example of this is that it does not overestimate UDs during resting phases. As previously mentioned, the dBBMM method relies on two parmeters that are to be specified by the researcher, window size *w* and margin size *m*.

Increasing the window size increases reliability of σ^2_m estimation at cost of missing short term variation changes. On the other hand, increasing the margin size increases the power to identify 'weak' breakpoints at the cost of not detecting breakpoints within the margin. These parameters should therefore be determined based on biologically relevant information on behavioural change (Kranstauber et al., 2012).
Validation of the parameters is done by calculating the f statistic of the normal distributions of the window size and margin size (see figure 10). Higher values for the F-statistic indicate better performance of the dBBMMs σ^2_m to separate a movement track into different behaviours (Kranstauber et al., 2012).

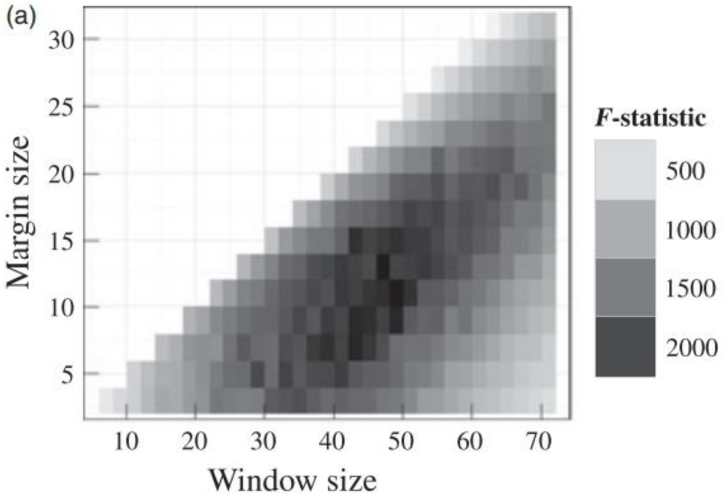


Figure 10: plot for evaluating optimal parameter settings for distinguishing behavioural changes (Kranstauber et al., 2012)

The dBBMM performs better than the BBMM when estimating home ranges with irregular sampling schemes, does not overestimate space use during resting phases and does not assign unrealistically high confidence intervals to migration segments (Kranstauber et al., 2012). It has also been attributed better performance than MCP and fixed KUD under low-resolution sampling (Silva et al., 2020).
A final important remark about both BBMM and dBBMM models is that in the strict sense, they must be referred to as occurance estimaors rather than home range estimators, as the probability distribution that is computed is constrained by the pairs of locations on both ends of the random walk (Fleming et al., 2015).

3 Data and methodology

3.1 Data

The telemetric data was obtained from a population (*n*) of 79 tagged juvinile Raja clavata. Among these animals are 46 female and 35 male individuals, with an age between 14 and 26 months at time of release. These rays were released over multiple occasions, with a total of seven batches being released in the period of June 2018 to October 2020 (Table 4). The transmitters used to tag the animals were Vemco V9 type tags. These tags were being monitored by a network of 107 acoustic receivers (VR2W-69) from the VLIZ LifeWatch System (Lifewatch Belgium, n.d.). The structure of these recievers consists of three meridional arrrays within the Western Scheldt, and a more distributed pattern in the North Sea (figure 12). The total study time in which detections were collected ranges from July 1st 2018 to December 10th 2021. A total of 88.104 detections were captured, containing information on:

- Station name
- Detection date and time
- Ray ID
- Ray sex
- Coordinates (Latitude and longitude)
- Transmitter ID

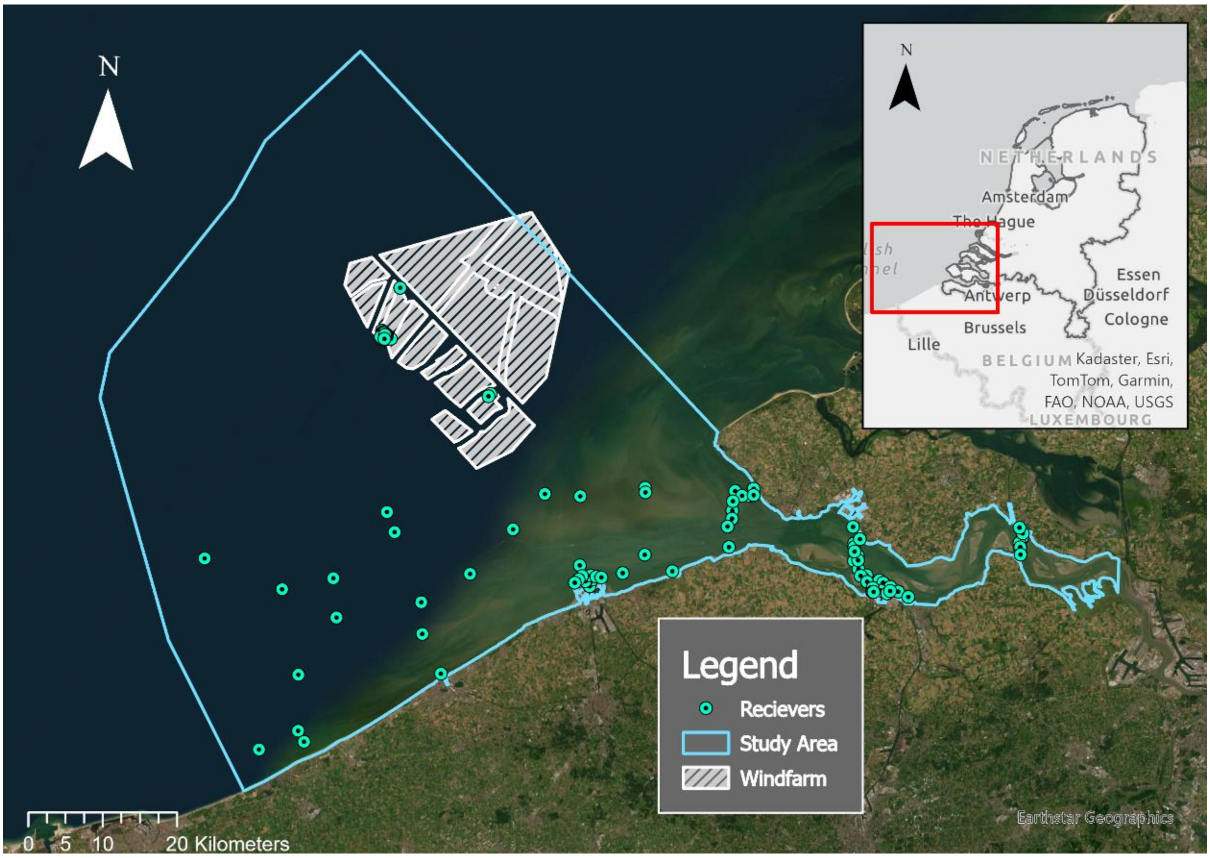


Figure 11: Study area with the positions of recievers and windfarm Borssele

Batch	Release date	Number of released rays	Number of rays with data	Male	Female
1	27th of June 2018	10	8	5 (62.5%)	3 (37.5%)
2	29th of June 2018	10	8	4 (50.0%)	4 (50.0%)
3	27th of August 2018	10	10	2 (20.0%)	8 (80.0%)
4	28th of August 2019	28	27	10 (37.0%)	17 (63.0%)
5	4th of October 2019	2	1	0 (0.0%)	1 (100.0%)
6	28th of August 2020	20	19	9 (47.4%)	10 (52.6%)
7	3rd of October 2020	10	8	5 (62.5%)	3 (37.5%)

Table 4: Overview of the batches with their release date, total number of released rays, number of rays with data and division in male and female (Essink, 2023)

3.2 Methodology:

In this section, the methods as applied in this study are specified. Figure 13 shows the general workflow of analyses, pre-processing and input and output datasets:

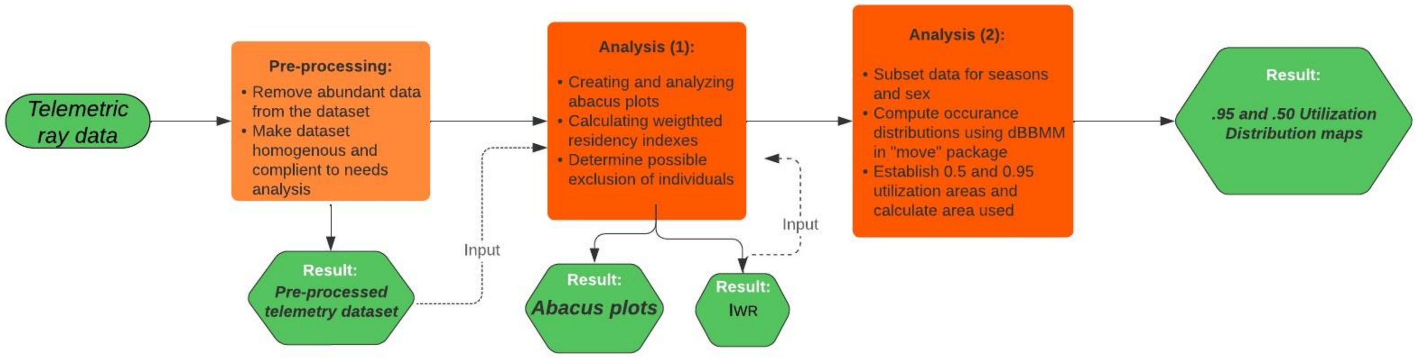


Figure 12: Conceptual analysis model

3.2.1 Estimating occurance distribution using the dynamic Brownian Bridge Movement Model

Method selection:

The method used in this study to estimate the utilization distribution (UD) of Raja clavata in the Western Scheldt uses the dynamic Brownian Bridge Movement Model as described by Kranstauber et al., 2012. There are several considerations that support the use of this specific estimitor compared to others. First of all, this study prefers a probabilistic approach over a hull-based approach. This is contributed mainly to the fact that the telemetric network cannot be assumed to cover the entire home range of the animal. A hull-based method would therefore be inappropriate, as its primary function is to outline home ranges. Also, a probabilistic approach better meets the initial goal of the organizations setting up the project, answering the question of whether the tagged individuals survive in the area, and if so where they reside.

Next to the fact that dBBMM provides more biologically relevant results (Kraft et al., 2023), its property to make distinctions in behavioural shifts makes it a promising estimator for Raja clavata specifically. As this species does not show consistent movement behaviour, but seasonal behaviour patterns (Walker et al., 1997; Hunter et al., 2005), it is incremental to select a method that warrants this trait. The dBBMM method can fulfil this by its property of not overestimating static phases and not assigning inappropriately high confidence intervals to migration segments (Kranstauber et al., 2012).

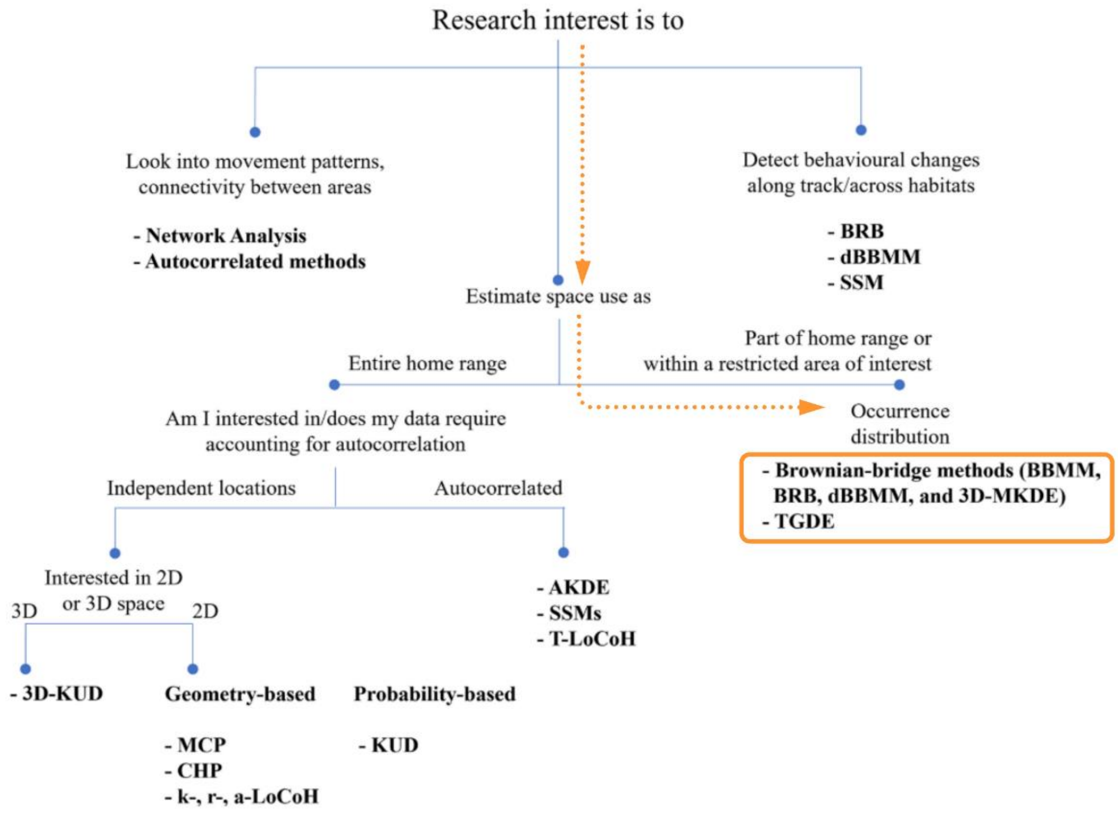


Figure 13: Decision tree with described space use estimation methods, categorized by relevant research interests and questions (Kraft et al., 2023)

Preprocessing
The telemetry data as collected by the organizations in the project is quite "rough" and needs some pre-processing steps in order to ensure data integrity and prevent flaws in the analysis. In his Msc thesis, Essink (2023) performed some valuable preprocessing on the dataset. However, there are also some steps in this process that adjust the dataset in ways not complient to presumptions of the dBBMM (for instance creating timeframes instead of point detections (Essink, 2023)). Also, previous preprocessing was performed in Python, while most analyses in this study will be performed in R. In order to use the steps of previous work that are valuable to this research, these steps will be recreated and fitted for this specific research in R. Some of these steps include organising data points into tracks, removing NULL data, removing abundant information, correcting syntax errors and dropping duplicate detections.

Residency estimation and abacus plots
The first rough step that will be performed to explore behaviour of Raja clavata in the research area is done by creating abacus plots and calculating weighted residency indexes (I_{WR}) for the individual rays. Apart from being a metric for residency in the study area, I_{WR} could also provide information on the temporal data quality of individuals. A low I_{WR} could point to the individual not residing in the study area, but could also be explained by data difficiency. Individuals with low residency values can then be visually assessed by using abacus plots. This way, choices can be made on whether an individual should or should not be included in further analysis. Individuals with a very low residency index cannot be assumed to depict natural behaviour within the extent of the study area. Determining from the results of the residency index and abacus plots, individuals might be left out of further analysis.

Both I_{WR} calculations and abacus plot visualizations are included in the glatos (Great Lakes Acoustic Telemetry Observation System) package in R (Ocean Tracking Network, 2022). Part of data exploration is visualizing the tracks in multiple ways. These visualizations are performed in R by plotting trajectories as well as generating abacus plots where dots in the plot are coloured by detection locations in order to indicate spatial behaviour of the animal on the plot.

Occurance distributions using dBBMM

Once the telemetric data is pre-processed and reviewed, it can be used as input to the dBBMM model. The dBBMM model is included in the “move” package for R (Smolla et al, 2024). Extensive documentation is provided on the use of this package. This includes information on how to compute KUDs using dBBMM, but also on relevant issues regarding data processing and different vizualizations. The central concept of the move package is that a move object for each individual is created, containing all relevant data. For multiple animals these objects can be stacked into a MoveStack, containing data on multiple individuals which can be used in batch processing. These can be used in order to calculate Brownian Bridges as specified in the dBBMM method, which accordingly can be used to calculate UDs for respectively 50% and 95% kernel utilization contours. As described by Kranstauber et al. (2012), there are two parameters that need to be specified before using the dBBMM model in the move package: margin (m) and window size (w). These parameters will be validated according to the method as suggested by Kranstauber et al. (2012).
The move package also has a functionality called burst, which splits up a track to see differentiation in patterns between parts of the day or seasons. This functionality will be used in order to generate subsets UDs for (a) different seasons (May to October and November-April) as specified by Winter & Jongbloed (2018) and (b) different sexes (male-female). The output of these multiple iterations of the model will be multiple utilization distributions, which will be compared visually as well as by metrics (e.g. total surface area per contour level).

4 Results

4.1 Telemetry data exploration and pre-processing

The telemetric dataset as described in section 3.1 is a rather ‘raw’ dataset containing all kinds of inconsistencies, inefficiencies, and other discrepancies. In order to clean the dataset and structure it to fit the input needs to the proposed methods, quite some data exploration and pre-processing are required. The results of exploring and pre-processing the dataset are (1) an assessment of data integrity and (2) a ‘clean’ dataset that can be used for input to following processes. Figure 16 shows the most important pre-processing steps that were taken, and the number of observations that were lost and kept for each step.

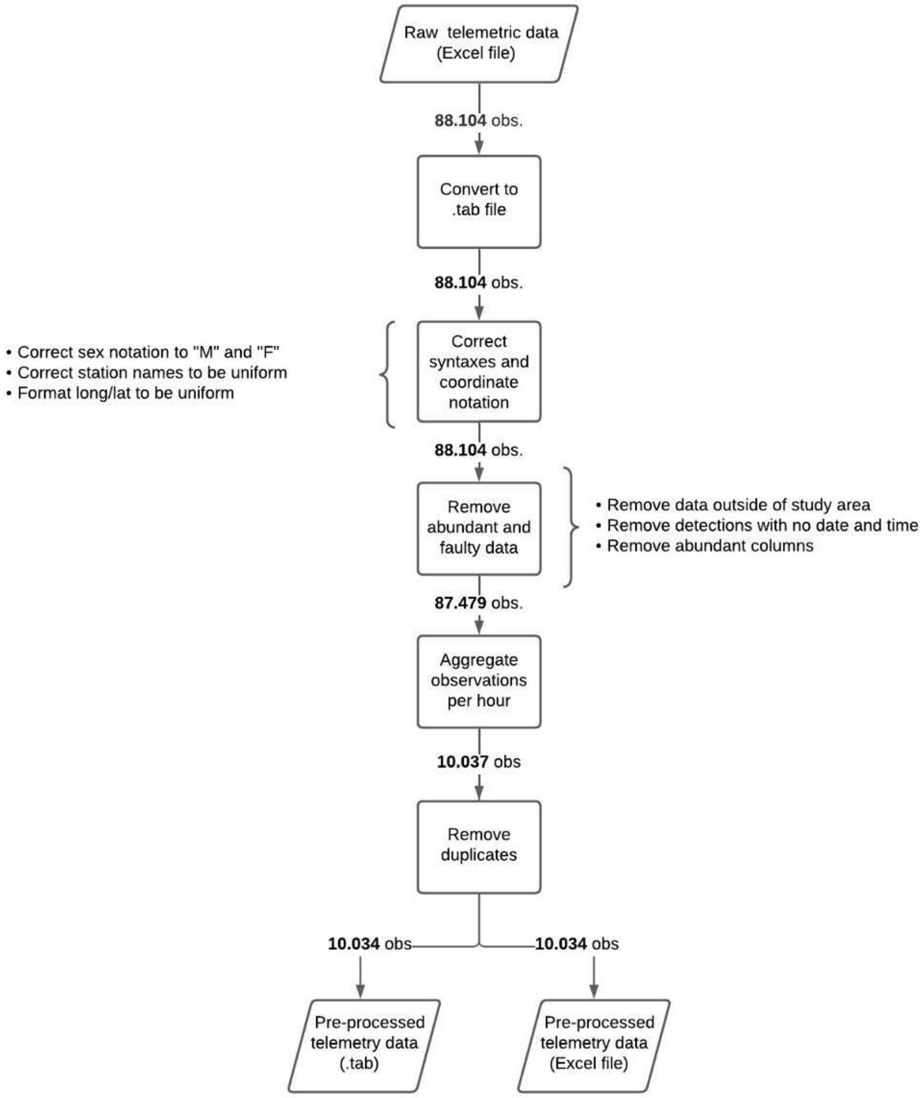


Figure 14: Pre-processing workflow

The first apparent flaw in the raw dataset’s quality is a lack of uniformity in variable notation. Both “Sex” and “Station Name” variables contained many syntax differences. Also, the coordinate values were stored in different formats, sometimes including separators and sometimes not. In other words, the data consistency of the dataset could be considered low.

These differences were corrected by assigning either “M” of “F” to the variable for sex and assigning station names based on a list of the proper station names for stations in the study area. All coordinates were set to the right format including a separator. Furthermore, the raw dataset included detections with missing values for certain variables, most often being coordinates. If these detections did have a valid station name, the average coordinates for that station as calculated by Essink (2023) were assigned. Detections with missing date and time values were emitted from the dataset, as well as detections captured outside of the study area. As only 0.7% of detections were emitted from the dataset, the data quality in terms of completeness can be considered high.
When a tag is withing sensing reach of a receiver, a signal is registered. These signals can have time differences of hours, minutes or sometimes even seconds. While this is practical for obtaining detailed information on the location of the animal, it also causes the dataset to be unnecessarily big in some instances. For example, when an animal decides to stay in one place under one receiver, this receiver will keep registering the tag. This can result in multiple observations of the same animal for the same receiver within the same hour, or even minute. This data can be considered abundant within the time scope of a year of tracking information. To prevent performance issues in further analyses, the number of observations of the same animal for the same receiver was reduced to one observation per hour (taking the first observation). This still provides detailed information on the animal’s location, while also accounting for travel between different buoys in the same hour. This preprocessing step reduced the number of observations by 88,5%. Hence, a lot of observations were done consecutively at the same station within the span of an hour. This can logically be explained by the fact that Raja Clavata is a nocturnal species, spending the hours in the daylight partially buried in sand (IFCA North West, 2018). Other explanations can be tag loss or death of the animal.
One last anomality in the dataset is that an animal can be measured by the same station at the exact same time. This happens when station coverages overlap, and the animal is located in this mutual measuring zone. It is impossible for an animal to be at two places at the same time, which is why the dBBMM function in the ‘Move’ package does not run when a dataset contains duplicate timestamps. Therefore, the last pre-processing step was performed by removing timestamps that were recorded for the same individual at the exact same point in time (HH:MM:SS). One of the duplicates remains in the dataset, selected at random (as the ‘real’ location of the animal is unknown). This step omitted three duplicate observations from the dataset. The pre-processing process as a whole reduced the original dataset from 88.104 observations to 10.034 observations, a total reduction of 88.6%.

4.2 Abacus plots and IWR

4.2.1 Abacus plots

The generated abacus plot for all 79 animals (figure 15) shows the detections (as dots) of each individual animal over time. In order to visualize a spatial component as well as the temporal information, the study area was divided into eight regions (figure 16). The colours of the dots on the abacus plot correspond to the region where the detection was done. This makes it possible to see roughly where an animal has resided in the study area throughout time.
Immediately apparent from the plot are a number of individuals with a low number of detections, a short measuring interval and large time gaps between detected locations. Animals with a low D_d or D_i are not appropriate to include in the computation of an occurrence distribution. This limited data does not rightfully represent animal behaviour, which is a process that is monitored successively over a longer period of time. The reason for absence of data for these animals is uncertain and can have multiple causes. Possible causes could be tag malfunction of any sort, as well as behavioural/natural causes like migration outside of the receiver array, death, or even the animal being preyed upon, causing the tag to be carried around by the predator.
The abacus plots also give information on the spread of individuals over the different regions throughout time. The regions within the Western Scheldt (WS-East, WS-West, and WS-Centre) are highly dominant in the plot. In the beginning of the timeline this abundance can be explained by the release location being located in the WS-Centre region. However, these regions stay dominant in the rest of the plot, insinuating that animals tended to stay inside of the Western Scheldt. Also, the Zeebrugge region (which encompasses the harbour of Zeebrugge, Belgium) seems to be visited by a substantial number of animals, also over longer periods of time. The western North Sea (NS-West) and Windfarm regions seem to be visited less frequently.

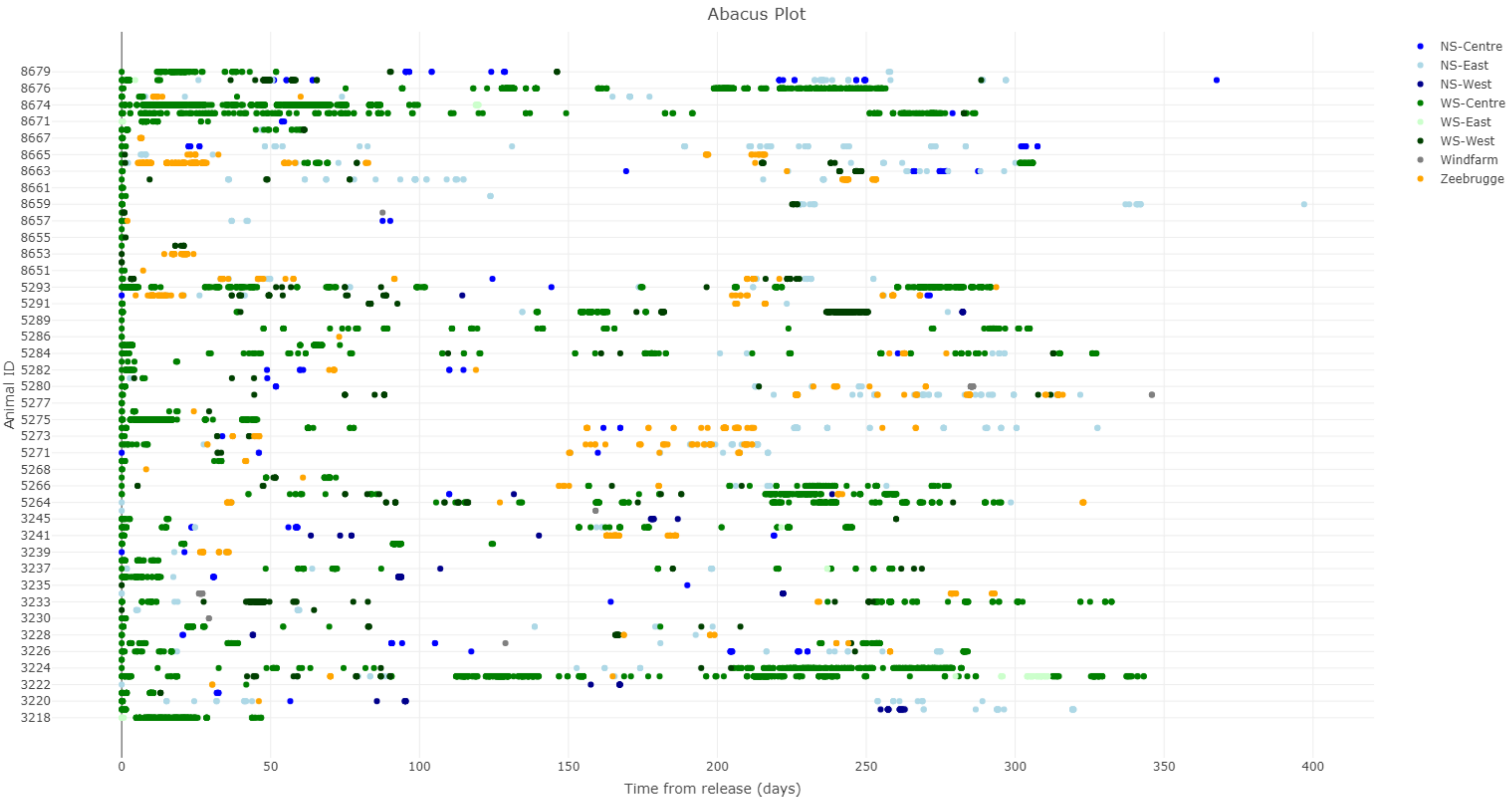


Figure 15: Abacus plot of all animals

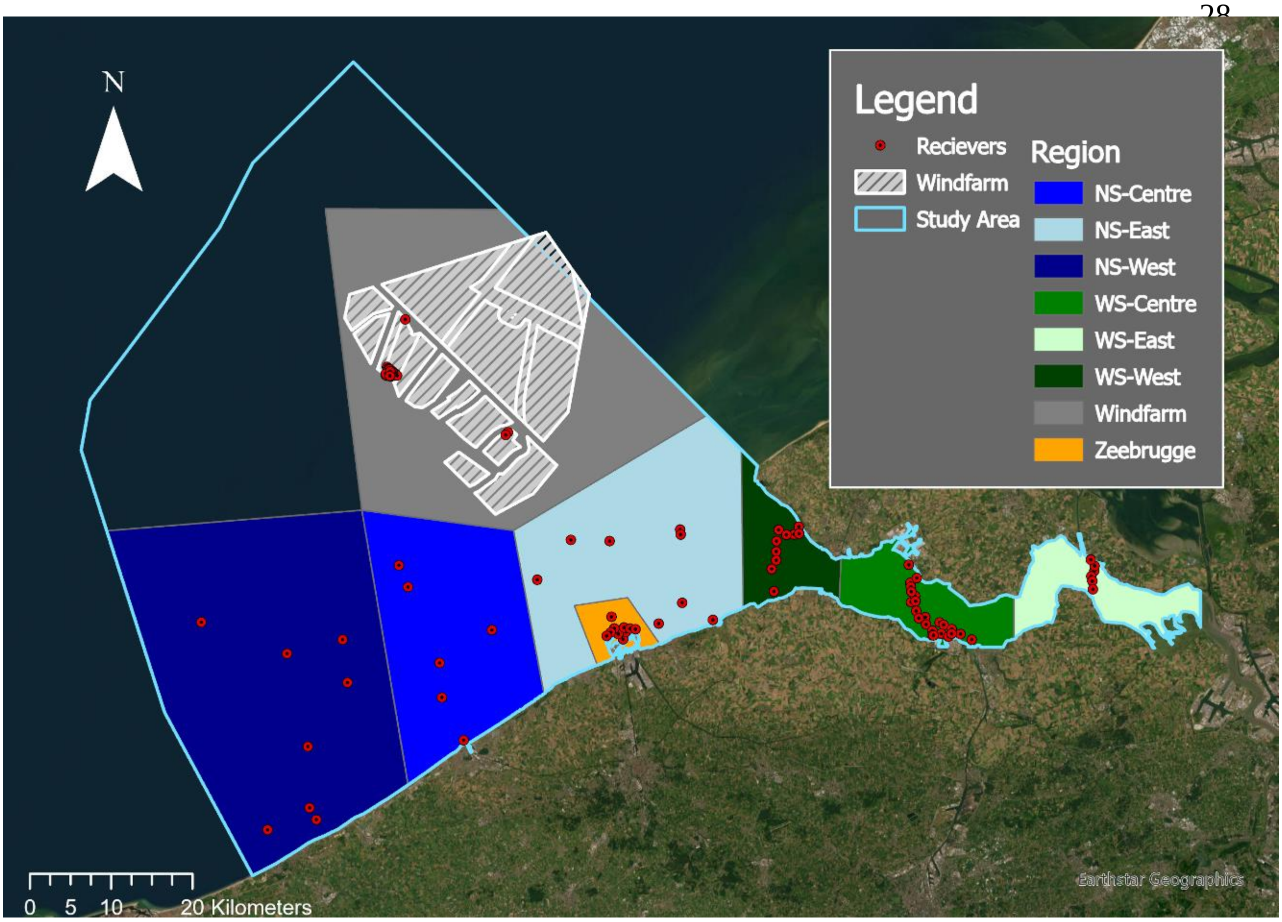


Figure 16: Regions to visualize the spatial behaviour of Raja clavata in the abacus plot

4.2.2 Weighted Residency Index

In order to assess which individuals are eligible to include in the estimation of occurance distributions, the I_{WR} for each animal was calculated through the following formula:

$$I_{WR} = \frac{D_d}{D_t} \times \frac{D_i}{D_t}$$

This formula first calculates a fraction of days the animal was detected (D_d) within the total study time (D_t). This fraction is then multiplied by the fraction of the total interval of the animal's detections (D_i) divided by the total study time (D_t). This second fraction generally filters out high I_{WR} scores for animals that have a high density of detections within a relatively small interval. The equation considers both the number of observations as well as the period of time over which the observations were done, which are two important factors for assessing behaviour.
In order to perform the calculation, the D_t, D_d and D_i values for each animal were extracted from the dataset. D_t is a static value that represents the total time extent of the study. This parameter was calculated taking the first and last observation of the entire study, resulting in a value of 1207 days.

D_i was calculated by taking the time difference in days between the first and last detection of an individual:

Total measuring interval (D_i)					
Minimum:	**1st Quartile**	**Median**	**Mean**	**3rd Quartile**	**Max**
0.0	45.5	190.0	168.3	282.0	397.0

The values for the measuring interval of individuals range between 0 and 397 days. This maximum value can be explained by the battery life of the Vemco V9 tags, which is expected to be around a year (Innovasea, 2020). The D_i can furthermore be interpreted as an indicator for whether the animals stayed within the study area. The median indicates that half of the animals were detected within the study area for 190 days or more or returned to the study area in this time period.

D_d was calculated for each animal as the number of different days on which detections were done:

Number of measuring days (D_d)					
Minimum:	**1st Quartile**	**Median**	**Mean**	**3rd Quartile**	**Max**
1.0	5.5	13.0	23.01	31.50	122.0

The range of the number of days with detections is very wide (1-122 days). The median value indicates that half of the individuals have less than two weeks of detections cumulatively. This low amount of detection days per animal can possibly be explained by the lack of study area coverage of the acoustic array, or the animal moving outside of the array.

The I_{WR} scores for every animal (appendix 1) were calculated by the formula formerly shown, taking the generated D_t, D_d and D_i values as variables:

Weighted Residency Index (I_{WR})					
Minimum:	**1st Quartile**	**Median**	**Mean**	**3rd Quartile**	**Max**
0.0	0.000208	0.001366	0.003933	0.006034	0.028724

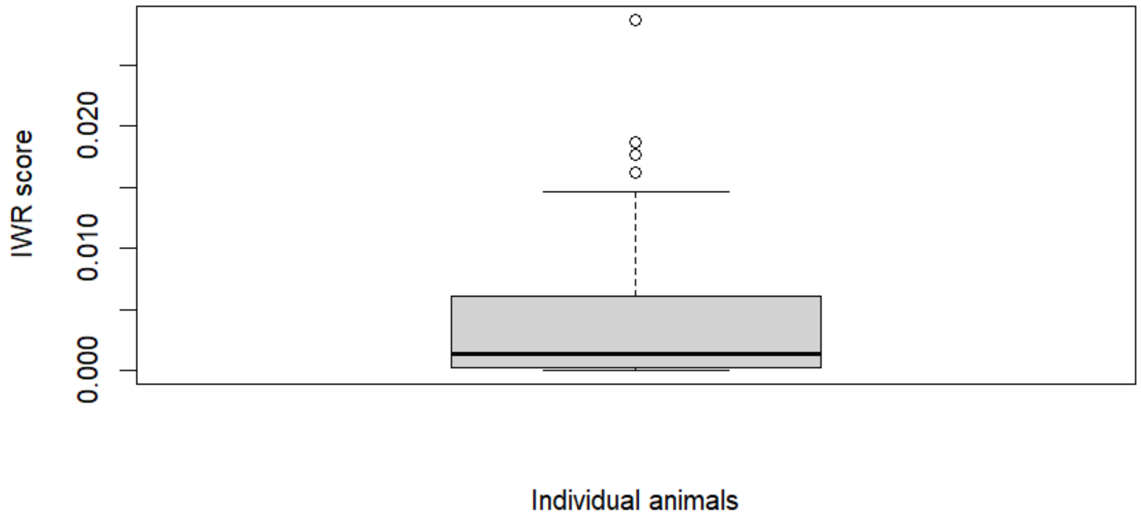


Figure 17: Boxplot of the I_{WR} for all animals

Figure 17 and the I_{WR}'s statistics show that the I_{WR} scores for many animals is very low. This can be attributed to either a low number of days measured, a short measuring interval or both. The low I_{WR} scores for this particular dataset are inherent to the lacking coverage of the receiver array. This trait inevitably causes a trade-off situation for selecting animals to include in the dBBMM. On the one hand, the estimation of occurrence distributions is more accurate with temporally high-quality data, while on the other hand individuals with temporally high-quality data are scarce, resulting the selection process to exclude data that might be valuable. Based on the results of the I_{WR} and its distribution combined with the output of the abacus plots, the decision was made to select animals in the 4th quartile of I_{WR} values. This corresponds to all animals with a I_{WR} of 0.006034 or higher. As the dataset contains 79 animals, this leaves the 20 animals that have data best suited for calculating behaviourally and biologically relevant occurrence distributions. Of these 20 rays, 9 are male and 11 female.

After the selection, the D_d and D_i values for the selected animals were reviewed to assess the quality of the selected data:

Total measuring interval (D_i) for selected animals					
Minimum:	**1st Quartile**	**Median**	**Mean**	**3rd Quartile**	**Max**
120.0	276.2	300.5	293.9	327.2	369.0
Number of measuring days (D_d) for selected animals					
Minimum:	**1st Quartile**	**Median**	**Mean**	**3rd Quartile**	**Max**
29.0	36.75	52.5	57.15	67.50	122.0

The selected animals have a minimum number of days detected of 29 and a minimum total measuring interval of 120 days. Especially the tracking intervals are considerably higher, with a mean value of 293.9 days. These are more appropriate values for modelling the spatial behaviour of Raja clavata in the study area, especially when comparing behaviour for seasons of the year.

To visualize the selected data and compare it to the original dataset, a second abacus plot was generated for the selected animals:

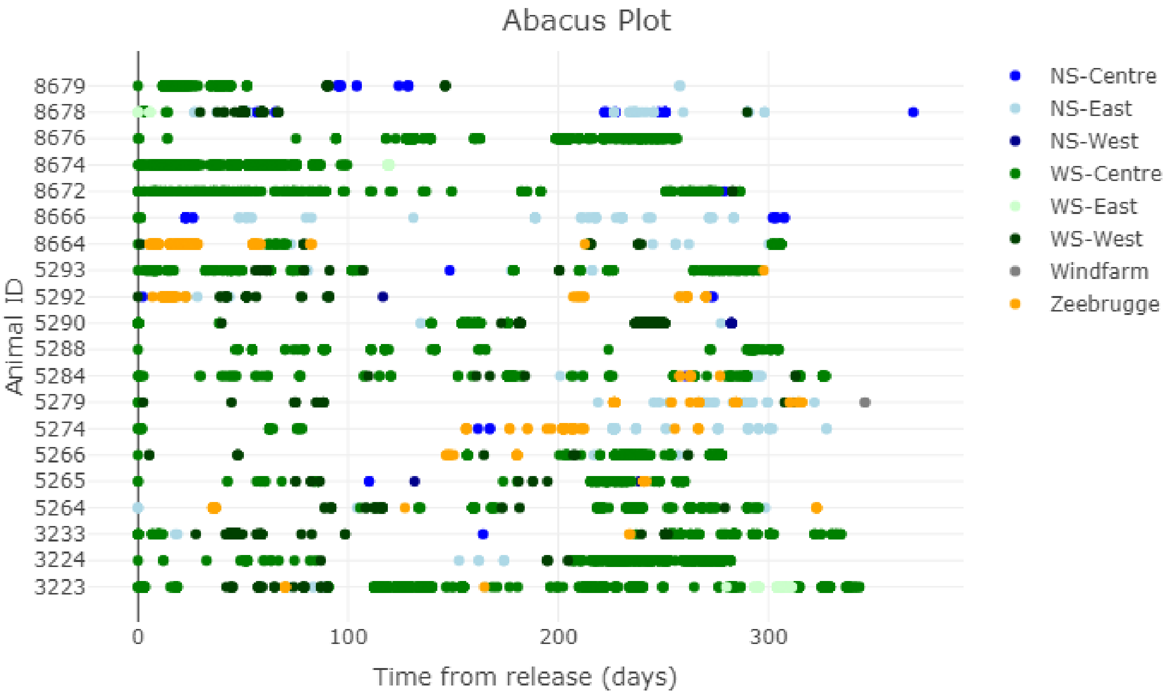


Figure 18: Abacus plot of animals with high weighted residency values in the Western Scheldt and Belgian Exclusive Economic Zone

This abacus plot overall shows that the selected animals have more observations, often spread out over approximately the lifespan of thee tag battery. However, it also portraits a deficiency present in the data. Multiple individuals still show large periods of time without observations, which means the location of the animal is uncertain for a period of time sometimes as long as a hundred days.

The regions visited by the animals do not differ greatly at first sight. The Western Scheld regions are still overrepresented, while the eastern part of the Nort Sea area (NS-East) and Zeebrugge are frequently visited as well. While occasionally detections are located in the centre of the North Sea area (NS-Centre), the selected rays show almost no visits to the western North Sea area (NS-West), whereas the Windfarm is only visited by one ray (ID 5279).

4.3 dBBMM and Utilization Distributions

3.3.1 dynamic Brownian Bridge Movement Model

In order to compute Brownian Bridges for the Raja clavata data, the data was ordered on animal ID and time. By doing this, the dBBMM function in the "Move" package iterates over the tracks as traversed by the animal and establishes a Brownian Bridge based on a variable Brownian motion variance dependent on time and distance between track points. Figure 19 shows a general overview of the tracks used to compute the dBBMM. In order to apply the dBBMM function in the 'Move' package, the dataset was made spatial (datum: WGS84, projected CS: UTM zone 31) and converted to a Move object. This Move object contains information on the X and Y coordinates, detection time and projection method.

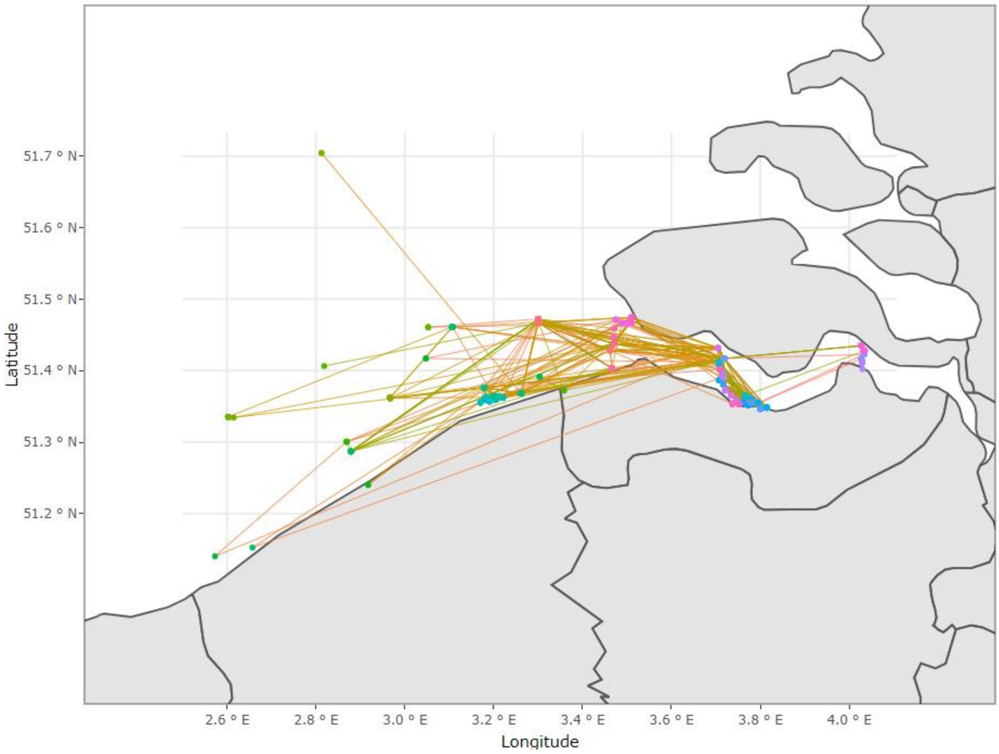


Figure 19: visualized tracks used as input for the dBBMM

The performance and output of the dBBMM depend on a number of parameters that can be defined in the model. In order to compute Brownian motion variance for sections of the tracks, a window size (*w*) and margin size (*m*) and location error are to be specified. Kranstauber et al. (2012) evaluated optimal parameter settings, finding that intermediate window sizes (41-47 locations) and relatively small margins (7-9 location) were best to separate behavioural stages of rest and activity. Larger window sizes provide more accurate estimates of Brownian motion variance, but are less well able to capture frequent changes in behaviour. Therefore the window size was set to 41, and the margin size to 7. The location error for the VEMCO Positioning System differs inside or outside the array, but was found to be between 2.4 and 4.2 (Roy et al., 2014). Therefore the location error was assumed to be 4.2 (the outside margin). As the Raja clavata data contains many ‘gaps’ inbetween detections, computing the dBBMM resulted in a big ‘blob’ for occurance distribution. This is caused by parts of the track where time between detections is very long. Because the dBBMM takes into account the time between detections, it generates a spread out distribution where there is a lot of uncertainty regarding the animal’s location. Moreover, it causes the probability distribution raster to extend to area’s far out of range of the study area, attributing very minimal probability values to a large extent. In order to generate more meaningful and realistic distributions, the variance of the segments corresponding to large time gaps can be removed from the model. This was done by calculation the Brownian motion variance, and setting the segments corresponding to large time gaps to FALSE beforre calculating the dBBMM. The barrier time lag for which segments were emitted was decreased until meaningful distriutions could be obtained. The resulting barrier time lag for the model was is 4320 seconds (or three days).

With a relatively large input dataset (6498 observations), the computations done to calculate the dBBMM were extremely big and took a long time. In order to minimize the size of the computation and output raster, the output raster size was set from the default 100m to 250m. To speed up the calculation, a time step can be defined. By default, the dBBMM will take the shortest time lag (in minutes) of the trajectory divided by 15 as the time interval taken for every integration step. This step time can be set manually. As the data on Raja clavata was aggregated to observations on the same receiver per hour and the time lag between observations is generally quite long, the time step parameter was set to 4 (*15 minutes = 1 hour).

With the parameters as described, the dBBMM was ran for the entire dataset, four subsets (male, female, summer and winter) and for each animal individually. The output of the dBBMM give the probability that the animal was present in a given pixel during the observed period.

4.3.2 Utilization Distributions

From the dynamic Brownian Bridge object, the utilisation distribution (UD) can be calculated. The UD shows the minimum area in which an animal has a specified probability of being located. From the dBBMM objects resulting from the model, both .95 (95%) and .5 (50%) UDs were calculated.

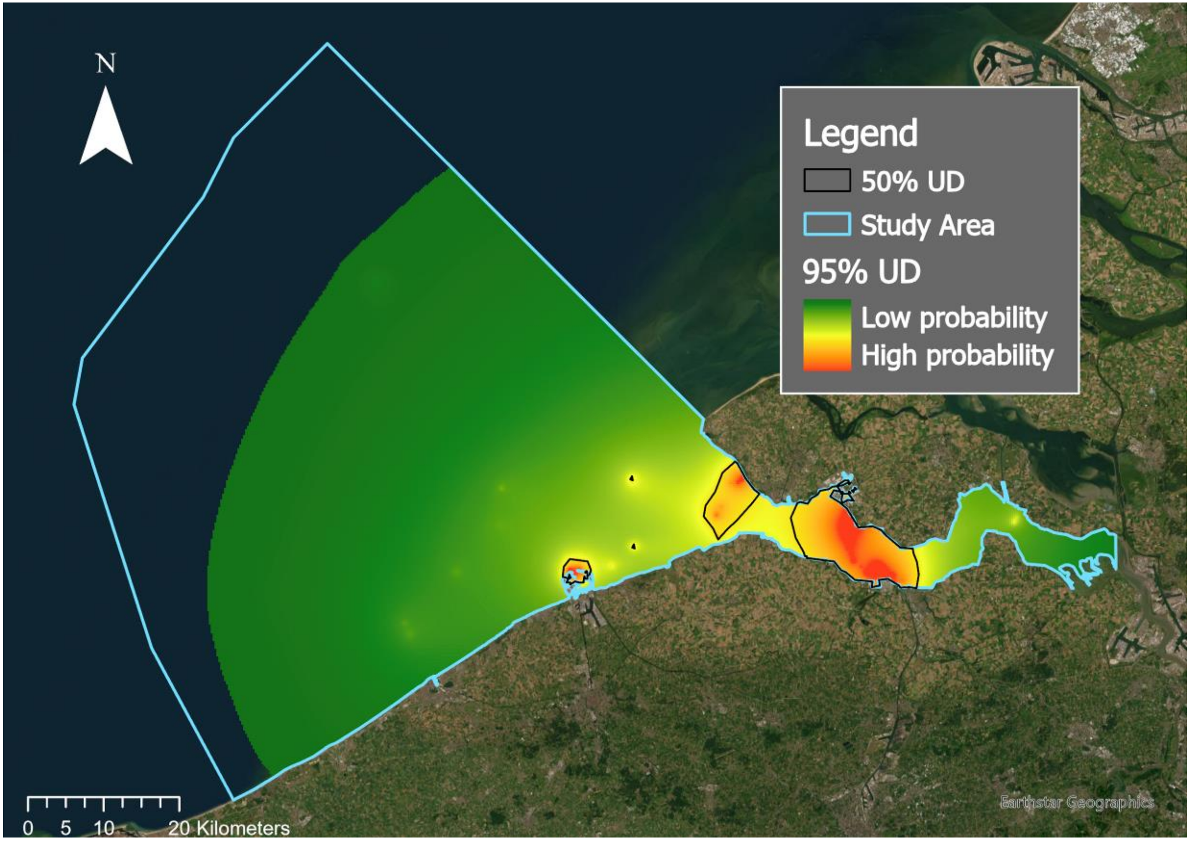


Figure 20: 95% and 50% Utilization Distributions (UD) for Raja clavata in the Western Scheldt and Belgian Exclusive Economic Zone

The 95% UD of all individuals combined (figure 20) extends from the eastern part of the Western Scheldt to the open water of the North Sea. This broad distribution can be explained by the time gaps present in the dataset. However, the offshore area in the North Sea gets attributed very low occurrence probability values. The higher occurrence probability is modelled in the outer and centre of the Western Scheldt, spreading to shore areas just outside and to the south of the Western Scheldt. There is also a small concentration of higher occurrence probability in the East of the Western Scheldt, and some areas along the Belgian coast that show somewhat higher values for occurrence probability.

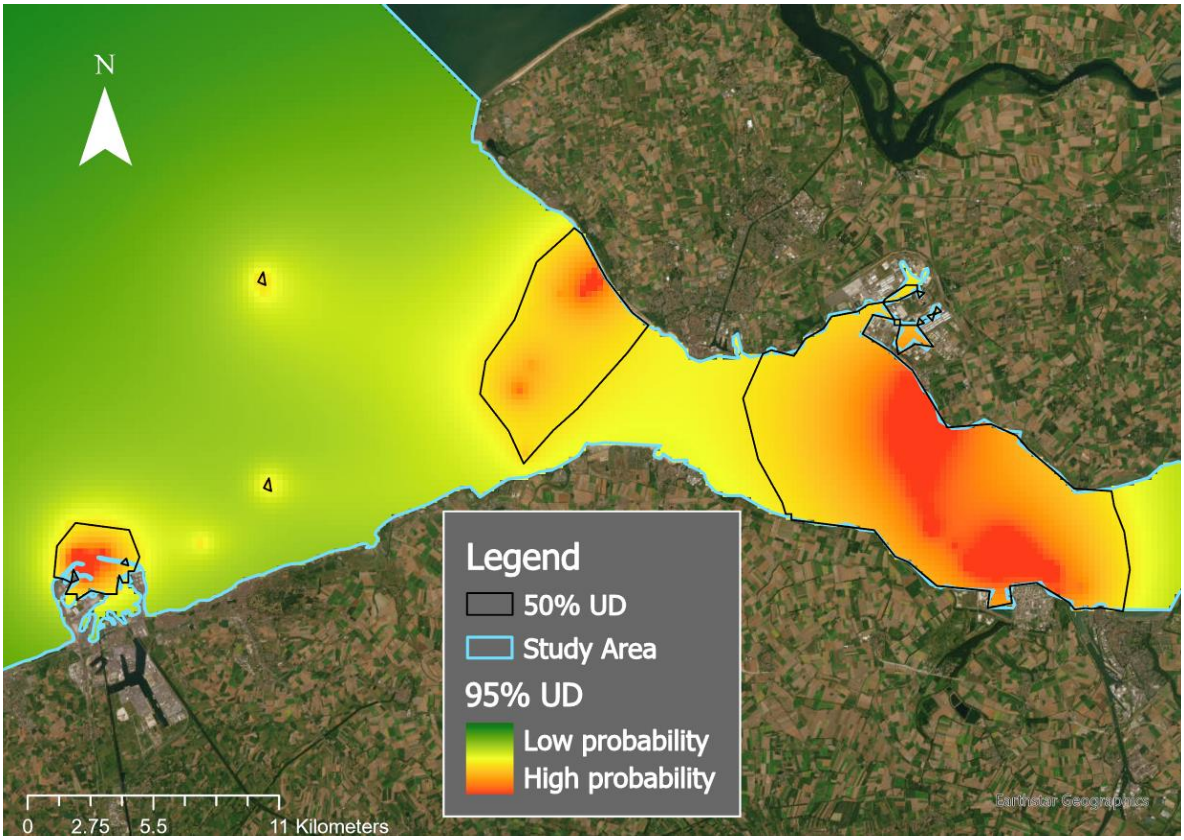


Figure 21: an overview of the 50% utilisation distribution (UD) for Raja clavata in the Western Scheldt and Belgian Exclusive Economic Zone

Zooming in to the 50% Utilization Distribution (or core use area), five different areas can be distinguished: an area in the centre of the Western Scheldt (between Vlissingen and Terneuzen), an area in the outer Western Scheldt (with higher probability close to the shore west of Vlissingen), and area to the shore south-west of the Western Scheldt (the Zeebrugge harbour) and two 'islands' to the west of the Western Scheldt.

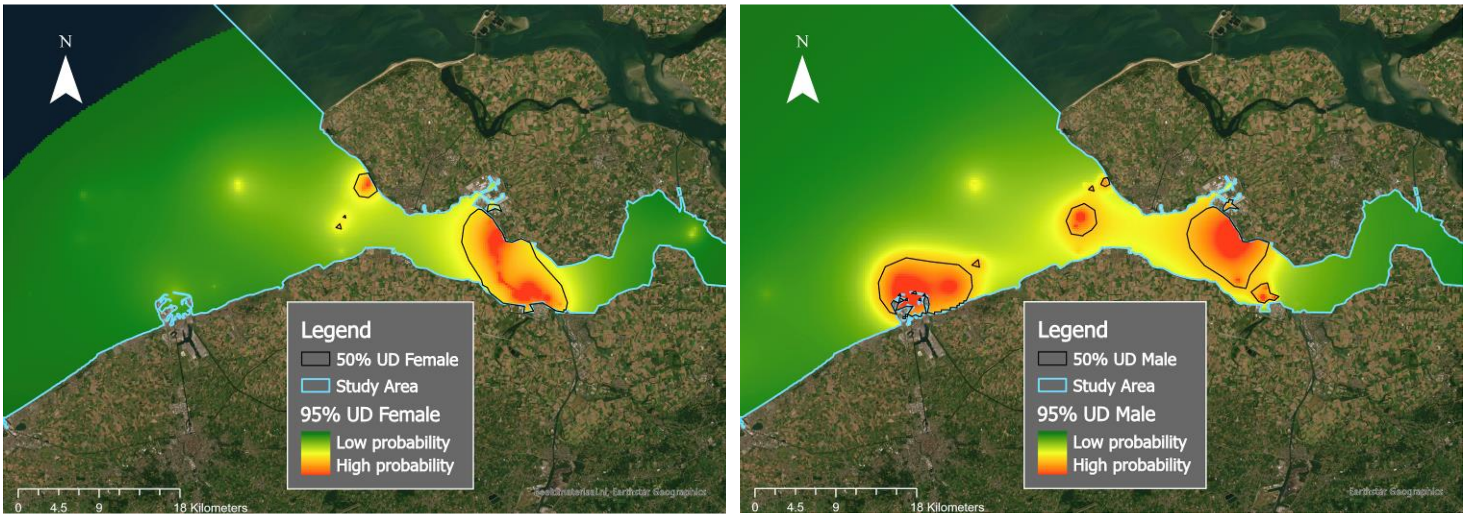


Figure 22: 95% and 50% Utilization Distributions (UD) for female (left) and male (right) Raja clavata in the Western Scheldt and Belgian Exclusive Economic Zone

The resulting UDs for female and male rays show a difference in spatial behaviour between the different genders. The 95% UD for females is a lot smaller, especially when considering the offshore areas. The 50% UD for females sits quite tight around the array of receivers in the centre of the Western Scheldt, with the exception of a small area to the west of Vlissingen and two spots in the outer estuary. The probability distribution of male Raja clavata contrarily is more spread out, especially in 50% utilisation areas. The core use areas of male Raja clavata are mainly located in the centre of the western Scheldt, the outer part of the estuary and Zeebrugge.

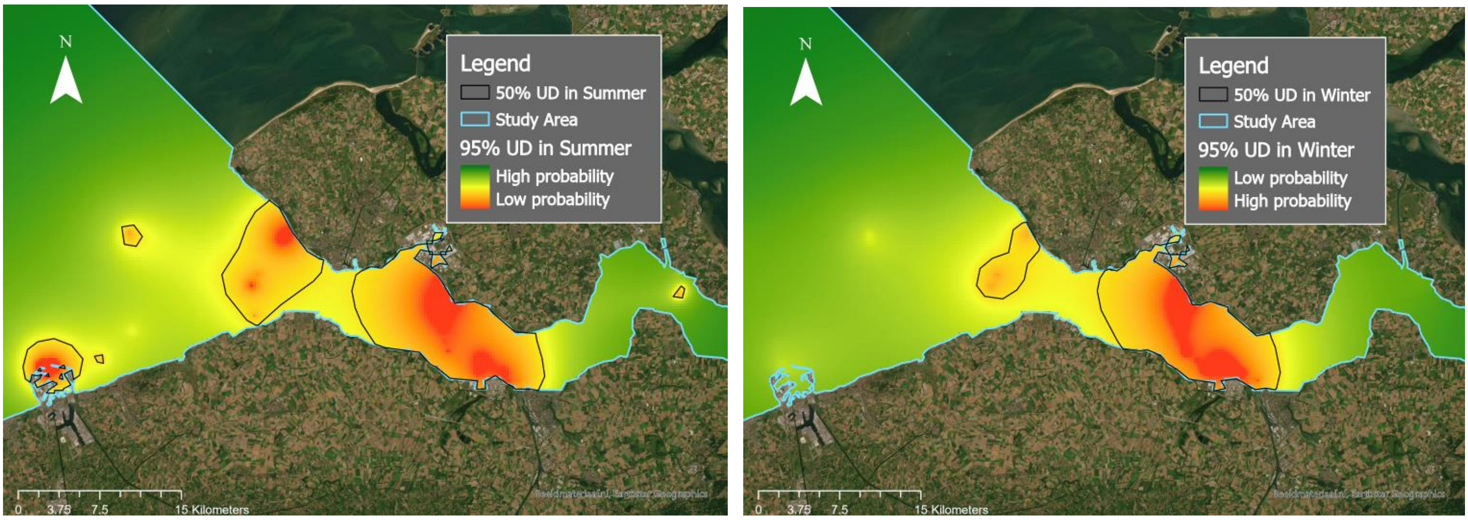


Figure 23: 95% and 50% utilisation distributions (UD) for Raja clavata in summer (left) and winter (right) in the Western Scheldt and Belgian Exclusive Economic Zone

Figure 23 shows the 95% and 50% UDs for Raja clavata in two different seasons of the year based on expected water temperature preference of juvenile Raja clavata (Winter & Jongbloed, 2018). Figure 23 shows opposite results to Winter & Jongbloed's expectations and studies performed on the English coast (Walker et al., 1997; Hunter et al., 2005). In the winter half-year (November-April), the animals tended to reside in the Western Scheldt, whereas in the summer half year (May-October) the utilization distributions expand more to the outer part of the estuary, off-shore and to the Zeebrugge area.

In order to quantify and compare the extent of utilisation of the study area by Raja clavata, the total area (in km$^{2)}$ for a UD can be calculated. This gives an indication on whether an animal (or a group of animals) has more 'static' or dispersive behaviour, and how much of the study area they utilize. As the outcome of the 95% UD is spread out, comparing used area does not make much sense. The area of the 50% UD however can explain how much space an animal (or group of animals) inhabits in their most regular natural behaviour.

Dataset	50% UD in km^2
All individuals	163.87
Male	110.66
Female	75.61
Summer	203.15
Winter	138.40

Table 5: Area of 50% utilisation distributions (UD) in km^2

The visual difference between spatial behaviour of male versus female rays is reflected in the area utilized 50% of the time. As male rays seem to show more 'active' behaviour expending their core habitat outside of the estuary, the total area of this core use area is substantially higher, while female rays seem to stay more clustered within the Western Scheldt. In the summer half-year, the 50% UD of Raja clavata is more dispersed than in winter, indicating more movement to outside of the Western Scheldt, as portraited in figure 23.

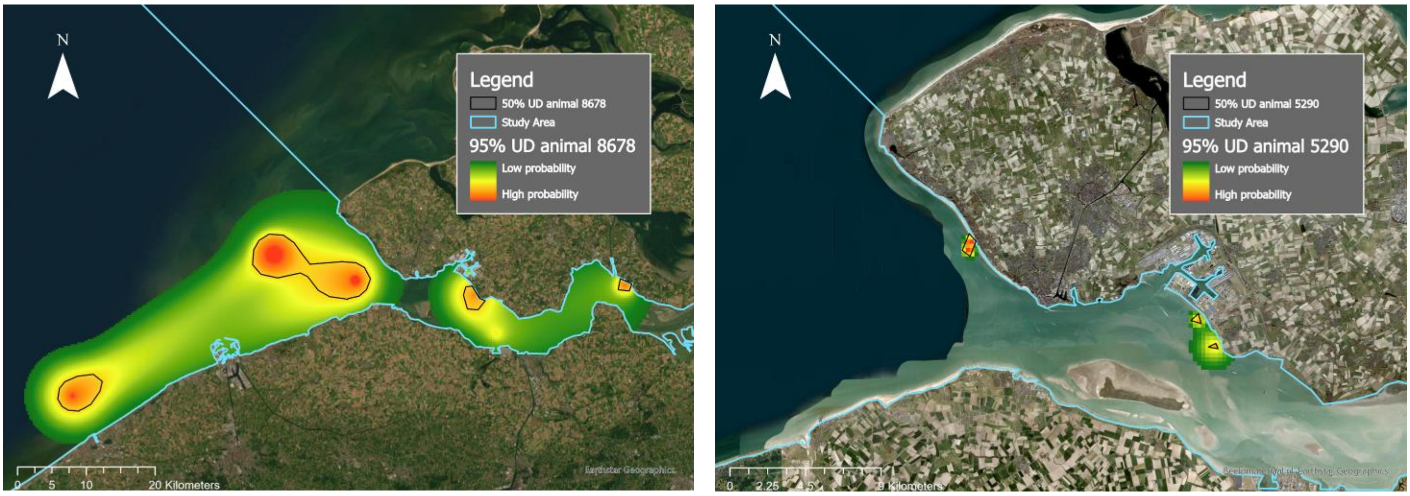


Figure 24: Raja clavata with a large (left) and small (right) 50% utilisation distribution (UD) in km^2

To show difference in behaviour between multiple individuals, figure 24 shows a comparison between a ray with a high utilization area (110.58 km^2) and a ray with a low utilisation area (0.82 km^2. Appendix 2 shows a high range and big differences in traversed 50% utilisation areas. As the UD values and visualisations do give a clear view on how the total population resided within the study area, this does not exclude active use of areas represented with lower UD values. The 95% UD of animal 8678 shows a clear movement pattern between core use areas, showcasing the core concept of a Brownian bridge, which can help to understand movement patterns of the animal. The 95% UD of animal 5290 on the other hand shows how the dBBMM method generates tighter UDs for animals with a more resting, static behaviour.

5 Discussion and conclusion

5.1: Discussion

5.1.1 Interpretation of results

When evaluating habitat suitability of the Western Scheldt and Belgian Exclusive Economic Zone for Raja clavata, the results of the dBBMM analysis support the conclusion of Winter & Jongbloed (2018) regarding the area as a suitable habitat. The results of the IWR and abacus plots show that at least a share of tracked animals was detected relatively frequently within the receiver array for an extended period of time. This implicates that these individuals use the Western Scheldt and Belgian Exclusive Economic Zone as their habitat for natural behaviour for at least approximately the first year after their release. For the remaining rays, telemetric data was deemed insufficient to model spatial behaviour within the study area over an extended period of time. Possible explanations for this data deficiency could be migration outside of the study area, a lack of coverage of the array within the study area, death, or others. These underlying processes for non-utilization of the study area are however not explored in this research.

The results of the utilization distributions show that resident Raja clavata prefer staying in the centre and west areas of the western Western Scheldt (where they were released) or migrate to the port of Zeebrugge to stay there (figure 20). Winter & Jongbloed (2018) suggest that for juvenile thornback rays, the western part of the Western Scheld (west of Terneuzen) appears most suitable in terms of water depth, sediment type and salinity. Within this area they suggest the area between Vlissingen-Terneuzen is very suitable in terms of bed shear stress. The 50% UD covers these areas intensively, confirming suitability of these areas within the Western Scheldt (figure 21). Winter & Jongbloed (2018) also question whether the habitats east from Terneuzen will be used. The utilisation distribution shows some use of this area, although not extensively, which suggests the area east of Terneuzen is a suitable habitat while thornback rays prefer the area west of Terneuzen.
The 50% UD and highest occurrence probabilities seem to be located in areas close to the shore. Most of these utilisation ‘hotspots’ are located close to harbour areas (Vlissingen, Terneuzen and Zeebrugge). This could be related to abiotic factors such as temperature or bathymetry (juvenile rays tend to prefer shallower waters), or presence of prey. Male rays used a bigger part of the study area than female rays, especially residing more in the outer estuary and Zeebrugge (figure 22). These results are in line with the study by Papadopoulo et al. (2023), finding more residential behaviour for female Raja clavata than for male animals. Male raja clavata showed a substantially bigger area of use, indicating more movement outside of the estuary as well as more activity overall. The cause for this difference can be explored further by comparing ray behaviour per sex for different abiotic and biotic factors.
Winter and Jongbloed (2018) predict that the temperatures in the Western Scheldt in summer are very suitable for Raja clavata, but too low in winter. Therefore, they predict migratory behaviour to warmer areas in winter, similar to studies on the English coast (Walker et al., 1997; Hunter et al., 2005). The UDs for summer and winter half-years suggest the contrary. In winter, the rays stayed within the Western Scheldt, whereas in the summer they moved to areas outside of the Western Scheldt (figure 23). This suggests that contrary to the predictions by Winter & Jongbloed (2018), the Western Scheldt can serve as a suitable habitat for Raja clavata in winter. It should be noted however that the rays were released in the beginning of the winter half-year, possibly being the reason for them residing in the Western Scheldt. Temperature analyses by both Winter & Jongbloed (2018) and Essink (2023) showed the temperatures in the Western Scheldt to reach values above the

preference value of 19,5 degrees, which could be considered as a reason for rays to migrate out of the Western Scheldt in future studies.

A reason often discussed as a reason for Raja clavata to reside in estuaries in summer is reproductive behaviour. In the summer breeding season, Raja clavata migrate to shallower, warmer areas in order to reproduce. The effect of reproductive migration can be ignored in this study, as data was only collected on juvenile rays, which do not yet show reproductive behaviour. This allows for consideration of abiotic factors and biotic factors (mainly food resources) exclusively. Studies measuring the impact of these factors are therefore highly recommended for this project’s dataset specifically.

Finally, the results of the dBBMM analysis show no clear reason for considering the windfarm Borssele to be a substantial part of the utilized area by Raja clavata, contrary to suggestions made by Derduwen et al. (2012).

5.1.2 Limitations

The biggest limitation of any acoustic telemetric study lies within the coverage of the receiver array. The array in the Western Scheldt and Belgian Exclusive Economic Zone has properties that limit as well as support the performance of dBBMM analysis. The three line arrays in the Western Scheldt could be considered an irregular sampling scheme, as locations in between the arrays are underrepresented. While receivers in the North Sea area are more regularly distributed, there are still ‘blind spots’ that rays can travel through while not being detected. These characteristics of the tracking network inevitably limit the spatial detail to which predictions can be done on area utilisation. On the other hand, the arrays in the Western Scheldt do practically guarantee detection of migratory events in and out of the Western Scheldt, as they serve as gates. Another limitation inherent to acoustic telemetry is the temporal limitation of the data caused by the tag life of the transmitters. This caused the maximum time window for observations to be around a year. For telemetric studies on animals that do no travel fast or far with less dynamic behavioural shifts, like Raja clavata, it would be recommended to decrease the nominal delay between detections when programming tags in order to optimize tag battery life.

The data in this study solely contains data on juvenile Raja clavata. This decreases generalization of study results for the species as a whole, as results and conclusions of this research cannot fully be applied to adult animals. Habitat preferences for adult rays slightly differ and adult rays show reproductive behaviour. Another factor decreasing generalization of results is the fact that the rays in this project were artificially reared before being reintroduced. For the first few months of their lives the rays were used to living in basins where they were fed instead of having to prey for food. Because of this the animals cannot be assumed to show natural behaviour immediately from the point of reintroduction.

However carefully selected and executed based on relevant scientific literature, the methods used for analysis imply certain limitations. While the IWR is an easy to interpret and effective pointer for residency and data quality, its is somewhat biased to specific data structures. For example, individuals that have multiple short intervals with high densities of observations get attributed high IWR scores, while having large periods of time without any observations. The IWR is slightly biased towards these specific ‘gappy’ tracks that do have a relatively large number of detection days over a long interval. Selecting animals based on IWR scores potentially leaves out data that could be valuable for estimating space use. However, this selection shifts the focus on animals that showed residential behaviour within the Western Scheldt and Belgian Exclusive Economic Zone, matching the research questions and project purpose.

Although the dBBMM showed to be effective in modelling occurrence distributions based on animal tracks, there are some limitations to the method as implemented in this research. Some of these limitations are data-dependent, while others are more general. Due to the relatively large dataset used as input to the model, computations were very large and took a long time. These performance issues ultimately led to the output pixel size being bigger, giving less spatially detailed predictions for occurrence distribution. The spatial resolution of 250 meters still provides plenty of valuable information, especially because Raja clavata are a species that don't move long distances in short times. For analysing species that do move faster, the pixel size could be limiting to analysing behavioural shifts. Long time gaps in the data caused the model to run with high uncertainty. While the time step parameter offers a solution to this problem, it also results in overrepresentation of resting phases while movement is represented less in the dBBMM output. This limited the analysis of potential moving corridors, but strengthens conclusions on areas where thornback ray reside. One final limitation of the dBBMM model in the 'Move' package is the inability to set boundaries to the computation of outputs. Specifically in the case of applying the model to an estuary, the model generates values within a general extent rather than considering physical boundaries. This causes the output of the dBBMM to cover areas on land, where occurrence is physically impossible. As the model has to be able to extend the raster to make all probability values to be 1, the extent to the model cannot simply be set to for instance the extent of the study area.

5.2 Conclusion and recommendations

5.2.1 Conclusion

Based on data on re-introduced juvenile Raja clavata, the results of this research confirm that the Western Scheldt and Belgian Exclusive Economic Zone can serve as a suitable habitat for the species. By using the dynamic Brownian Bridge Movement Method (Kranstauber et al., 2012) utilisation distributions were estimated, which confirm residential behaviour of Raja clavata in the Western Scheldt and Belgian Exclusive Economic Zone. Core use areas of the juvenile Raja clavata are located in the Western Scheldt around and west from Terneuzen, as well as in the harbour of Zeebrugge. Male and female Raja clavata showed different behavioural patterns, with male rays utilizing a bigger area outside of the Western Scheldt and females showing more resting behaviour within the Western Scheldt. In the winter half-year Raja clavata tended to stay more into the estuary, while in the summer half-year they migrated to the outer estuary and the coastal area south of the Western Scheldt (around Zeebrugge). The dBBMM overall performed well in terms of modelling occurrence distribution but tends to overestimate resting phases and underestimate movement phases for tracks with limited temporal and spatial detail.

5.2.2. Recommendations

While this research clearly illustrates the behaviour of Raja clavata in the Western Scheldt and Belgian Exclusive Economic zone, it raises the question of why the animal uses specific regions within the area. The most urgent recommendation resulting from this research is to investigate what abiotic and biotic factors drive this spatial behaviour. Literature suggests water temperature, bathymetry, salinity, bottom shear stress and sediment type to be predictors for Raja clavata habitat preference, thus it would be logical to compare the values for these factors with the occurrence distribution as modelled in this research. While this research focussed on animals that resided within the area, future research is needed to determine possible behaviour of Raja clavata outside of the area and drivers to this behaviour. Broader, more zoomed out studies could be performed in order to assess possible use of multiple habitats by Raja clavata. Research like this could profit from European initiatives such as the European tracking network in order to assess species distribution and habitat suitability on a continental scale.

This research contains information on the most frequent whereabouts of Raja clavata in the Western Scheldt and Belgian Exclusive Economic Zone. The results of this research can therefore potentially be used to design more detailed strategies in order to protect, maintain and potentially expand the population of Raja clavata in the Western Scheldt and surrounding areas. As the area seems to meet most natural requirements to function as a habitat for Raja clavata, more research on human interference and potential disturbance in the habitat of Raja clavata is also strongly suggested.

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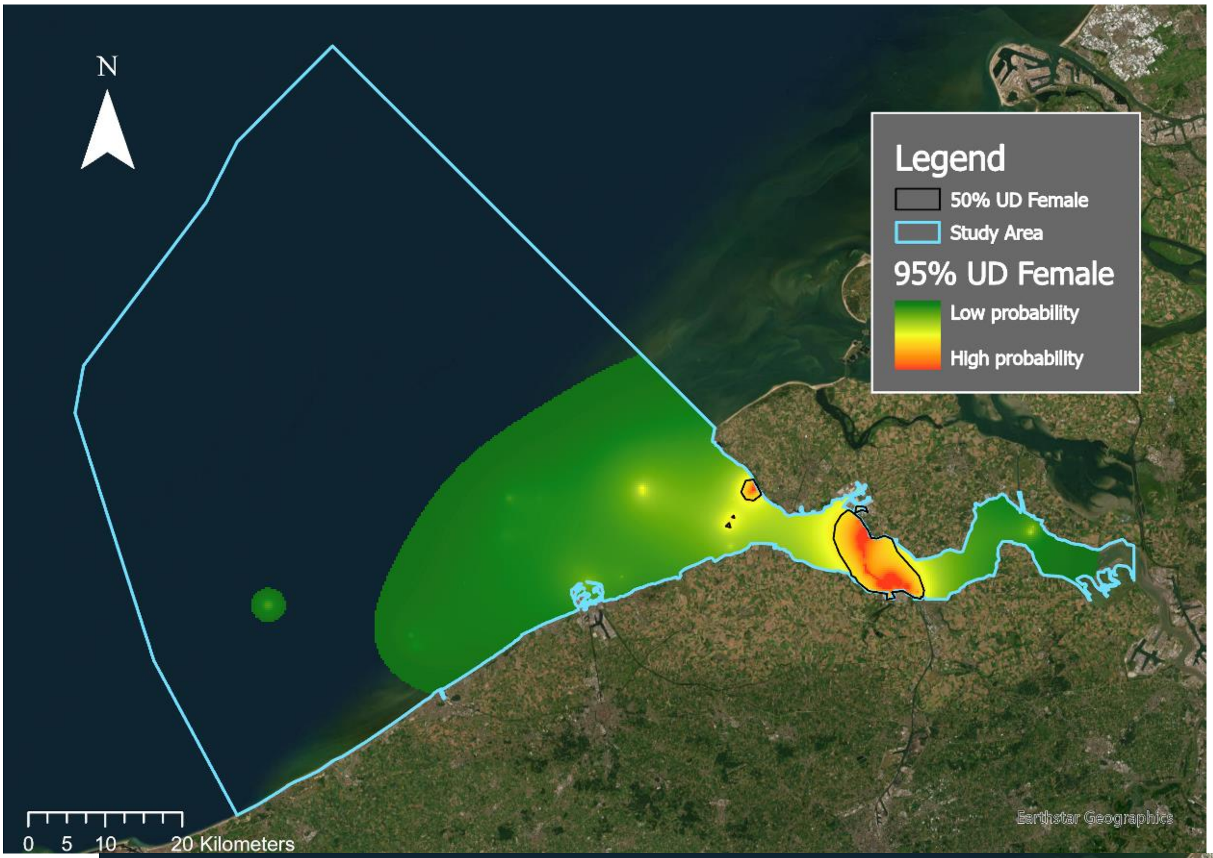
7 Appendices

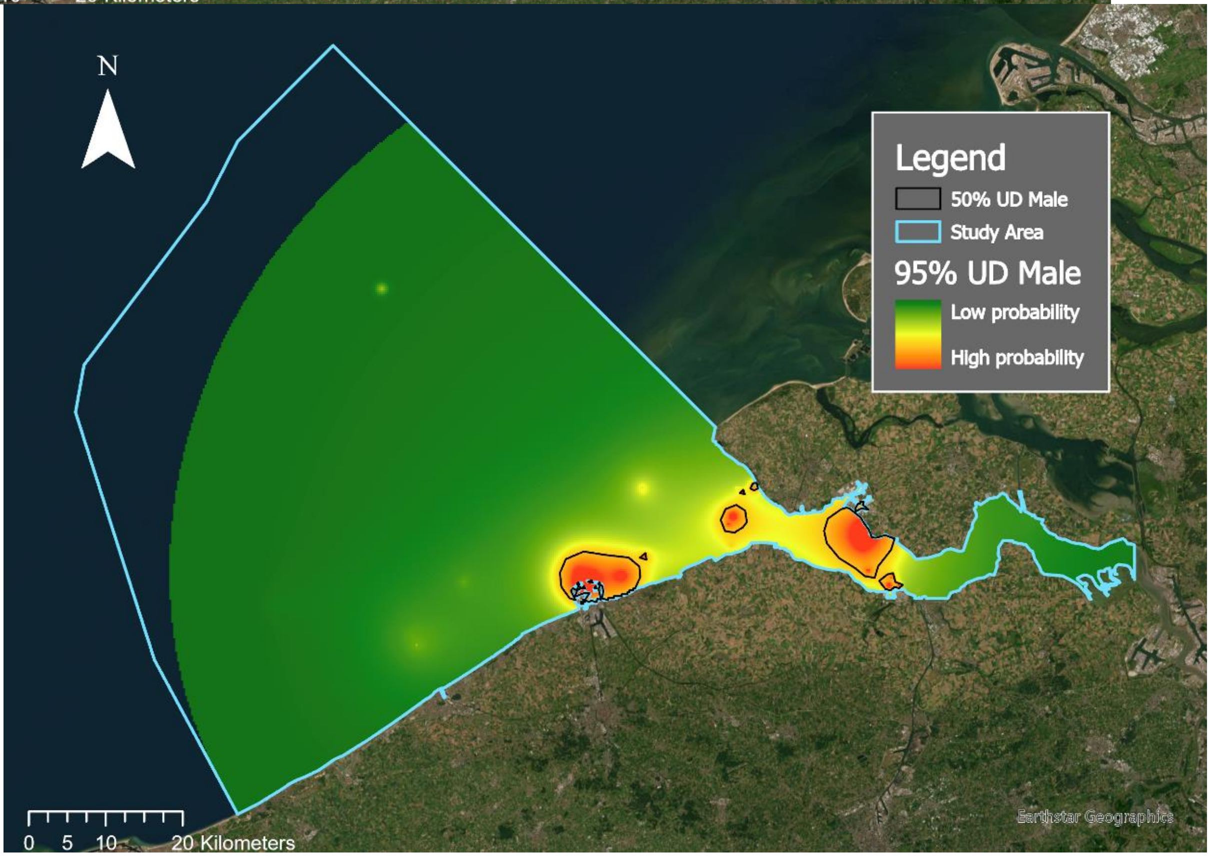
Appendix 1: IWR results

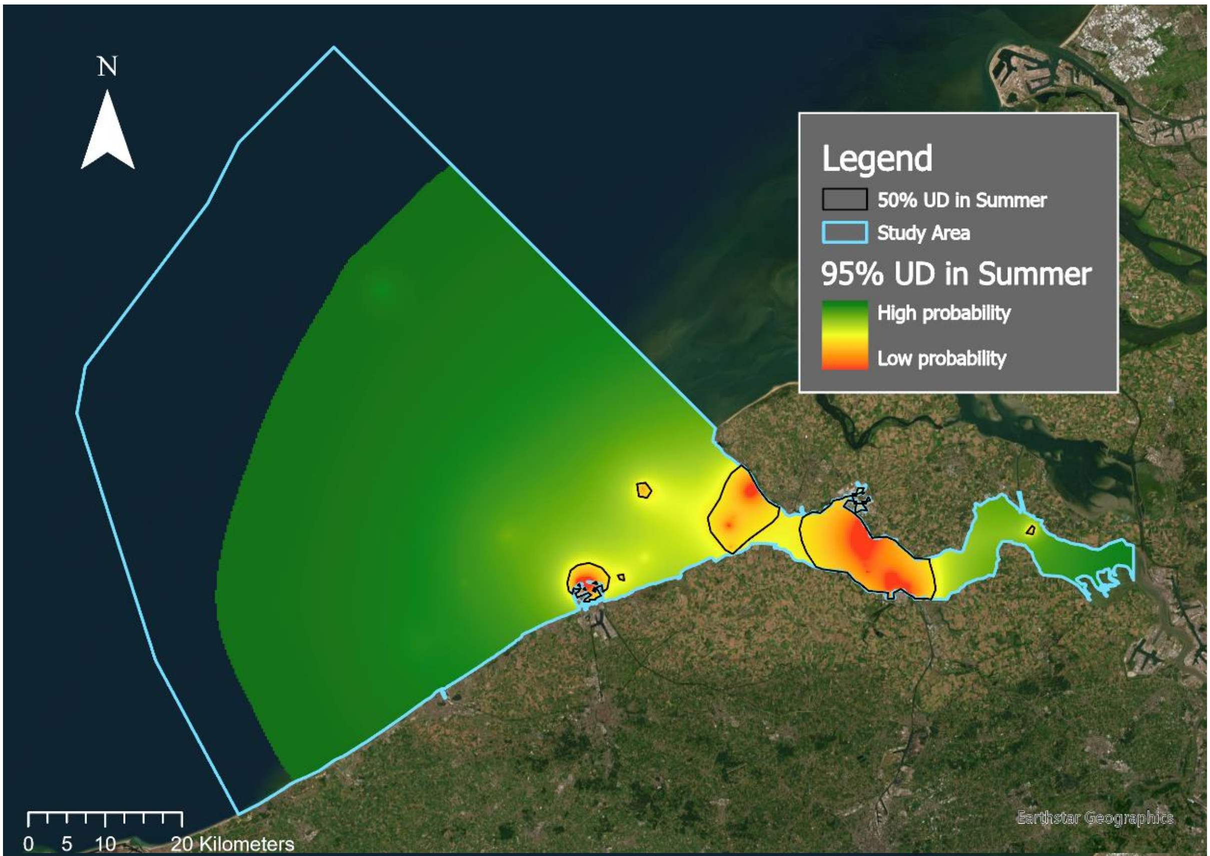
```
Animal_id_pk    Dd    Di    Dt        Iwr
   <fct>        <int> <dbl> <dbl>       <dbl>
 1 3218            29    47  1207 0.000936
 2 3219            13   320  1207 0.00286
 3 3220            21   291  1207 0.00419
 4 3221             8    42  1207 0.000231
 5 3222             5   167  1207 0.000573
 6 3223           122   343  1207 0.0287
 7 3224            84   282  1207 0.0163
 8 3225             1     0  1207 0
 9 3226            29   284  1207 0.00565
10 3227            29   257  1207 0.00512
11 3228            10   199  1207 0.00137
12 3229            15   208  1207 0.00214
13 3230             3    29  1207 0.0000597
14 3231             4    64  1207 0.000176
15 3233            58   334  1207 0.0133
16 3234             9   293  1207 0.00181
17 3235             2   190  1207 0.000261
18 3236            18    94  1207 0.00116
19 3237            31   279  1207 0.00594
20 3238            10    13  1207 0.0000892
21 3239             8    36  1207 0.000198
22 3240             9   125  1207 0.000772
23 3241            14   219  1207 0.00210
24 3244            27   245  1207 0.00454
25 3245             9   260  1207 0.00161
26 3246             2   159  1207 0.000218
27 5264            56   323  1207 0.0124
28 5265            51   260  1207 0.00910
29 5266            47   277  1207 0.00894
30 5267            11    72  1207 0.000544
31 5268             4     8  1207 0.0000220
32 5269             6    41  1207 0.000169
33 5271            11   217  1207 0.00164
34 5272            36   214  1207 0.00529
35 5273             9    46  1207 0.000284
36 5274            35   328  1207 0.00788
37 5275            25    45  1207 0.000772
38 5276             8    29  1207 0.000159
39 5277             1     0  1207 0
40 5279            37   345  1207 0.00876
41 5280            16   286  1207 0.00314
42 5281             8    49  1207 0.000269
43 5282            13   119  1207 0.00106
44 5283             5    18  1207 0.0000618
45 5284            65   327  1207 0.0146
46 5285            11    74  1207 0.000559
47 5286             3    73  1207 0.000150
48 5288            32   304  1207 0.00668
49 5289             1     0  1207 0
50 5290            37   282  1207 0.00716
51 5291             6   223  1207 0.000918
52 5292            35   274  1207 0.00658
53 5293            87   297  1207 0.0177
```

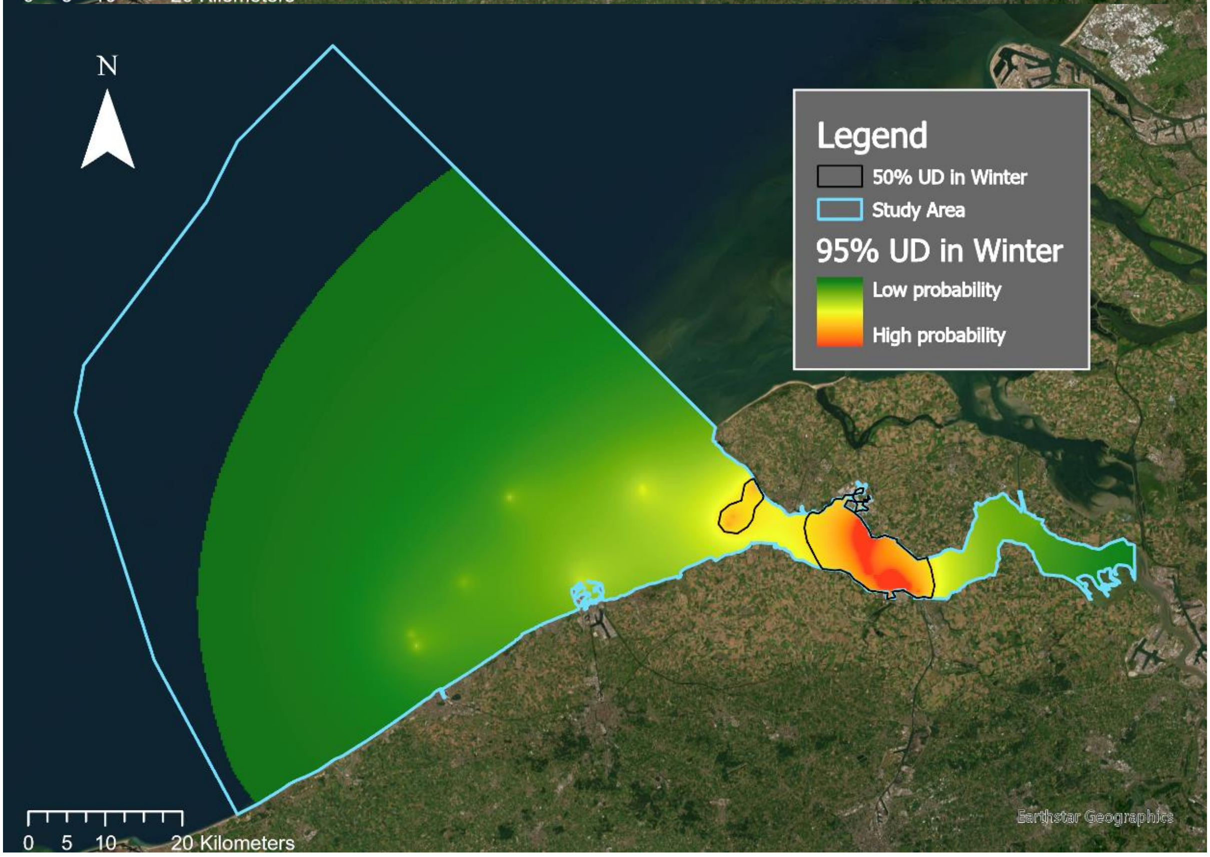
```
54 8650                 30   252  1207 0.00519
55 8651                  4     8  1207 0.0000220
56 8652                  2     1  1207 0.00000137
57 8653                 10    28  1207 0.000192
58 8654                  5    21  1207 0.0000721
59 8655                  3     2  1207 0.00000412
60 8656                  2     2  1207 0.00000275
61 8657                  7    90  1207 0.000432
62 8658                  4    89  1207 0.000244
63 8659                 13   397  1207 0.00354
64 8660                  4   124  1207 0.000340
65 8661                  2     1  1207 0.00000137
66 8662                 31   253  1207 0.00538
67 8663                 18   296  1207 0.00366
68 8664                 54   306  1207 0.0113
69 8665                 18   216  1207 0.00267
70 8666                 29   308  1207 0.00613
71 8667                  2     6  1207 0.00000824
72 8669                 14    62  1207 0.000596
73 8671                 11    54  1207 0.000408
74 8672                 95   286  1207 0.0186
75 8674                 75   120  1207 0.00618
76 8675                 15   177  1207 0.00182
77 8676                 65   256  1207 0.0114
78 8678                 43   369  1207 0.0109
79 8679                 36   258  1207 0.00638
```

Appendix 3: 95% and 50% utilisation distributions


N
Legend
50% UD Female
Study Area
95% UD Female
Low probability
High probability
0 5 10 20 Kilometers
Earthstar Geographics


N
Legend
50% UD Male
Study Area
95% UD Male
Low probability
High probability
0 5 10 20 Kilometers
Earthstar Geographics


N
Legend
50% UD in Summer
Study Area
95% UD in Summer
High probability
Low probability
0 5 10 20 Kilometers
Earthstar Geographics


N
Legend
50% UD in Winter
Study Area
95% UD in Winter
Low probability
High probability
0 5 10 20 Kilometers
Earthstar Geographics

Appendix 2: 50% UD area per animal

Animal	50% UD in square km
8679	15.46
8678	110.58
8676	6.76
8674	1.4
8672	2.3
8664	14.15
5293	4.53
5292	57.38
5290	0.82
5288	0.04
5284	75.24
5279	12.44
5274	1.31
5266	40.36
5265	16.39
5264	47
3233	11.98
3224	21.35
3223	53.38

Appendix 3: Literature reviews on HIS's and habitat selection functions:

Habitat suitability index (HSI)

Perhaps one of the most important question in fish habitat management is what exatly a fish habitat looks like. Or: how does the habitat support the species? The concept of habitat suitability adresses this capacity of a habitat to support a species population (Brownscombe et al., 2022). Knowing a species preference from ecological literature, a Habitat Suitibility Index (HSI) model can be developed. HSI modeling is a tool for developing maps and information upon which conservationists and environmental managers can bae decisions (Brown et al., 2011). By knowing which areas are potentially suited for a specific species, measures can be taken in order to conserve or protect this species. Brown et al. (2011) introduce a simple framework for the process of developing a HIS model (Figure 11). The process starts by selecting the species to be modelled, environmental variables upon which the models are run, and a modelling method. After that, the habitat affinities of the selected species are encoded (for each environmental variable: what are suitable ranges) and developing digital maps for each variable (in raster format). After this, the model can be run using a GI system. Running the model takes three steps. First, each environmental map should be reclassified to a suitability scale from 0 to 1, based on the established affinities. Then, the model calculation is run (in this case, the geometric mean of suitability scores is calculated). Lastly, the results of the model are mapped. After this, evaluation of the resulting map may lead to revision of the model. If this iterative process comes to an end, a final map can be generated and analyses can be conducted (Brown et al., 2011).

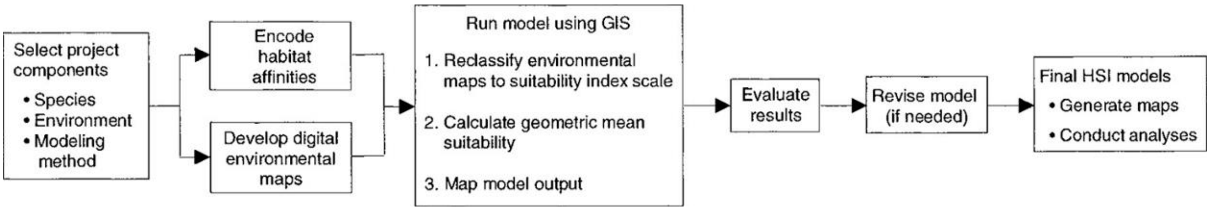


Figure 11: The process of HSI modelling (Brown et al., 2011)

Habitat-selection functions

Among the most widely used approaches for analyzing telemetry data are habitat-selection functions (HSFs). HSFs compare environmental attributes at locations visited by animals (used locations) to those at a set of locations considered available to the animals (available locations). This is generally done by using logistic and conditional logistic regression, respectively (Boyce & McDonald, 1999; Fortin et al., 2005; Thurfjell et al., 2014). These methods are widely available in most statistical software packages and offer a robust framework for examining habitat-selection patterns (Fieberg et al., 2021). HSFs help identify habitat features preferred or avoided by species, aiding in ecological inferences, distribution mapping, and demographic projections (Boyce & McDonald, 1999; Matthiopoulos et al., 2019).

Various arguments have been made to justify the use of logistic regression for use-availability data analysis, but a significant breaktrough was realised by Warton and Shepherd (2010). They made a connection between logistic regression and a spatial inhomogeneous Poisson point process (IPP). A spatial IPP is a model for random locations in space, where expected density of the loations deepends on spatial predictors (Fieberg et al., 2021). As the number of points is increased towards infinity, the slope parameters for logistic regression models converge to the slope parameters in an IPP model.

The IPP model provides a simple framework for modeling the density of points in space by using a loglinear function of spatial predictors through a spatially varying intensity function:

$\lambda(s) = \exp(\beta_0 + \beta_1 x_1(s) + ... + \beta_p x_p(s))$

In this function, s represents a location in geographical space, and $x_1(s), ..., x_p(s)$ are spatial predictors associated with location s. β_0 serves as the intercept, determining the log density of points within a small homogeneous area around s when all predictors are zero. $\beta_1, ..., \beta_p$ represent the slopes describing the effect of spatial covariates on the log density of points in space (Warton and Shepherd, 2010). The IPP model operates under three assumptions:

- The number of points in an area, denoted as N(A), follows a Poisson random variable with mean λ(A), which is the spatial integral of λ(s) over A.
- Locations are independent, so all clustering can be explained by spatial covariates.
- When all available spatial predictors are measured at a coarse scale (e.g. raster cells), fitting the IPP model is equivalent to fitting a Poisson regression model. In this case, the counts in discrete spatial units can be treated as a set of independent Poisson random variables.

When spatial predictors are available at the point level, it is desirable to model locations in continuous space. In telemetry studies, the density of points is determined by the frequency and duration of data collection. Therefore, the intercept term β_0 may not be of biological interest, and the focus may shift to estimating and interpreting the slope coefficients $\beta_1, ..., \beta_p$, which govern the relationships between spatial covariates and the relative density of locations across the study area.