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Habitat use, home-ranges and activity patterns of translocated European lobster *Homarus Gammarus* on artificial reefs as assessed by acoustic telemetry

On the functioning of the new artificial reefs of Ørsted in Borssele II

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With reviews on habitat requirements for European lobsters and their mobility

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Summary

Introduction
To meet the increasing need for renewable energy, the Dutch government has plans to use offshore wind farms (OWFs). With the resulting rapid upscaling of OWFs in the North Sea, there is increased stressors on nature and fisheries (with OWFs as closed areas for fisheries). Successful development and exploitation of OWFs require an integration that is inclusive of marine activities and foremost nature. Co-use is mentioned to meet these wishes and needs. Nature restoration projects are proposed as well as other types of co-use like passive fisheries with pots on crab and European lobster.

Artificial reefs and relevance for European lobster
In the Netherlands, artificial reefs are considered as an option for OWFs in their obligation to improve the marine biodiversity and thereby fortify the natural North Sea ecosystem. Artificial reefs could contribute in the restoration of formerly present hard substrates (like oyster banks and moreen deposits).

There is a need to improve knowledge on the use of artificial reefs in order to improve design and application. This includes: 1) gaining practical experience with nature enhancement options and 2) gain insight into the biodiversity development and functioning associated with such nature enhancement options. In that context, artificial pipe reef structures were deployed in the Dutch Borssele II OWF.

European lobster (*Homarus gammarus*, L) can be found on most hard substrates in the North Sea, like wrecks, anti-scouring, artificial reefs and (moreen) stone patches. They have a high site fidelity hiding in crevices. European lobster can be an important keystone species (i.e. acting as trophic system structurer) in local communities. With the deployment of artificial reefs, they are potentially an important species for the functioning of the food web, biomass and biodiversity. However, the use and relevance of such artificial structures by European lobster has not been investigated to date.

Passive fisheries
In addition to investigating the suitability of artificial reefs for European lobster, knowledge is needed on their behaviour and mobility in relation to catchability by baited pots and cages, i.e. for fisheries purpose. It is obligatory to place the baited pots and cages at considerable distances from hard substrate and crevices. The Dutch Ministerie van Binnenlandse Zaken defined a 250 m maintenance zone around monopile and anti-scouring. In order to evaluate the effectiveness of passive fisheries if animals inhabit the structures, it is essential to identify whether European lobsters have enough daily mobility to encounter bait scent at distances of ≥250 m. For example, a study on *H. gammarus* identified attraction distance of maximally 125m[1], which could warrant against effective passive fisheries because of the 250 m maintenance zone. Such findings need to be explored further for European lobsters in the context of an OWF and obligatory distances to relevant objects as anti-scouring.

Knowledge need
The goal of the study was to develop more knowledge on the behaviour and habitat utilisation of individual translocated European lobster at the artificial reefs. More specifically, individual home ranges, movement characteristics and seasonal and diel activity patterns were monitored at fine spatial and temporal scales. These were further investigated in relation to substrate, sex and size of the European lobsters. In relation to fisheries, this research describes the natural behaviour of translocated European lobsters but without any influence of bait to estimate catchability.

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[1]   Lees KJ, Mill AC, Skerritt DJ, Robertson PA, Fitzsimmons C (2018). Movement patterns of a commercially important, free-ranging marine invertebrate in the vicinity of a bait source. Animal Biotelemetry 6: 8 1-12
https://doi.org/10.1186/s40317-018-0152-4

Methods

The study consists of two parts:

- A literature review on habitat quality in relation to European lobster preferences and mobility (ranges of movement, habitat use and territories).
- An experiment at sea on translocated European lobster around artificial reefs in the Borssele II OWF. The monitoring consisted of short-term movements and space-utilization inferred using acoustic telemetry. European lobsters were tagged with acoustic transmitters and released at the artificial reefs. Individual behaviour was tracked using a 200m grid network with 16 acoustic telemetry receivers. The monitoring took place with 2 batches of 12 animals each carried out in 2021 and 2022.

Results

The review showed that the European lobster is a large, long-lived decapod crustacean of ecological and commercial importance, distributed from the north of Norway to Morocco in North Africa. Longevity potentially spans several decades. The species is considered a nocturnal animal, where light hours are generally spent solitary inside shelters on rocky bottoms. European lobsters rarely move more than a few kilometres. Instead, they have a territory around their shelters which they know thoroughly. Territories were found between 1,728 m^2 and 173,053 m^2. The daily mobility ranged from 75 m to 477 m.

The at sea monitoring exemplified only a small proportion of tagged European lobster attracted to the artificial reefs. Residency to these new hard substrate structures was also limited. Most individuals moved out of the study area quickly after release, or after moving around in the study area. After a period of 51 days all European lobsters had left the receiver arena. Results show difficulties of the animals to settle in the area. The factors for this low attachment could not be fully identified. Potential explanatory factors could be: the effect of animal translocation (as a result of strong homing sense), lack of food on the young reefs or lack of suitable crevices.

The territories estimated (i.e. home range area) ranged from 102 to 254 m^2. This was smaller than encountered in other studies.

In addition to area utilization, behavioural patterns were estimated using Hidden Markov Models (HMM). In total, five behavioural states were estimated. Three behavioural states were defined with the help of a spatial HMM using position data: locally inactive (indicative of resting), locally active (indicative of foraging behaviour), transit (travelling and exploring across the monitoring area). A non-spatial HMM was used to infer the behavioural state of hiding in the artificial structures and being on the rim of the measurement arena.

The artificial reefs deployed in the Borsele OWF offered the animals the opportunity to hide in the concrete pipes. This hiding behaviour was identified with a dedicated non spatial HMM. It revealed that the animals residing in the area for extended periods of time exemplified extended hiding in the structures.

Correlations were made of type of behavioural state with current speed, hour of the day and temperature. Due to the limited amount of European lobsters settled, the resulting limited amount of data and the individualistic behaviour of European lobsters, no general correlation could be established.

An important aspect of the data set presented here is the large inter-individual variation in behaviour and area utilization. This heterogeneity limited the replication (e.g. in home range of hiding) and in turn the statistical significance of part of the results presented here.

In a next approach it is recommended to attempt the catch of local European lobsters first, which are likely to exemplify stronger residency. In addition, adding additional reef units with smaller crevices could also be beneficial.

1 Introduction

To meet the increasing need for renewable energy the Dutch government has plans to use offshore wind farms (OWFs). With the resulting rapid upscaling of OWFs on the North Sea, pressures are mounting on other users, such as nature and fisheries. Successful growth of development and exploitation requires integration in the environment, in terms of ecology and in relation to other users. Co-use is mentioned to meet these wishes and needs. Nature restoration projects are proposed as well as other types of co-use like passive fisheries with pots on crab and European lobster (Ministry of Binnenlandse Zaken, 2020)

1.1 Artificial reefs to enhance nature restoration

Artificial reefs[2] are used for coastal management purposes in many countries and regions across the world, and are thought to have developed in parallel in a variety of locations. They can be considered as interventions of engineering technology to recover and/or improve the natural habitats, increase productivity and coastal defence (London Convention and Protocol/UNEP, 2009, FAO, 2015, DeGraer et al., 2020). In the Netherlands, artificial reefs are considered as an option for OWFs in their obligation to improve the marine biodiversity and thereby fortify the natural North Sea Ecosystem (Hermans et al., 2020, Glarou et al., 2020). The general idea is that artificial reefs have a contribution in the restauration of formerly present hard substrates that have been lost (like oyster banks and moreen deposits) (Olsen et al., 1883, Kardinaal, 2020).

There is a need to improve knowledge on these type of interventions in order to improve design and application, in particular 1) gain practical experience with nature enhancement options (i.e. recently deployed artificial pipe reef structures in Borssele II, *Figure 1-1*) in Dutch OWFs and 2) gain insight into the biodiversity development and functioning associated with such nature enhancement options (Kardinaal & Didderen, 2020).

1.2 European lobster as example species

European lobster (*Homarus gammarus*, L) (and also various species of crab) can be found on most hard substrates in the North Sea, like wrecks, anti-scouring, artificial reefs and (morene) stone patches (Krone & Schröder, 2011, Bouwma et al., 2012, Skerrit et al., 2015, Rozemeijer & van de Wolfshaar, 2019). They have the potential to significantly impact a local ecosystem such as (artificial) reefs as they require large amounts of food. This large intake is due to their relatively large, voluminous tail and high energy density of the cells. Lobsters are calculated to be able to down regulate a benthos community to low levels of standing stock of benthos (within the assumptions of the modelling, Rozemeijer & Van de Wolfshaar, 2019).

It is likely that crabs and lobsters will migrate to the artificial reefs in OWF Borssele II. The extent to which lobsters can migrate is limited but this can be increased by tidal currents (passive migration, Rozemeijer & Van de Wolfshaar, 2019). Given their potential impact on the hard substrate benthos by predation, European lobsters can be an important key note species (trophic system structurer) in local communities. Therefore it is eminent more information is needed on functioning in and impact on the food web, biomass and biodiversity of the artificial reefs.

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[2]   An artificial reef is a submerged (or partly exposed to tides) structure deliberately placed on the seabed to mimic some functions of a natural reef, such as protecting, regenerating, concentrating and/or enhancing populations of living marine resources. This includes the protection and regeneration of habitats. It will serve as habitat that functions as part of the natural ecosystem while doing 'no harm'. (FAO, 2015)

Habitat, behaviour and movement are key determinants of animal distribution, and in turn local abundances and local impacts (Geraldi et al. 2009, Skerrit et al., 2015). Understanding the movement, distribution and activity pattern of lobsters can be linked to predation pressure. This is vital to understand how the biodiversity and biomass of benthos on artificial reefs will develop. However, this type of information is scarce in literature with a clear knowledge gap. van der Meeren, (1997), Smith et al. (1998), Picciulin et al. (2003, 2005), Moland et al. (2011a,b, 2019), Wiig et al. (2019), Skerrit at al. (2015) and Lees et al. (2018, 2020) were the first working on detailed European lobster movement. This study has the ambition to extend this knowledge.

In general lobsters are considered nocturnal and cannot physically regulate their body temperature; therefore, warmer temperatures and periods of darkness are thought to produce greatest movements (Smith et al., 1998, Skerrit et al., 2015). Previous analyses using capture-mark-recapture (CMR) have provided limited movement data that suggest *H. gammarus* has restricted movements; <3 km for periods of up to a year (Thorbjørnsen et al., 2018, Rozemeijer & van de Wolfshaar, 2019). *H. gammarus* are generally believed to make short movements away from shelter, which could be prompted by local competition for food, shelter and mates. Only a small number of individuals have been observed to travel up to 45 km in a season (Smith et al., 2001). Furthermore, movements and distributions are largely influenced by the spatial distribution of hard substrates, interpreted, by positions of capture and recaptures (Skerrit et al., 2015, Rozemeijer & Van de Wolfshaar, 2019). Therefore lobsters can be expected to forage locally in order to retrieve their entire nutritional need (Thorbjørnsen et al., 2018, Skerrit et al. 2015).

1.2.1 Behaviour in relation to fisheries

In addition knowledge is needed on the behaviour and mobility of European lobsters in relation to catchability by baited pots and cages. Lobsters primarily identify and navigate towards potential sources of food using their highly developed olfactory system (Derby & Atema, 1982, Atema & Voigt, 1995). The cages will need to be placed at, for a European lobster, considerable distances from hard substrate and crevices. The Dutch Ministry of Home Affairs (Ministerie van Binnenlandse Zaken) (2020) defined a 250m safety zone around monopile and anti-scouring. Some studies investigating behaviour of *Homarus spp.* in relation to bait sources have been undertaken in aquariums or mesocosms (Derby & Atema, 1981, Moore et al., 1991). Bell et al. (2011) calculated different radii of rapid declining influence with a maximum radius of 100m (as used by Skerrit, 2014). Lees et al. (2018) studied behaviour of free-ranging *H. gammarus* in the field in relation to bait sources demonstrating no clear overall change in movement or behaviour between pre-trap period as compared to the post trap period. As a first step to estimate catchability, this research describes the natural behaviour of translocated European lobsters, not influenced by bait.
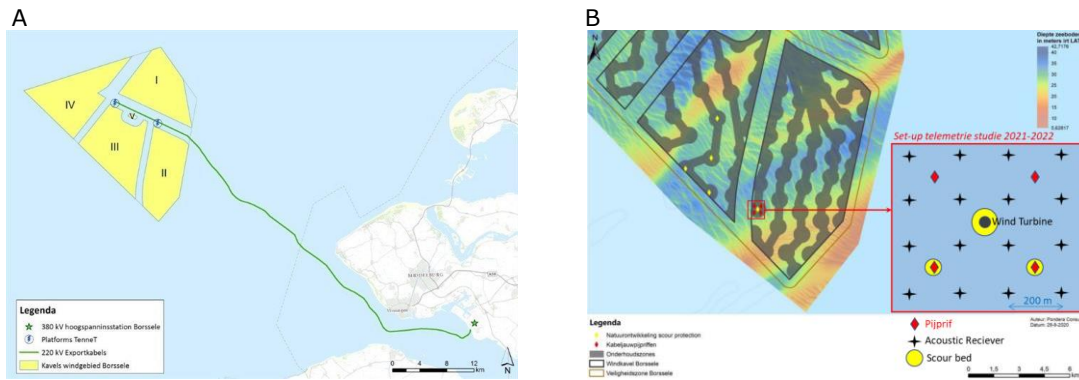
Figure 1-1

A location of OWF Borssele II. with site I and site II that were built and are operated by Ørsted.

B Bathymetry of the Borssele II Area with the positions of the artificial reefs (red diamonds) and antenna's (black crosses). Artificial reefs were positioned around monopile L08. The red diamonds depict the location of the artificial reefs where the study took place. Yellow circles represent anti-scouring. Grey bands: demarcation of monopiles and infield cables.

1.3 Goal and methods

1.3.1 Goal and research questions

The goal of the study was to develop more knowledge on the behaviour and habitat utilisation of individual translocated European lobster (*H. gammarus*) at artificial reefs. Specifically to quantify individual home ranges, movement characteristics and seasonal and diel activity patterns, and relate these to substrate, sex and size of the lobsters.

Research questions:
  (1) What are the ranges of movement, habitat use and territories of European lobster? What does this imply for fisheries with pots at 250m from the preferred habitat?
  (2) How do the hard substrate of artificial reef and the anti-scouring protection of the reefs and wind turbine influence European lobster home-ranges and movements?
  (3) How do sex and size of the animals influence space-utilization and movement distances?
  (4) How do seasons and diel cycles influence movement and space-use?

1.3.2 Methods

A literature review on habitat quality in relation to European lobster preferences and mobility (ranges of movement, habitat use and territories) was carried out.

The short-term movements and space-utilization of freely moving *H. gammarus* were explored in their natural habitat using a VEMCO Positioning System (VPS). Lobsters were tagged with acoustic transmitters and released in OWF Borssele II, in an area around one monopile where four artificial reefs were placed. Individual behaviour was tracked using a 200m grid network with acoustic telemetry receivers. This allows one to track movement and behaviour of individual lobsters for extended time periods.

2 Autecology of European lobster

Given their potential impact on the hard substrate benthos, European lobsters have a high trophic level (between 3.7 and 4.1, Mavraki, et al., 2020, Jurrius & Rozemeijer, 2022). They have the potency to be an important key species (trophic system structurer) in local communities (Jurrius & Rozemeijer, 2022). By studying the behaviour of European lobster in an offshore wind farm (OWF) setting with four artificial reefs, lessons on habitat demands of the lobster can be learned as well as on ecological functioning of an OWF with added structures for biodiversity. Aspects which could influence habitat criteria for a species can include life cycle traits such as development phase, food or nutritional needs, and needs for shelter or socialisation.

Preferred lobster burrows have outcrops and hollows, which are dependent on the size of the lobster. The lobster will often excavate its burrow underneath boulders and stones (Dybern, 1973). This makes adult *H. gammarus* prefer hard substrate biotopes for shelter and a suitable burrow (Krone & Schröder, 2011). However, soft sediment nearby can be used as food- or nursery-grounds (Rozemeijer & van de Wolfshaar, 2019). This makes locations at the boundary between soft and hard sediments especially suited (Galparsoro et al, 2019).

2.1 Distribution and abiotic requirements

H. Gammarus are found between 0 and 150 m depth but usually not deeper than 50 m on the continental shelf, see **Figure 2-1**. They prefer current speeds of 0.6 m/s or lower. If current speed gets higher than that they can get carried away (Howard, 1980a, Howard & Nunny, 1983). According to Galparsoro et al. (2009), the most suitable habitat is coincident with seafloor depressions with a steep slope, with medium to high wave energy conditions (0.3-0.6 kW h m^{-1}), and located within a range of water depths of 35–40 m. *H. gammarus* can be found in fully marine waters but can also inhabit low saline coastal waters of only 10 PSU (Linnane et al., 2000). Desirable levels for key water quality parameters such as oxygen, pH and ammonia can be found in Table 1.
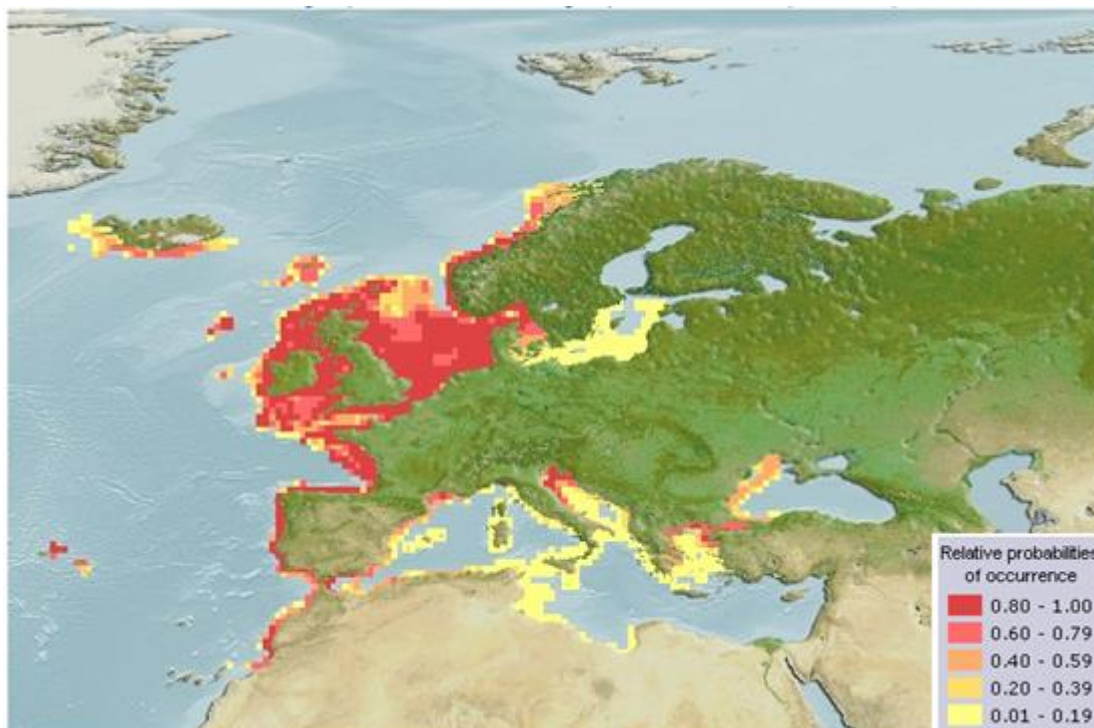
Figure 2-1. *Habitat distribution map for H. gammarus. Note: Distribution range colours indicate degree of suitability of habitat which can be interpreted as probabilities of occurrence. AquaMaps (2019, October). Computer generated distribution maps for Homarus gammarus (European lobster), with modelled year 2050 native range map based on IPCC RCP8.5 emissions scenario. Retrieved from https://www.aquamaps.org.*

Table 2-1 *Desirable levels for key water quality parameters for Homarus sp., from Rozemeijer & van de Wolfshaar, 2019.*

Desirable levels for key water quality parameters for Homarus sp. (van Olst et al. 1980 (*H. americanus*) and Wickins & Lee 2002, (*H. gammarus*)), Table compiled by Kristiansen et al. (2004). Data from Oosterschelde lobster from Wolf and Sandee (1971) and Schuiling and Smaal (1998). The bold figure here is claimed to be the optimum.				Natural ranges in which *H. gammarus* is encountered (https://eol.org/pages/46505673 d.d 27-09-2022)	
Parameter	**Optimal condition**	**Natural range**	**Lethal condition**	**Parameter**	**Encountered range**
Temperature (°C)	18-22	1-25	<0, >31	Temperature (°C)	8.214 - 12.243
Salinity (‰)	28-35	28-35	<8, >45	Salinity (‰)	33.5-35.6
Salinity (‰) Lobsters Oosterschelde	21-**27**-32	9-35		O2 (mg l^{-1})	5.4-6.7
O2 (mg l^{-1})	6.4	4-8.2	<1, >saturation	Depth range	0-165
pH	8	7.8-8.2	<5, >9	Nitrate (µmol l^{-1})	2.7-8.5
Ammonia (mg l^{-1})	<0.14	0-0.3	>1.4	Phosphate (µmol l^{-1})	0.32-0.63
				Silicate (µmol l^{-1})	1.9-4.5

2.2 Life history

The average life-span of male *H. gammarus* in the wild is 31 years (maximum 42 years ± 5 years) and for females on average 54 years and maximally 72 years (± 9 years, Sheehy et al., 1999). During its life history, the European lobster undergoes several stages of development, starting as pelagic larvae, growing into scavenging juveniles and finally into predatory adults. Two distinct phases are discussed: the pelagic and benthic phase.

2.2.1 Pelagic phase

Female lobsters carry eggs for up to twelve months. Hatching of *H. gammarus* is primarily controlled by temperature. Eggs hatch in a period of a few days up to a few weeks. Hatching occurs at night, with temperatures in the range of 5-15°C. The larva is capable of vertical movement through the water column (Cobb, 1993) to feed on zooplankton near the surface (Beard & McGregor, 2004). After approximately three moults taking 15 to 35 days the larvae moult to the fourth, post-larval or megalopa stage. *H. gammarus* is able to propel itself both vertically and horizontally by the use of pleopods. This enables the larvae to move and find a suitable habitat. Transition to the early benthic phase is now made. In the post-larval stage the larva takes a similar form to its adult stage (Cobb, 1993).

2.2.2 Benthic phase

In the post-larval stage the *H. gammarus* settles onto the benthic habitat. Swimming and moving behaviour is replaced by burrowing and sheltering behaviour once a suitable habitat has been found. Preferred habitats in this stage appear to be cobbles, boulders and stone piles with plenty of crevices to burrow in. Further growth is achieved by moulting and the adult will become more mobile with size (Cobb, 1993). With each subsequent moult stage the calcification of their integument is increased (Hinchcliffe et al., 2021) and carapace length is on average increased with 7 mm each moult stage (Agnatt et al., 2007). The lobster is sexually reproductive after 5-8 years (Sheehy et al., 1999). Maturity is reached with a carapace length between 80-140mm (Hinchcliffe et al., 2021).

2.3 Sediment and shelter

H. Gammarus prefer hard substrate such as hard mud or rock and are found mostly in close vicinity to rocky substrates and boulder fields, living in holes or crevices (Holthuis, 1991; Krone & Schröder, 2011; Beard & McGregor, 2004), with the exception of the pelagic larvae stages. The dependency on shelter lowers as the lobster ages, as predation will be less of an issue, however even adult lobsters will keep a preference for hard substrate. They can shape their own burrow between hard substrate and soft bottom but do not dig their own burrows in pure soft bottoms, making them dependent on biotopes with hard substrate (Krone & Schröder, 2011). This makes pre-adult and adult lobsters reef-obligate species, selecting living sites which supply enough shelter from currents and predation, sufficient oxygen and food. Soft substrates can be used as food- or nursery-grounds (Rozemeijer & van de Wolfshaar, 2019). According to a modelling study by Galparsoro et al. (2009) on habitat suitability of *H. Gammarus* along the Basque coast, the most suitable habitat are locations lying at the boundary between sedimentary and rocky bottoms. Adult European lobsters are territorial and do not travel far from their burrow, however in juvenile stage they may shelter communally (Cobb & Phillips, 2012). As dependency on shelter lowers during the lifetime of the lobster, in cobble patches smaller lobsters are usually more common in the middle whereas large individuals are more common around the edges (Skerrit, 2014). As the lobster ages and grows, they will need to move to increasingly larger burrows. The burrow itself needs to fulfil several criteria which influence suitability such as oxygen supply, length, entrance size, presence of multi-openings (escape routes) and internal aspect ratio (manoeuvring space) (Rozemeijer & van de Wolfshaar, 2019).

Lobster shelters can be present in natural formations such as crevices in natural rock, boulders or scree formations, but lobsters can also occupy man-made structures such as shipwrecks, harbour

walls or artificial reefs (Jensen et al., 2000, Krone & Schröder, 2011, Krone et al., 2015). This opportunistic approach gives *H. gammarus* the opportunity to inhabit larger parts of the North Sea where sand-and mud-dominated habitats (**Figure 2-2**), are alternated with often occurring harbour shipwrecks or other man-made structures (**Figure 2-3**). These man-made structures might serve both as permanent habitat for lobster, but also as stepping stones to connect hard substrate habitats (Krone & Schröder, 2011). Density of lobsters is not yet well studied and reported densities vary greatly in literature, depending on location and local conditions.
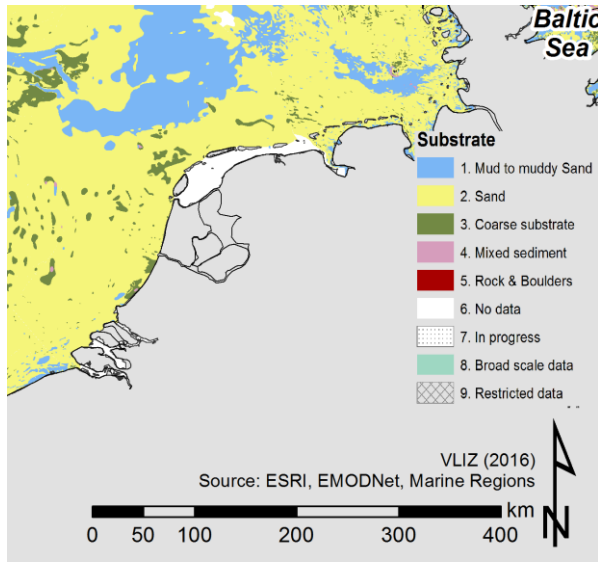

Figure 2-2. *Seabed substrate. Figure adapted from EMODnet and Marineregions (VLIZ, 2016)*
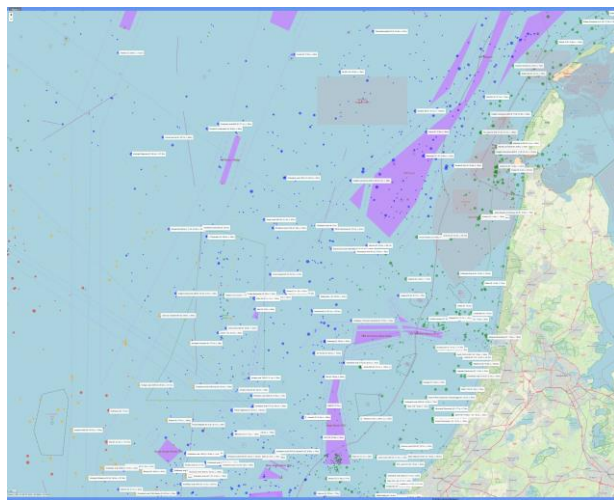

Figure 2-3. *Wreck map North Sea west of Netherlands. Each blue dot represents a man-made structure or wreck*

2.4 Diet

H. gammarus appears to be omnivorous (for overview see Jurrius & Rozemeijer, 2022). The diet varies between individuals, but in general they forage, prey and scavenge. Stomach analyses of adult *H. gammarus* have shown presence of a wide range of crustaceans, molluscs, worms, starfish and fish (Beard & McGregor, 2004). A stomach content study by Hallbäck & Warén (1972) on *H. gammarus* during summer found that the most important prey groups were malacostraca (60.6%), gastropods (36.6%), polychaete worms (23.1%), and unspecified diet items (18.9%), while there were a few occurrences of unspecified fish, calcareous pieces, bivalves, echinoderms, and algae. Smaller lobsters were found to prefer polychaete worms among smaller malacostraca and gastropods. A DNA-based method was used by Leiknes (2023) to describe the diet of adult *H. gammarus*. Cnidarians (hydrozoans and 'true jellyfish'), fish, and tunicates were the important prey items for adult *H. gammarus*. Other important taxa were echinoderms, crustaceans, and green plants (Streptophytina). Compared to the DNA study of Leiknes (2023) past studies might have neglected or largely underestimated soft-bodied organism presence in the lobster diet. Further, the study found that *H. gammarus* sex had no effect on the observed diet composition which suggests that males and females have similar foraging strategies.

Diet composition is mostly independent of European lobster size (Leiknes, 2023). This is contrary to findings on *H. americanus* (Sainte-Marie & Chabot, 2002). They showed smaller sized lobsters dominantly foraged for food that is considered to be easily acquirable, such as animal tissue, (juvenile) bivalves, macroalgae, meiobenthic crustaceans and foraminifera's. Larger lobsters fed more on mobile prey usually of higher nutritious value, incl. heavy shelled crayfish and fish. The contrast could reflect species differences between *H. Gammarus* and *H. americanus* or local differences in food availability or difference in methodologies of assessing diet composition (tissue analysis versus DNA analysis). Compared to the DNA study of Leiknes (2023) past studies might have neglected or largely underestimated soft-bodied organism presence in the lobster diet.

The encountered diets differ substantially, most likely they reflect the combination of local ecology (=food availability) and individual preferences (see Rozemeijer & Van de Wolfshaar, 2019, Jurrius & Rozemeijer, 2022 for an overview).

Under normal circumstances, a healthy adult lobster can survive without food for several weeks to a few months. The cells have a high energy density, and they have a large flesh tail, both serving as reserves. Larger lobsters tend to have more energy reserves and can go longer without feeding compared to smaller ones (Rozemeijer & Van de Wolfshaar, 2019). European lobsters can endure months without food, by lowering their metabolism (Albalat et al., 2019).

2.5 Predators and competition

Predation on hatchery-reared lobsters (*H. gammarus*) in the wild was studied by Van der Meeren et al. (2020) to identify predators in southwestern Norway on rocky and sandy substrates in winter and summer conditions. Approximately 51,000 juvenile lobsters (carapace length 12-15 mm) were released at three locations on 10 occasions during both summer and winter. In summer, loss to predators occurred on both rocky and sandy substrates. The risk of fish predation was highest in the first hours after release, when the lobsters were out of shelter. The genus *Labrus* (wrasses) were the major predators of lobsters during summer, while Atlantic cod (*Gadus morhua*), shorthorn sculpin (*Myoxocephalus scorpius*), and crab (*Cancer pagurus*) were the main predators during winter. During summer predators were more abundant than during winter. To minimise predatory loss o lobsters, the recommendation is to release lobsters onto rocky substratum in winter or early spring to avoid predation due to the summer-active Labridae (Van der Meeren, 2000). Lobster mortality could also be due to temperature-enhanced lobster activity during summer, resulting in reduced shelter use and in creased predator exposure (van der Meeren, 1993) as higher temperatures induced prolonged interactions in naive artificially reared *H. gammarus*. Hughes et al (1972) showed that the *H. gammarus* need for food is increased with higher temperatures up to a certain point.

Especially male European lobsters are highly competitive. Food quantity, availability and nutritional variety, mating and availability of suitable crevices are causes for this competition (Jensen et al., 2000, Lees et a., 2020)[3]. Females can have overlapping territories (Skerrit et al., 2015, Lees et al., 2020). This is alike American lobsters (Karnofsky & Price, 1989, Atema & Voigt, 1995).

2.6 Shelter composition

2.6.1 Crevices

In situations where rocks rest on a soft substrate, there is a limit to the burrow size a lobster can create before the rock becomes unstable. Larger shelters may be necessary to accommodate bigger lobsters effectively. The distribution of crevices varies based on the size of the rocks, affecting the available shelter sizes. Howard (1980b) hypothesised that the mean size composition of some lobster populations could be increased by providing larger shelters. In response to the hypothesis of Howard, Steneck (2006) showed that larger American lobsters choose shelter and habitats with a lower population density compared to smaller American lobsters (demographic diffusion). Steneck concludes that there is a lower proportion of large lobsters at high population densities and aggression to surrounding lobsters leads to a high shelter vacancy, especially in high population densities. Relative frequency of habitats for *H. gammarus* along the Swedish west coast on a scale from 0 (very low) to 5 (very high) shows that most habitats are located at a mixed bottom seabed in natural hollows under boulders and stones (4) and in excavated burrows under boulders and stones (4-5). When looking in more detail to mixed bottom excavated burrows under boulders or stones, a few similarities between burrows appear. For example, the main opening of the burrow is often facing the downslope direction, possibly so the lobster can use its burrow as a lookout, as lobsters have a habit to dwell half inside and half outside their burrow main entrance during the day (Dybern, 1973). In literature and aquarium tests it was found that there are often burrows with multiple openings. The ratio between burrows with one opening and burrows with more than one opening have been reported to be 2:1 for American lobster (Cobb, 1971) and up to 4:1 for European lobster (Dybern, 1973).

2.6.1.1 Artificial reefs

H. gammarus were tracked on an artificial reef in Poole Bay on the south coast of England. The reef consists of eight piles of blocks (0.4 x 0.2 x 0.2) made of concrete or cement-stabilised pulverised fuel-ash (Collins et al. 1991, Jensen et al., 1994). The piles were 5 m in diameter and 1.5 m high, and were arranged in two rows of four; they occupied an area of sedimentary seabed 15 m x 35 m at a mean water depth of 12 m. During the day, most lobsters were detected predominantly on a particular reef unit (not necessarily the same unit for each individual), with small numbers of records for other units. The majority of movements were between the mainly inhabited unit and an adjacent unit, and were predominantly nocturnal, peaking 1.5 -3 h after sunset and returning to low movement before dawn (Jensen et al., 1994, Smith, 1998).

One of the earlier studies on the role of artificial reefs for American lobster is by Scarratt et al. (1968) where an area of 2740m[2] was seeded with rocks to monitor development of flora, fauna and especially lobsters. It was shown that average size of American lobsters was larger than on productive American lobster grounds nearby, however American lobster biomass after 2 years was less compared to natural American lobster grounds. The rocks deployed ranged from 5 to 100 cm in diameter and were up to 15 cm high.

Reef design should provide a range of crevice sizes in order to maximize provision of lobster habitat in artificial reefs and minimize the need for recently moulted lobsters to leave a reef in search of new shelter (Jensen et al., 2000).

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[3] Homarus gammarus (European lobster) | CABI Compendium (cabidigitallibrary.org)

3 Review on mobility, habitat use and territories

3.1 General aspects of mobility

Mobility of European lobster can be divided in daily activities and more migratory movements. European lobsters are sedentary animals with migration ranges varying from 0 to 3.8 km and a rare 45 km (Smith et al., 2001). They prefer to remain at the locations where they have settled and do not move more than 3.5 km during their life span in general (Smith et al., 2001). In term of long term movement and migration, Bannister et al. (1994) observed most recaptures of tagged lobsters within 6 km of known release positions. Only a small number of larger individuals have been observed to travel up to 16 km in a season (Jensen et al., 1994) or even up to 45 km (Smith et al., 2001), presumably finding new territories .On a daily basis *H. gammarus* seems to make short random movements away from shelter with a range of at least 1000 m (Skerrit et al., 2015, Lees et al., 2018), which could be influenced by local competition for food, shelter and mating.

3.1.1   Locomotion types

Locomotion of European lobster predominantly consists of walking on the seafloor. They are also capable of fast propulsion using their telson, but cannot maintain this momentum, relying on walking for sustained movements. In one case European lobsters walked with a maximum speed of 3-5 m min^{-1} (Picciulin et al., 2003). Lees et al (2018) even measured a maximum speed as high as 15.6 m min^{-1} for an individual and averages of 0.24 to 1 m min^{-1}. E.g. *H. americanus* typically walks in five minute bouts; with a mean walking speed of 0.9 m min^{-1}, increasing to 2.5 m min^{-1} (Skerrit, 2014). Skerrit et al. (2015) measured average walking speeds between 0.15 m min^{-1} on hard substrate with large turning angles to 4.2 m min^{-1} on soft substrates with more unidirectional movement. The behaviour on hard substrate seems to reflect either the difficulties of dealing with this substrate or feeding or searching behaviour. The higher, unidirectional speed seems to reflect the need of traversing distance or to evade predation (Martin et al., 2009, Skerrit et al., 2015).

Propulsion using their telson is used to flee stressful circumstances like conflicts with other lobsters or to escape predators. Typical distances for this propulsion are 10-15 m (Cooper & Uzmann, 1980, Karnofsky et al., 1989a, Altema et al., 1998).

3.2 Tidal currents

Tidal currents determine the time available for *H. gammarus* to wander and forage. *H. gammarus* adolescents (50-mm CL) act normally in current speeds of 5 cm/sec, but as currents increase to 10–15 cm/sec, walking is impaired and control over antennae is lost. With currents of 21–43 cm/sec, some lobsters slip downstream, while others remain standing still (Dow, 1998). Smaller lobsters seem to have a larger tidal window with *H. gammarus* of ±5 cm CL (15 cm TL) are dragged away by the currents with a speed of ~49-54 cm/s (Howard & Nunny, 1983, Howard, 1988). Maximum Dutch tidal currents are ~150 cm/s, around Borssele OWF area velocities up to 100 cm/s are expected (Cleveringa et al., 2012). Howard & Nunny (1983) estimate velocities between 53-203 cm/s in this area, the higher numbers when more shoreward.

Howard (1988) observed European lobsters in the wild mostly one hour before and after slack tide, further underlining the limitation by tidal currents. For this reason Howard & Nunny (1983) and Howard (1988) suggested the need to take cover against currents is a limiting habitat factor and that

therefore the larger European lobsters are also restricted to bolder and crevice rich areas to have that shelter against currents.

3.3 Daily and seasonal rhythm

European lobsters are mostly active during night time. The emphasis of their action is just before or after dusk and just before and after dawn although daytime activity also occurs (Cooper &. Uzmann, 1980, Van der Meeren, 1997, Walter et al., 1998, Moland et al., 2011a). Skerrit et al. (2015) demonstrated a nightly active, daytime passive rhythm in spring and a more even rhythm in autumn.

Cooper &. Uzmann (1980), Smith et al. (1999, 2000) and Moland et al (2011a) mentioned a high activity pattern in summer and a low activity pattern in winter (probably governed by temperature). Moland et al. (2011a) showed that lobster activity levels declined from September, reaching a minimum during February and March. From April, activity levels resumed. Seasonal variation in activity was correlated to water temperature. Skerrit et al. (2015) demonstrated European lobsters were more active during spring (driven by temperature) than during autumn (probably governed by prey availability and amount of light: shorter days).

3.4 Daily mobility

The daily mobility can be measured with acoustic tags (take e.g. Skerrit et al., 2015, Lees et al., 2018, Moland et al., 2019) or scuba diving (Karnofsky et al., 1989a,b), yielding a direct image of the tracts taken by individual lobsters. Indirect results are obtained by catch-mark-recapture results of e.g. flee tag studies (Bannister et al., 1994, Skerrit, 2014, Thorbjørnsen et al, 2018 Kjerulf Petersen et al., 2022) or V-notching of the tail or other means of external marking (Skerrit, 2014). Also laboratory results can yield some insights in mobility (Walter et al., 1998).

3.4.1 Direct measurements

In the laboratory juvenile European lobsters (30 mm CL) walked a maximum of 28m hr^{-1} during night time and 6.3m hr^{-1} during day time (Walter et al., 1998). Lees et al. (2018) investigated free-ranging *H. gammarus* behaviour and movement in relation to baited commercial traps. The bird eye's view distance at which lobsters began approaching a trap varied considerably: 5.40 m to 125 m. The actual distances covered while wandering could be much larger. E.g. animal F in Figure 3-1 covers approximately 1 km (1,04) walking from sub-territory to sub-territory. Figure 3-1 shows more of these larger daily dynamics of single walks.

Skerrit et al., (2015) measured a daily cumulative step-length of maximally 482 m distance and minimally 86 m in spring and daily cumulative step-length of maximally 608 m distance and minimally 57 m in autumn.

Moland et al. (2019) calculated a daily cumulative step-length of maximally 5860m distance and minimally 217 m in September and an average 1272 m per day for male lobsters.

Concluding, daily movements can range to accumulated distances of 5.8 km daily and at least 1 km for a trip. The average daily movement can be approximated from the recapture experiments and the size of the territories.
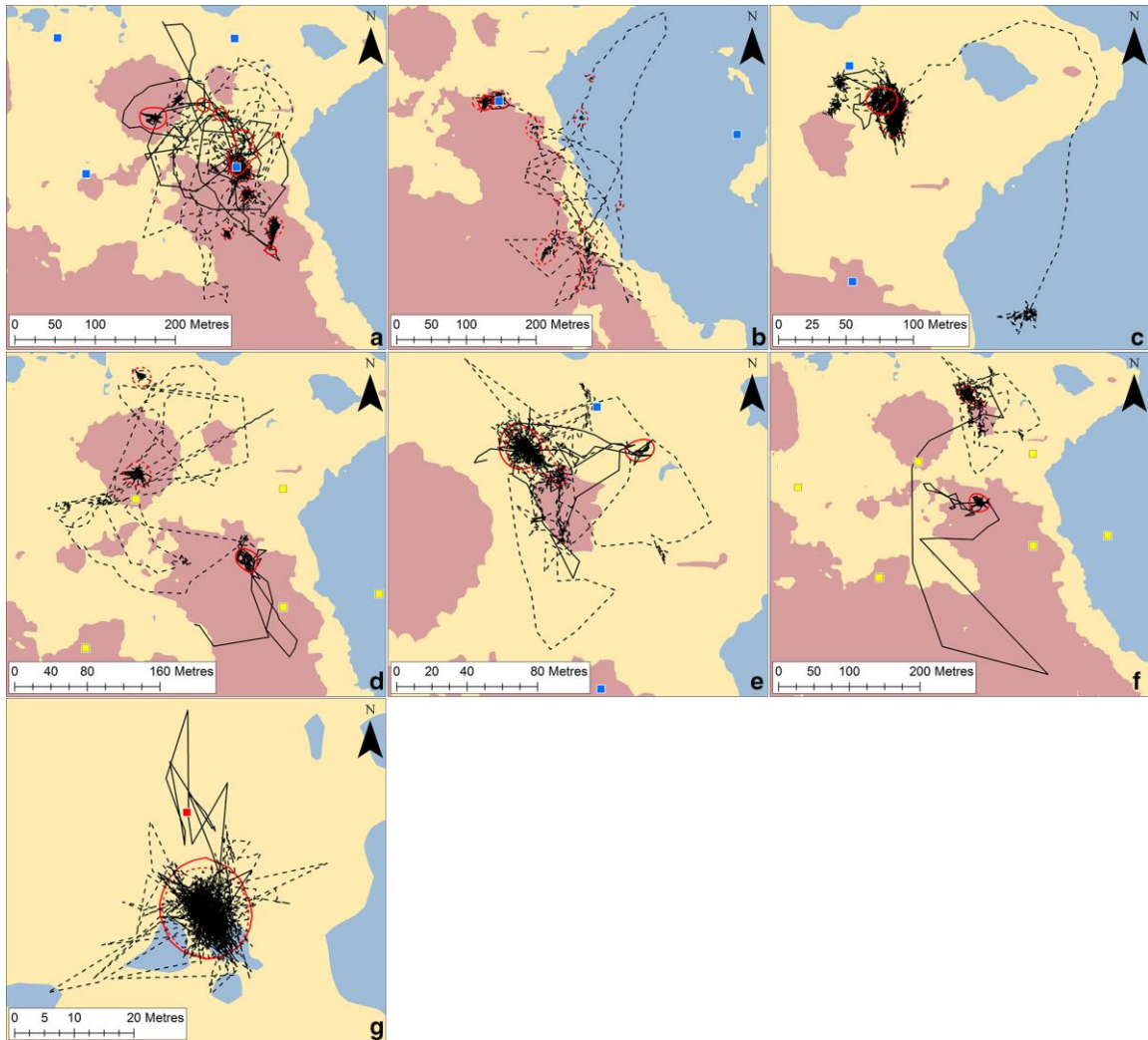
Figure 3-1. *Movement in the absence and presence of traps. a Lobster 28179, b lobster 28187, c lobster 28189, d lobster 28192, e lobster 56815 deployment 2, f lobster 56815 deployment 3, g lobster 56816. Pre-trap trajectories = black dashed line, post-trap trajectories = solid line, pre-trap 50% utilisation distribution = red dashed line, and post-trap 50% utilisation distribution = red solid line. Coloured squares represent traps deployed at the time of approach (Fig. from Lees et al., 2018, Hard substrate = red, mixed substrate = yellow, soft substrate = blue).*

3.4.2 Indirect measurements

Through indirect measurements the long-term dispersal can be investigated. These will depend on the individual lobsters, the sampling period and the characteristics of the local area.

Smith et al. (2001) tagged European lobsters for almost 3 years and released them on their home grounds (near Bournemouth, south coast of England). The 95% group of recaptured lobsters moved <3.8 km from their original release positions over periods of up to 862 days. Average distances ranged from 0.8 km to 1.4 km for the three areas. The distance of the 5% leaving the area tended to increase gradually with time at liberty. Maximum distance from release site was 45 km and an average of 1.5 km. Bannister et al. (1994) found that most recaptures occurred within six kilometres of known release positions (with a maximum of 2 years of dispersal) (see also **Table 3-2**). In other reared lobster release projects most lobster remained within the 5 km and migrated maximally 20 km (Jensen et al., 2000).

Thorbjørnsen et al. (2018) tagged European lobsters in three areas for 8 years. Each area had a Marine Protected Area (MPA) and a fishing ground part. The median distance moved by lobsters inside MPAs was 75 m, with distances ranging from 4 to 1535 m. Migrating lobsters originating from MPAs had a median movement distance of 1037 m (range: 35−24670 m). Inside fishing grounds, the median distance moved by lobsters was 93 m (range: 1−1311 m) (**Figure 3-2**). Migrating lobsters originating from control areas had a median movement distance of 1047 m (range: 34−16690 m).
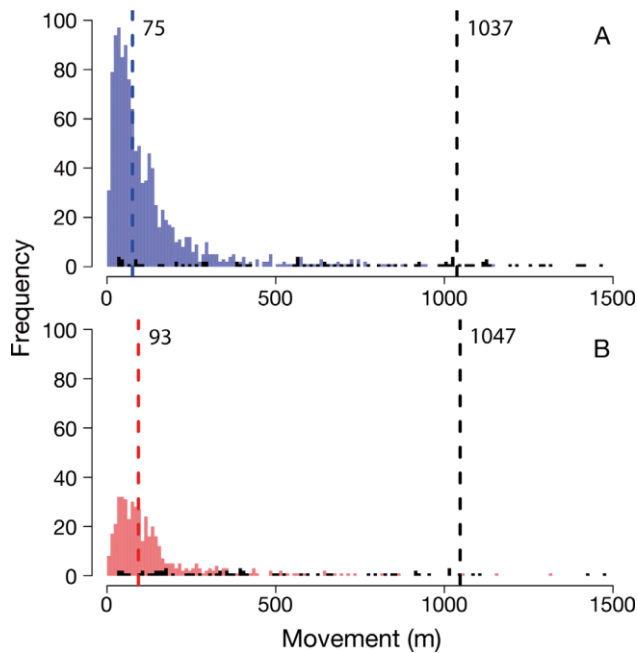
Figure 3-2 *Extent of movement undertaken by European lobsters tagged in (A) marine protected areas (blue) and (B) control areas (red) recaptured during the monitoring fishing, and (A,B) those recovered and reported by fishers (black). Only movement observations of <1500 m are shown. Vertical lines denote median distance moved for the different groups (Thorbjørnsen et al., 2018).*

3.5 Territories

The size of a lobster territory is depending on the size, sex and personal characteristics of the European lobster. Also the characteristics of the habitat itself can be of influence, e.g. availability of suitable crevices and of food sources (species, distribution, amounts) and season (temperature, light) (Cooper & Uzmann, 1980, Skerrit et al., 2015, Moland et al., 2011b, 2019, Wiig et al., 2013). The experimental set-up can be of influence in the assessment of territory size. Moland et al., (2011b) showed that at least 98 and 259 days, respectively, were necessary to reach 50% and 95% of minimum convex polygon home range area. The total study lasted 354 days. However, each study. The home-range estimates were based on manual tracking in which a single position was obtained per individual during daytime every 5 days. Daytime is a period when lobsters are less active so also the home range could be less. Most studies determining home ranges last much shorter.

Moland et al. (2019) analysed home ranges (utilisation distribution, UD) with a surface of 22,733−638,216 m^2 for lobsters in Norway (**Table 3-1**). The average territory was 173,053 m^2 (± 125,887 m^2) The home range size correlated in this case with month of the year (temperature regulated activity). Territories can overlap or be separated from each other (
Figure 3-3). They can be in one coherent piece or exists of several sub territories (Wiig et al., 2013, Skerrit et al., 2015. Moland et al., 2011b, 2019, Lees et al., 2018, 2020). E.g. the elongated light blue territory in
Figure 3-3b has a length of ~ 1.2 km and a width of 0.3 km. The light pink territory in
Figure 3-3b stretches at the longest distance 1 km from edge to edge (bird eye view)

Skerrit et al. (2015) measured a seasonal variation: European lobster had a 95% UD ranging from 244 to 7,722 m^2 during spring with a mean of 11,104 ± 397 m^2). The 95%UD declined to 237−784 m2 during autumn (mean ± SE: 455 ± 66 m^2).

Thatcher et al. (2023) determined home ranges from 9,313.76 to 23,156.48 m^2 (95% kernel densities) while core territories ranged from 1,084.05 to 6,037.38 m^2 (50% kernel densities) for European lobster in an offshore wind farm (OWF).

Figure 3-3 *September UD95 home ranges for European lobster harvested (a and c) and surviving (b and d) the 2011 (a−b) and 2012 (c−d) fishing seasons (1 October−30 November) estimated from acoustic monitoring. For illustration purposes, a randomly selected subset of 10 home-range estimates from the harvested individuals included in the analyses (n = 55) are shown in each of panel (a) and (c), while home ranges for all survivors (n = 17) are included in (b) and (d). Pyramids are capture and release locations of individuals shown in corresponding color. Red asterisks (a−b) mark the cumulative GPS locations of all lobster traps deployed in the study area during the 2011 fishing season (Moland et al., 2019).*
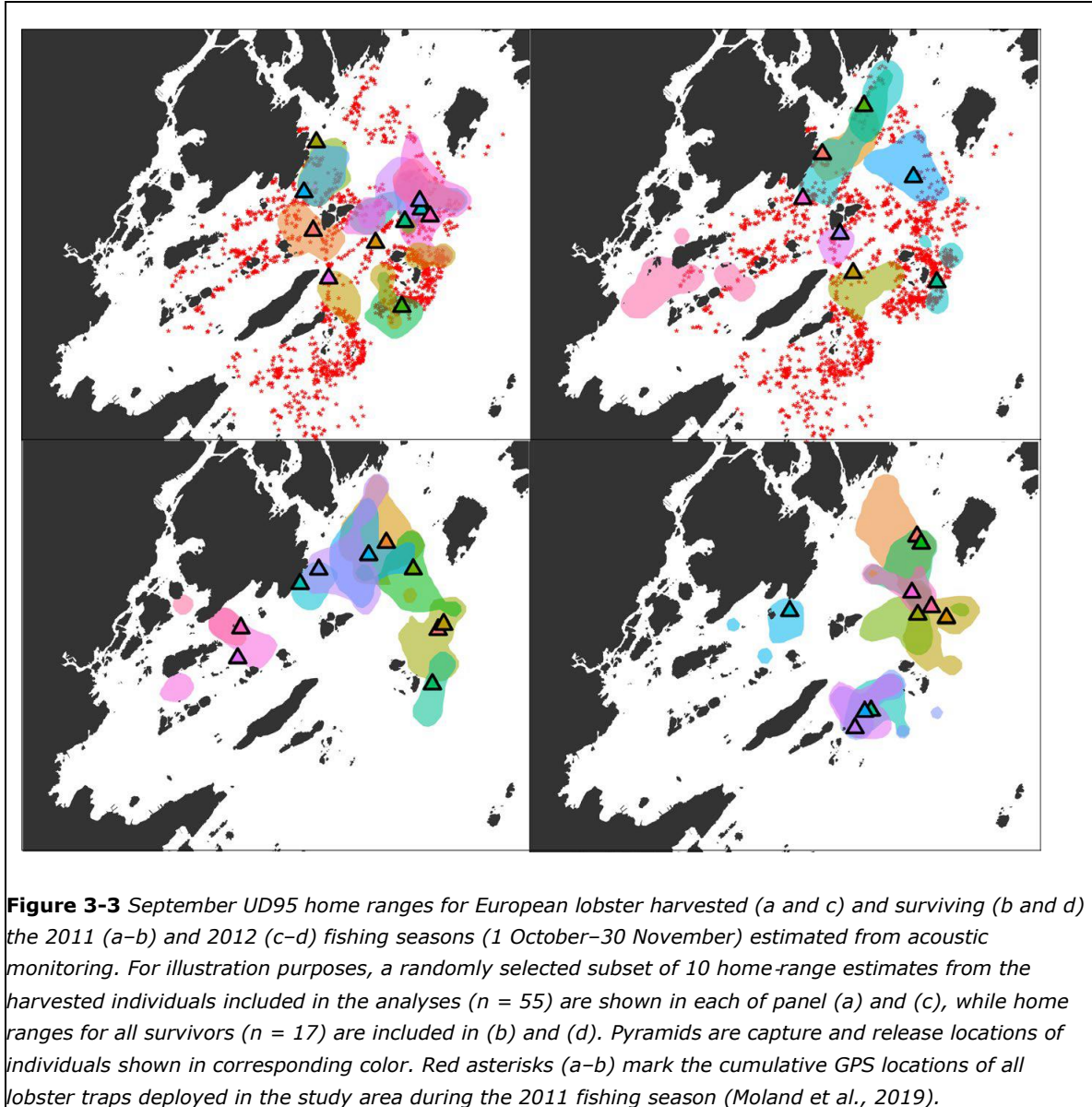
Table 3-1 *The home ranges (95% utilisation distribution, UD95) for the lobsters that had a period of residence. The results of Figure **4-9** were averaged for the two reefs having anti-scouring and the two reefs without anti-scouring, directly with sandy sediments surrounded. Data are given for minimum and maximum UD95, the average with Standard Deviation (StDev) and Standard Error (SE). Other others were added for comparison. In order to get more feeling on the significance of the areas, the areas were assumed a quadrant and the length of the side of the quadrant was calculated by calculating the square root of the area. Comparison with the other authors was discussed in Section 5.3*

Reference	Substrate	Minimum	Maximum	Average	StDev	S.E.	N	Remark	length of the side of an assumed quadrant (Sqrt, m)
Moland et al. (2011a)	Varied hard substrate, soft sediment, eel grass beds, and kelp forest	5728	41548	19879	2152		19	During day time	141
Skerrit et al. (2015)	mixed hard and soft substrate; large rocky-reef	244	7722	11104		397	37	Spring	105
		237	784	455		66	10	Autumn	21
Wiig et al. (2013)	Varied hard substrate, soft sediment, eel grass beds, and kelp forest	43129	641731	170660	125519		37	2011 males	413
Moland et al. (2019)	Varied hard substrate, soft sediment, eel grass beds, and kelp forest. Same area as Wiig et al. (2013)	22733	638216	173053	125887		72	2011, 2012 Males 2011 data same as Wiig et al. (2013)	416
Lees et al. (2020)	mixed hard and soft substrate; large rocky-reef	834	5336	2068		371	Females		45
		991	30033	6547		1759	Males		81
Thatcher et al. (2023)	gravel and sand sediment, anti-scouring in an Offshore Windpark	9314	23156	15240		980	33		123
This study	Artificial reef and sandy sediments	433	4203	1524	817	102	11	Continuous	39

This study	Artificial reef and Anti-scouring	719	3607	1849	760	211	5	Continuous	43
This study	Monopile and Anti-scouring	731	3259	2009	949	254	3	Continuous	45
This study	Receiver and sandy sediments	555	6327	1728	1098	143	9	Continuous	42
This study	Unknown, sandy sediments	1792	9189	5394	3702	2138	2	Continuous	73

3.6 Larger scale migration

The distances of larger scale migration is described partially in section 3.4.2. In general most European lobsters will stick to their home grounds. In general the animals that do migrate tend to be larger, older, male and also with large crusher claws (Skerrit et al., 2015, Thorbjørnsen et al., 2018, Moland et al., 2019). Though females also migrate, especially older females (Agnatt et al., 2007), Smith et al. (2001) noticed that average migration distances were still small (1.4 to 1.5 km), and only 5 % of the population tended to migrate. Skerrit et al (2015) saw two of the twelve tagged lobsters migrate out of the measuring area (17%). Thorbjørnsen et al. (2018) measured 4% of the European lobster population at a median movement distance of 1 km from the original site of first catch (indicating migration). Kjerulf Petersen et al. (2022) measured significant spill-over of lobsters from the MPA to surrounding areas . Lobsters moved several hundred meters to over 1,000 m within a few days to a few weeks. The extremes of distances measured away from point of first capture were up to 45 km, but most showed no large scale movement beyond their home grounds (**Table 3-2**).

Despite this tendency not to migrate, a new artificial reef in the UK nearby Bournemouth, 500 m from the rocky shore, was occupied by European lobster (and brown crab, *Cancer pagurus*) from the surroundings (soft seabed or nearby coast) but also from further away within three weeks, while having hardly any epibiotic colonization (Jensen et al., 1994, 2000). The availability of a wide range of crevice sizes may be part of reason of attraction or residence.

In our review we found it difficult to distinguish between long-term migration and a lobsters' home range. Home ranges vary significantly between studies (Moland et al. 2011, Skerritt et al. 2015, and **Table 3-1**) especially taking into account the various home range size when longer monitoring of lobsters' home range is conducted. Thorbjørnsen et al. (2018)stated that most registered movements had time intervals of one year or more; hence short-term monitoring might not give the full data on possible migration or home range. Large distances from first point of capture are indications at best as full migration is difficult to assess. In this review we have not found a defined study about full scientifically significant migration of lobsters. Difficulties in monitoring, catching and the abovementioned home range differences make this a possible hiatus in scientific knowledge.

Table 3-2 *Overview of data on lobster migration after tagging on home grounds or released from a hatchery.*

Reference	Country	Location	region	Type of Area	Origin	CL	TL	Maximum range Homebound population (km)	% homebound of total population	Average range homebound (km)	Maximum distance (km)	Average distance migration (km)	% population migrating	n	year
Bannister et al., 1994	UK	Bridlington Bay	East Coast England	Fishing grounds	Hatchery		15 stage XII juveniles	6						49000	1983-1992
Jensen et al., 1994	UK	Poole Bay	South Coast England	Fishing grounds	Homeground			>0.01	88	0.005	16	6.1	12	114	1990-1992
Smith et al. (2001)	UK	Poole Bay	South Coast England	Fishing grounds	Homeground	50-85		3.8	95	0.8	45	1.5		1954	1990-1993
Smith et al. (2001)	UK	Christchurch Ledge	South Coast England	Fishing grounds	Homeground	55-85		3.8	95	1.4	45	1.5		999	1990-1993
Smith et al. (2001)	UK	Swanage Bay	South Coast England	Fishing grounds	Homeground	60-85		3.8	95	1.4	45	1.5		272	1990-1993
Jensen et al., 2000	UK	Aberystwyth	Wales	Fishing grounds	Hatchery			5			20				1983-1988
Thorbjørnsen ea (2018)	Norway	Bolærne	South coast	MPA	Homeground		24.2-27.5								2006-2014
Thorbjørnsen ea (2018)	Norway	Bolærne	South coast	Fishing grounds	Homeground		22.4-25.3								2006-2014
Thorbjørnsen ea (2018)	Norway	Flødevigen	South coast	MPA	Homeground		24.1-28.4								2006-2014
Thorbjørnsen ea (2018)	Norway	Flødevigen	South coast	Fishing grounds	Homeground		24.0-25.6								2006-2014
Thorbjørnsen ea (2018)	Norway	Kvernskjær	South coast	MPA	Homeground		23.2-27.4								2006-2014
Thorbjørnsen ea (2018)	Norway	Kvernskjær	South coast	Fishing grounds	Homeground		22.8-25.1								2006-2014
Thorbjørnsen ea (2018)	Norway		South coast	MPA	Homeground		23.2-27.4	1.5		0.075	24.7	1		4682	2006-2014
Thorbjørnsen ea (2018)	Norway		South coast	Fishing grounds	Homeground		22.8-25.1	1.3		0.093	16.7	1		3317	2006-2014

Kjerulf Petersen et al. (2022)	Denmark	Limfjorden	Inland north of Denmark	MPA reef. Research measurement	Homeground						0.053	0.306				2021
Kjerulf Petersen et al. (2022)	Denmark	Limfjorden	Inland north of Denmark	MPA non reef. Research measurement	Homeground						0.061	0.476				2021
Kjerulf Petersen et al. (2022)	Denmark	Limfjorden	Inland north of Denmark	Non-MPA:Fishing ground. Research measurement	Homeground						0.172	0.343				2021
Kjerulf Petersen et al. (2022)	Denmark	Limfjorden	Inland north of Denmark	MPA reef. Fisher measurement	Homeground						0.579	1391				2021
Kjerulf Petersen et al. (2022)	Denmark	Limfjorden	Inland north of Denmark	MPA non reef. Fisher measurement	Homeground						0.594	1586				2021
Kjerulf Petersen et al. (2022)	Denmark	Limfjorden	Inland north of Denmark	Non-MPA:Fishing ground. Fisher measurement	Homeground						0.361	1477				2021

3.7 Role in the food web

H. gammarus ascends the food chain as it develops from opportunistic larva, to a scavenging juvenile, to an active predator as adult. As an adult they eat hydrozoans, scyphozoans ('true jellyfish'), fish, tunicates, echinoderms, and crustaceans, gastropods, and polychaetes, with mussels and starfish comprising a minor portion of the diet (Cooper & Uzmann, 1980, Leiknes, 2023, section 2.4). *H. gammarus* can reach a trophic level of 4.1 (Mavraki et al., 2020). They have a high energy content and need a lot of food to grow. In addition, due to this high energy content and the large tail they have ample reserves to withstand periods with low food availability (Rozemeijer & van de Wolfshaar, 2019). Although the larvae and early benthic settlers of *H. gammarus* are quite vulnerable to predation, adult *H. gammarus* is not a target for predators accept for top predators like seals. If happening at all, Atlantic cod, wolf fish, goosefish, and several species of shark can and do consume lobsters up to about 100 mm CL, but the magnitude of predation by these relatively large animals is considered minimal (Cooper & Uzmann, 1980, Moland et al. 2019).

H. gammarus has a high position in the food web (**Figure 3-4**). Jurrius & Rozemeijer (2022) suggested a trophic level ranging between 2.8 and 3.9 comparable to edible crab (North Sea crab, *Cancer pagarus*). Mavraki et al. (2020) suggested European lobster to have a higher position than edible crab. It is suggested that *H. gammarus* inhabits top-down control on the benthic ecosystem by predation and is controlled bottom-up by food availability (Rozemeijer & van de Wolfshaar, 2019). Most likely it will predate on the mid-level predators. As a result, there is a possibility that the trophic layer predated by those mid-level predators, benthic invertebrates, will have higher biomass and maybe a higher biodiversity.
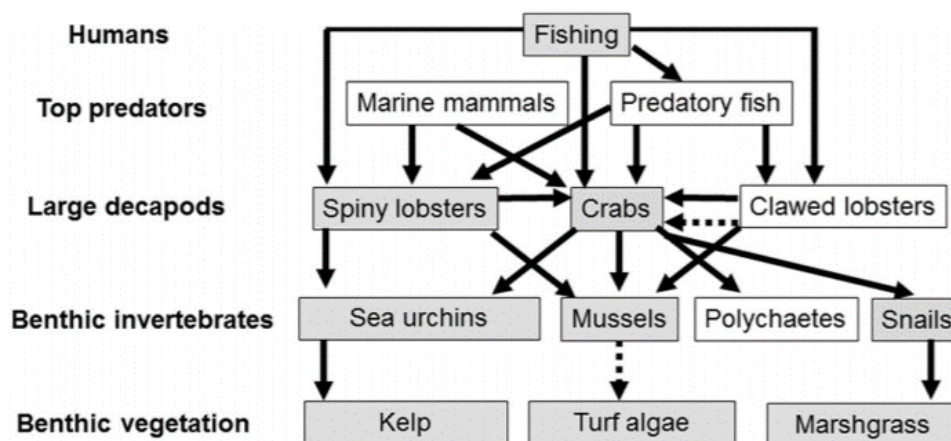

Figure 3-4 *Simplified scheme of ecosystem interactions of large decapod species. Dotted arrows indicate competitive interactions, while solid arrows indicated predation. Note: cannibalism is not displayed, yet occurs for both crabs and lobsters. The species in grey have strong implications in trophic cascades (Boudreau & Worm, 2012).*

3.8 Catchability

H. gammarus can be attracted to baited static traps, commonly together with *Cancer pagurus* (passive fisheries). Lobsters primarily identify and navigate towards potential sources of food using their highly developed olfactory system. Still, despite the continuous diffusing scent of the bait, lobsters as near as 20 m do not react to the scent. Nb the radius of the area of influence of the bait plume is also quit small (≤11 m, McQuin et al. 1988, Watson et al, 2009). There was no clear overall change in movement or behaviour of the European lobster between the pre-trap period compared to the period

with static traps (Lees et al., 2018). Still it is also true that more mobile animals like large, socially dominating males are more readily caught than domicile lobsters presumably because they make more explorative trips (Moland et al., 2019, Skerrit et al., 2015).

4 At sea experiment in wind farm Borssele

4.1 Materials and Methods

4.1.1 Study area and acoustic telemetry network

The study took place between 25th February 2021 and 30th January 2023 in the Borssele II wind farm zone, located along the Dutch coast (Figure 4-1(a)). The distance between monopiles in the Borssele OWF is roughly 1 km (Figure 4-1(a), black dots). The study site was limited to an area where four artificial reefs were deployed around a single monopile between 1st and 17th July 2020 (Figure 4-1(a) and (b)). The water depth at the study site was ~30 m. The four reefs were all placed at ~280 m from the monopile in NW, NE, SE, and NW direction (Figure 4-1(c), R01-R04). Each individual reef deployed was of the same design, i.e. same dimensions and pipe sizes used for construction. The reefs are each made of 21 pipes of 0.5 m diameter, 12 pipes of 1 m diameter and 12 pipes with 1.5 m diameter. The two most southern reefs also include an anti-scouring bed of 20 m diameter, similar to the monopile (Figure 4-1(c), L08). This hard substrate is a rock pad with a top-/footprint radius of 12.5/14.5 m and a layer thickness of 0.7 to 1.2 m.

To investigate the presence and track the movement of European lobster around the monopile and the artificial reefs, acoustic telemetry was used, using a grid of acoustic receivers (Innovasea VR2AR) and deploying lobsters with acoustic tags with pressure and acceleration sensors (InnovaSea V13P), which allows for detailed 3D tracking and fine scale behavioural assessment of tagged lobsters that are present within the study arena (Lennox *et al.*, 2023). The acoustic receivers were mounted on customised frames with the receiver placed on top of a 1.5 m tall stainless-steel tripod (weighing 80 kg) (Goossens *et al.*, 2020). A total of 16 sets were deployed (Figure 4-1(c)), to enable fine scale positioning at each of the four artificial reefs and around the monopile in the centre of the arena. The acoustic receivers were first deployed on 25th February 2021, retrieved, and redeployed on 13th April 2022 and finally retrieved on 30th January 2023. During retrieval operations, 5 acoustic receivers were lost. For the interim retrieval of receivers on 13th April 2022, 14 receivers were retrieved and 13 were redeployed. For the final retrieval on 30th January 2023, 11 receivers were retrieved. The loss of acoustic receivers reduced the acoustic network of each data set as shown in Figure 4-1(c). The coverage was particularly reduced with the 2022 network in the southwestern corner of the study area where reef R03 is located. However, the fine grid of acoustic receivers allowed a satisfactory coverage despite these losses.

Environmental data were collected from a weather station through the entire monitoring period. The weather station was located 17.7 km away from the study area (Figure 4-1(a)). A range of environmental data were recorded and the one of interest here are temperature and current speed (Figure 4-2).
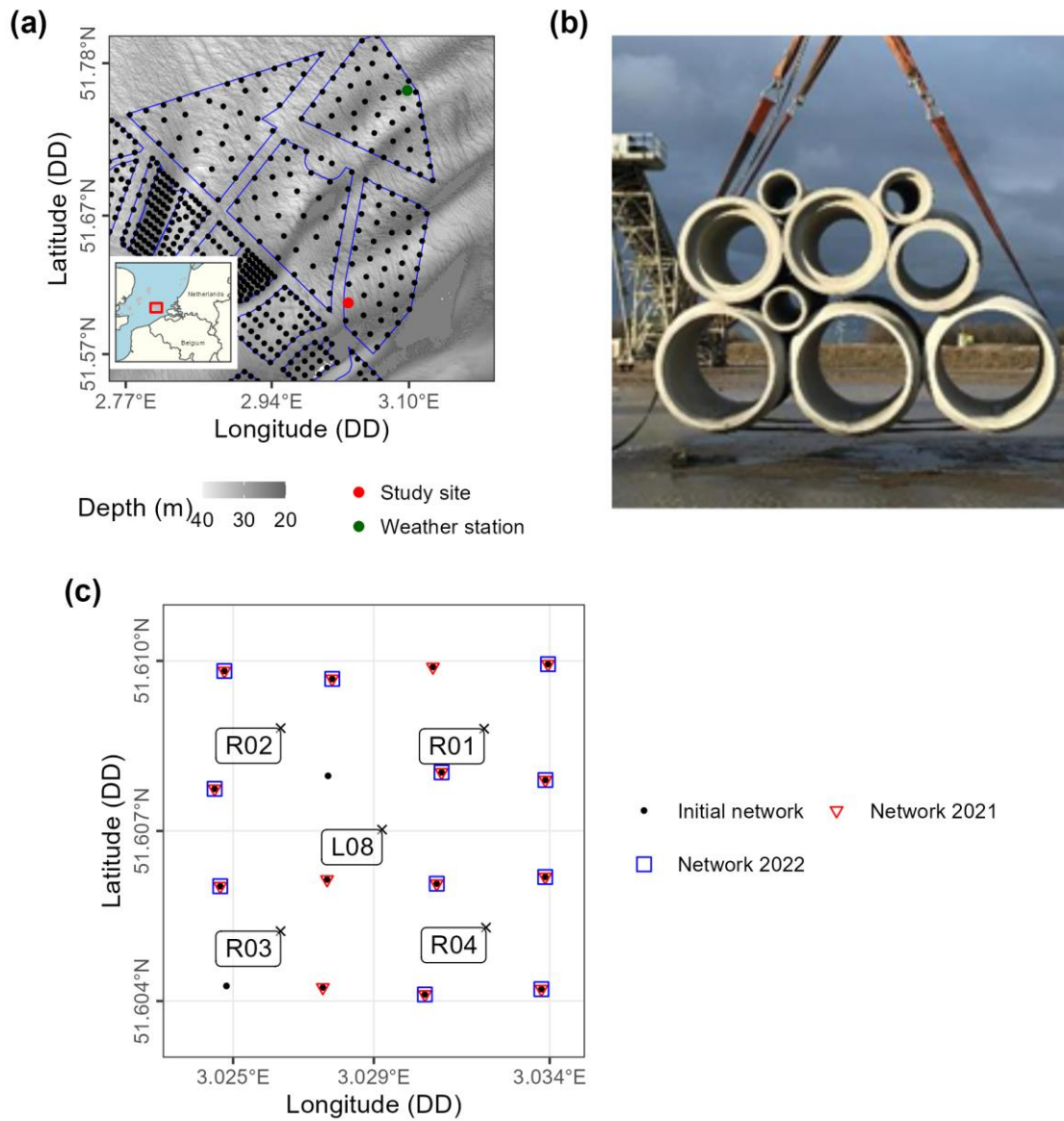
Figure 4-1: *Study setup. (a): Overview of the study area (red rectangle). The monitoring took place around a single monopile in the Borssele offshore wind farm in Dutch waters. (b): Photograph of the concrete pipes deployed on the seabed as artificial reefs. (c): Acoustic telemetry network and surrounding structures. Because of the loss of equipment, the two data sets considered in this study had altered coverage (red downward triangles and open blue rectangles).*

Figure 4-2: *environmental data. (a) temperature profile with green and blue lines representing the periods over which the monitoring took place. (b) Current speed profiles over the 2021 and 2022 monitoring periods.*

4.1.2 Animal tagging and release

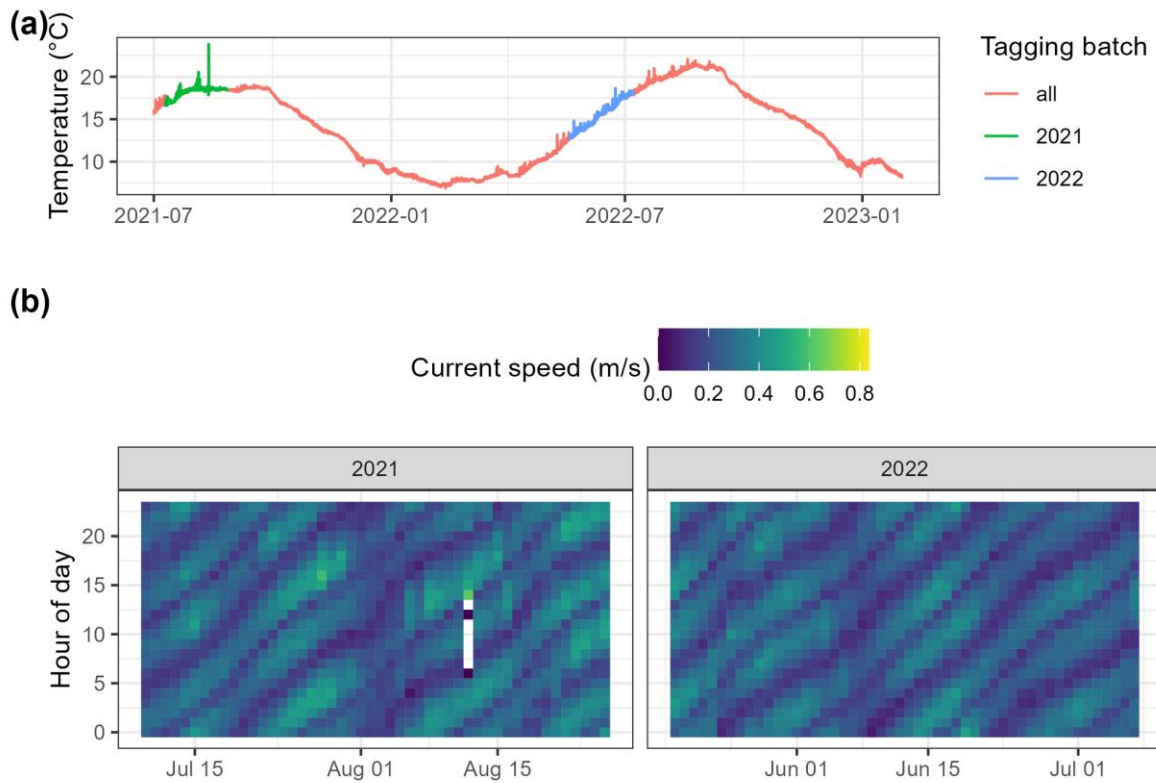The principle of acoustic telemetry is to detect and record acoustically transmitted data from each individual tag by acoustic receivers. Each tag can transmit acoustic signals with a specific sequence. This sequence is specific to each tag and can carry information about an additional parameter like e.g. depth via a dedicated pressure sensor. In this study, European Lobsters were be equipped with acoustic transmitters Vemco V13P. The specifications of these tags are as follows: diameter 13 mm, length 39 mm, mass in seawater 5.5 g, frequency 69 kHz. The transmitters were set to send a pulse train random between 100 and 150 seconds which yielded a battery life of ~460 days. In the context of lobster monitoring, Wiig et al., (2013) and Moland et al (2019) used 110–250 s random intervals (mean 180 s). Moland et al. (2011b) used a 40-120 second range and Skerrit et al. (2015) used a 200-400 second range. For this study there was the need to avoid signal collision with tags deployed for a concurrent monitoring on Atlantic cod which used pulse train intervals between 100 and 150 seconds (Berges et al., 2022, 2023). The interval yielded a high enough resolution to follow the slow-moving European lobster (Skerrit et al., 2015).

It was decided not to try to catch local lobsters because it was anticipated that the probability of catching lobsters on the reefs at the time of experiment would be very small. Such a decision was based on the fact that the reefs were only deployed in July 2020 and would not have benefited from enough seasonal cycles to exemplify abundance of local lobster populations. This was confirmed by ROV Video footage in 2022 where no European lobsters were observed. In order to prevent migration back to their original territory, the sourcing of the lobsters was done away from the Borssele area. More specifically, the animals were sourced from Ireland for the 2021 tagging batch and The Netherlands for the 2022 batch.

The commercially available lobsters in the Netherlands often come from the German Bight, representing the genetic crossover clad between the Baltic clad and the Atlantic Europe clad. For the 2021 batch, it was decided to source lobsters from the same clad as the Southern Bight clad that inhabit Borssele area. Evaluating Triantafyllidis et al. (2005) and Ellis et al. (2017), it was found that lobsters from West

Ireland have the largest similarities with the Southern Bight clad, in contrast to for example the lobsters from Denmark that are closest to the Baltic Sea clad. Fourteen lobsters were purchased from West Ireland. The animals were all males (carapace length ranging 11-13.3 cm, mean value 12.9 cm) and were retained in WMR aquaria. Prior to the release of the animals at sea, testing of the tagging procedure and tag fixation was performed on two individuals. Similarly to Moland et al. (2011), it was found optimal to fix the harness and tag to the middle segment (carpus) of one of the two chelipeds (Figure 4-3(a) and (b)). The 12 individuals that did not undergo testing in the aquaria were deployed at sea around the artificial reefs (Figure 4-4(a)).

I 2022 batch lobsters was obtained from Dutch fishing vessels since none of the translocated lobster from western Ireland had remained in the study area. It is hypothesized that the transition between western Ireland and the south of Holland might have been too large. Therefore for the 2022 batch more local lobsters were obtained from Dutch fishing vessels. Both male and females were tagged (carapace length ranging 10.9-16.1 cm, mean value 12.6 cm), (Figure 4-4(a) and (b) and Table 4-1).

For the deployment at sea for the 2021 and 2022 tagging batches, the animals were transported to the harbour of Vlissingen. The animals were released from a CTV vessel at slack tide at the four artificial reefs of the Borssele II OWF by means of a release device of WMR, to bring the lobsters near the seabed before release. Three lobsters were released at each reef per deployment.

(a)   (b)

Figure 4-3. *Animal tagging setup. (a) a male European lobster equipped with a Vemco V13P‑L acoustic transmitter. Note the T-Bar tag. CW: claw width (Moland et al., 2019). (b): zoomed in view. The Vemco V13P acoustic transmitter and harness are attached to the middle segment (carpus) of the left cheliped in a European lobster. Note the placement of the cable tie between two denticles, which prevents the harness from sliding towards the carpus' tapered end (Moland et al., 2011b).*
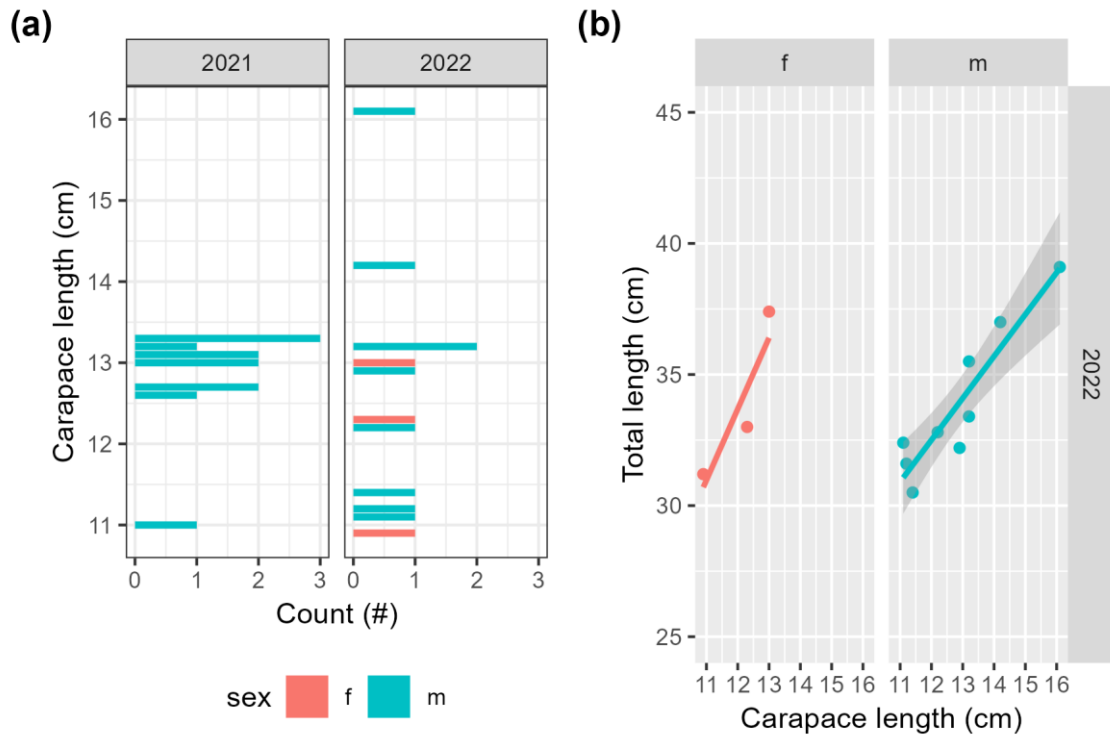
Figure 4-4: *Biological information of lobsters released on site for the 2021 and 2022 batches. (a) Carapace length frequency over the two tagging rounds. (b) Carapace length-total length relationship based on the 2022 data. For the 2021 specimen, length data were not available. Solid lines are the linear regressions.*

Table 4-1: *information on individual lobsters – animal name, length, carapace length, weight, release location, first detection, number of detections, last detection and tagging batch. The number of acoustic detections is expressed as Number of synchronous detections binned per 10-minute intervals, a standardized proxy for the number of detection for each individual.*

Animal name	First detection	Last detection	Number of days	Number of synchronous detections per 10 minutes	Carapace length (cm)	weight (g)	length (cm)	batch	Release location
lobster_10a	7/9/2021 10:40	7/9/2021 15:10	1	28	13	NA	NA	2021	
lobster_11a	7/9/2021 10:30	7/20/2021 14:50	12	798	13.1	NA	NA	2021	
lobster_12a	7/9/2021 11:00	7/13/2021 8:10	5	370	13.3	NA	NA	2021	
lobster_1a	7/9/2021 10:40	7/9/2021 19:00	1	51	13	NA	NA	2021	
lobster_2a	7/9/2021 11:10	7/9/2021 15:00	1	24	12.7	NA	NA	2021	
lobster_3a	7/9/2021 11:00	7/15/2021 17:30	7	251	12.7	NA	NA	2021	
lobster_4a	7/9/2021 11:10	7/29/2021 5:30	11	501	11	NA	NA	2021	
lobster_5a	7/9/2021 11:20	7/24/2021 16:00	6	266	13.1	NA	NA	2021	
lobster_6a	7/9/2021 10:40	8/27/2021 21:30	28	1771	13.2	NA	NA	2021	
lobster_7a	7/9/2021 11:00	7/10/2021 3:40	2	81	12.6	NA	NA	2021	
lobster_8a	7/9/2021 10:50	7/27/2021 0:40	14	445	13.3	NA	NA	2021	
lobster_9a	7/9/2021 10:20	7/11/2021 18:00	3	156	13.3	NA	NA	2021	
lobster_10b	5/18/2022 12:00	6/28/2022 19:40	42	4382	13.2	1840	35.5	2022	R03
lobster_11b	5/18/2022 11:40	5/18/2022 18:20	1	29	13	1510	37.4	2022	R01
lobster_12b	5/18/2022 11:40	7/6/2022 21:50	50	3726	11.4	1065	30.5	2022	R01
lobster_1b	5/18/2022 11:20	5/18/2022 13:00	1	8	14.2	1925	37	2022	R02
lobster_2b	5/18/2022 11:30	5/21/2022 21:50	4	82	11.1	1050	32.4	2022	R02
lobster_3b	5/18/2022 12:00	6/8/2022 3:10	6	162	11.2	1240	31.6	2022	R04
lobster_4b	5/18/2022 11:50	5/19/2022 1:20	2	54	10.9	940	31.2	2022	R04
lobster_5b	5/18/2022 11:50	7/8/2022 22:30	52	6232	13.2	1365	33.4	2022	R04
lobster_6b	5/18/2022 11:30	6/9/2022 1:20	23	2757	12.3	1160	33	2022	R01
lobster_7b	5/18/2022 11:20	5/23/2022 20:00	6	503	12.2	1100	32.8	2022	R02
lobster_8b	5/18/2022 12:10	5/19/2022 6:30	2	48	16.1	2700	39.1	2022	R03
lobster_9b	5/18/2022 12:10	6/30/2022 7:20	3	55	12.9	1090	32.2	2022	R03

4.1.3 Data analysis

4.1.3.1 Fine scale positioning

The data from each acoustic receiver yielded acoustic detections of the different tags. These tags provided data on depth on each emission. These detections were processed using the Fathom Position web platform by Innovasea[4]. First, using reference acoustic emission from each acoustic receiver, the clock drift at receiver was corrected using linear regressions over the time difference between different receivers (Smith, 2013). This correction allowed the time synchronisation of detections across the receiver network and was an essential step to further compute accurate positioning. From the synchronised detections, 2D locations in the horizontal plane were computed using Time Difference Of Arrival (TDOA) (Lennox RJ et al., 2023). The minimum requirement for the calculation of a 2D position was the detection of a transmissions over at least 3 receivers.

Alongside positioning using TDOA, an indicator of accuracy for each position was computed (Smith, 2013), so called Horizontal Position Error (HPE). The HPE is a dimensionless quantity calculated through multiple receiver combinations and is only applicable for each acoustic network setup. The HPE associated to each lobster positions was used to filter out deviates. Here, the highest 2% HPE quantile was filtered out. In addition, detections associated with dubious temporal and spatial trends (e.g. loss of tag, death of animal, moulting) were further removed.

4.1.3.2 Area utilization

In order to investigate the spatial utilisation of the study area and determine home range size, Utilization Distributions (UD95) were computed using kernel densities with the "adehabitatHR" R package (Calenge, 2006). Such method estimates the 2D spatial probability density given the animal positions. When fitting kernel densities to estimate home range, one of the most important parameters is the smoothing factor as it underpins the fitting of the kernel density. A fixed value of h=4 was chosen over a parametric estimation because of the large number of cases and the need to standardize the calculations over the different individual animals. As for the magnitude of smoothing, based on examining the daily spatial distribution of animal positions, a value that best capture point densities was chosen, optimizing the degree of under- and over smoothing (Worton, 1995, Seaman et al., 1996, Skerrit et al., 2015).

Home ranges were fitted daily for each individual lobster. Individual home ranges were defined as the smallest area containing 95% of the UD (UD95). Home ranges were further filtered based on the following criteria: 1) the polygon should be derived from at least 5 positions, 2) the time extend of the positions within the polygon should be greater than 2 hours. Each home range polygon was further associated with structures in the study area (reef, turbine, acoustic receivers). To associate each polygon to a structure, it was first envisioned to have a condition on the containment of the position of the structure in the home range polygon. However, it was not satisfactory on a few cases where the home range polygon was in the vicinity of the structure but did not contain it (e.g. because of uncertainty in effective position on the seabed, against logged GPS position from surface of the acoustic receivers). Consequently, the association between home range polygons and structures was done based on the distance from the structure to the centroid of the home range polygon. The association was made with polygon centroids at a distance less than 100 m of a structure. The stay at the different structures was further used to determine fidelity. The fidelity was computed for each home range as the ratio between the number of positions within the home range polygon to the total number of positions in the period of interest (binned per day).

4.1.3.3 Behaviour analysis

To investigate changes in behaviour in the study area, a spatial Hidden Markov Model (HMM) was fitted to the animal positions using the "momentuHMM" R package (McClintock & Michelot, 2018). The HMM was configured with step length and turning angle as data streams. Step length was modelled using a Gamma distribution, parametrized with mean and standard deviation. Turning angle was modelled using a von Mises distribution parametrized with mean and concentration. The HMM was based on positions grouped per 10 minutes. The number of Behavioural States (BS) was based on biologically plausible

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[4] https://www.innovasea.com/fish-tracking/products/fathom-software/

states, more specifically: locally inactive (BS1), locally active (BS2) and transit (BS3). Initial conditions for the model were inferred based on examining the distributions of data streams in time and space. The HMM model was fitted using an individual random effect by adding the individual lobster ID as covariate to transition state probabilities. In addition, the following covariates were tested: current speed (m/s), Sea Surface Temperature (SST, °C), hour of day, individual tag extent (0 at time of release, 1 at time of departure) and distance to closest reef (m). Using the HMM, the sequence of states was decoded using the Viterbi algorithm (McClintock & Michelot, 2018) and could be associated with each position.

4.1.3.4   Inferring hiding in artificial structures

Several aspects can alter acoustic detection such as the receiver network, the number of tagged animal present or the effective acoustic propagation (van der Knaap et al., 2021). The latter can be affected by the properties of the water column, water depth and most importantly potentially obstacles. An important aspect of the data set presented here is the ability of the animals to hide in the concrete pipes of the artificial structures which is clearly detrimental to the acoustic propagation of the acoustic signal emitted by the tags. A distinctive feature of the data was that individuals positioned in the concrete pipes of the artificial reefs exemplified detection of each acoustic emission at a lower number of receivers. Importantly, for fine scale positioning, if a transmission was detected at less than 3 receivers simultaneously, no positioning could be performed, events that happened more frequently when the animals were hiding in the concrete structures. To determine the time at which the animals hid in the pipes, a non-spatial HMM was used using the "momentuHMM" R package (McClintock & Michelot, 2018).

Using this feature, a dedicated HMM was built to identify hiding in the structures.

The input data consisted of data binned per 10 minutes based on all detections (with and without successful positioning). The HMM was configured with 3 data streams:
-   The mean distance to the closest reef within 10-minute bins.
-   The number of unique receiver IDs within 10-minute bins.
-   Boolean on the presence of at least one successfully inferred TDOA position within 10-minute bins.

It is important to note that the distance to the closest reef could only be computed when TDOA was successful. For detection intervals without successfully TDOA positioning, the distance to the closest reef was interpolated based on closest values. The distance to the closest reef and the number of receivers data streams were modelled using a Gamma distribution parametrized with mean and standard deviation. The Boolean on TDOA positioning presence was modelled with a Bernoulli distribution, parametrised with the probability of occurrence. Four different states for the HMM were defined:
-   Hidden state: animal at reef but hiding within the concrete pipes.
-   At reef: animal at reef, not hiding within the concrete pipes.
-   Not at reef with TDOA position: animal not at reef with TDOA
-   Not at reef without TDOA position: animal not at reef without TDOA,

The HMM model was fitted using an individual random effect by adding the individual lobster ID as covariate to transition state probabilities. Further to individual lobster IDs, the following covariates were tested: current speed (m/s), Sea Surface Temperature (SST, °C), hour of day, individual tag extent (0 at time of release, 1 at time of departure) and distance to closest reef (m). Using the HMM, the sequence of states was decoded using the Viterbi algorithm (McClintock & Michelot, 2018) and could be associated with each 10-minute interval.

4.2 Results

4.2.1 Residency, site fidelity and area utilization

Both in 2021 and 2022, 12 lobsters were released, 3 at each artificial reef. The acoustic receiver network consisted of 13 receivers in 2021 and 11 in 2022 (Figure 4-1(c)). Because of the loss of equipment during recovery operations, the coverage was sub-optimal but remained satisfactory across the whole monitoring period. The resulting time series of lobster detections is shown in Figure 4-5(a) with the corresponding decay in Figure 4-5(b). Overall, low residency was observed with a higher residency for the 2022 batch. In 2021 and 2022, three and two individuals left the area within 1 day respectively. Excluding these early leaving individuals, the mean residency was 9.8 days with a maximum of 28 days in 2021, and the mean residency was 19 days with a maximum of 52 days in 2022. In addition, there were differences in the patterns of presence between the two batches. In 2021, the individuals exemplifying residency above 5 days often had intermittent presence. For example, lobster 6a was observed from 2021-07-09 to 2021-08-27 but had a long absence within this period. In contrast, the individuals of the 2022 batch showed more consistency in their presence (e.g. lobster 5b, 6b 10b and 12b).
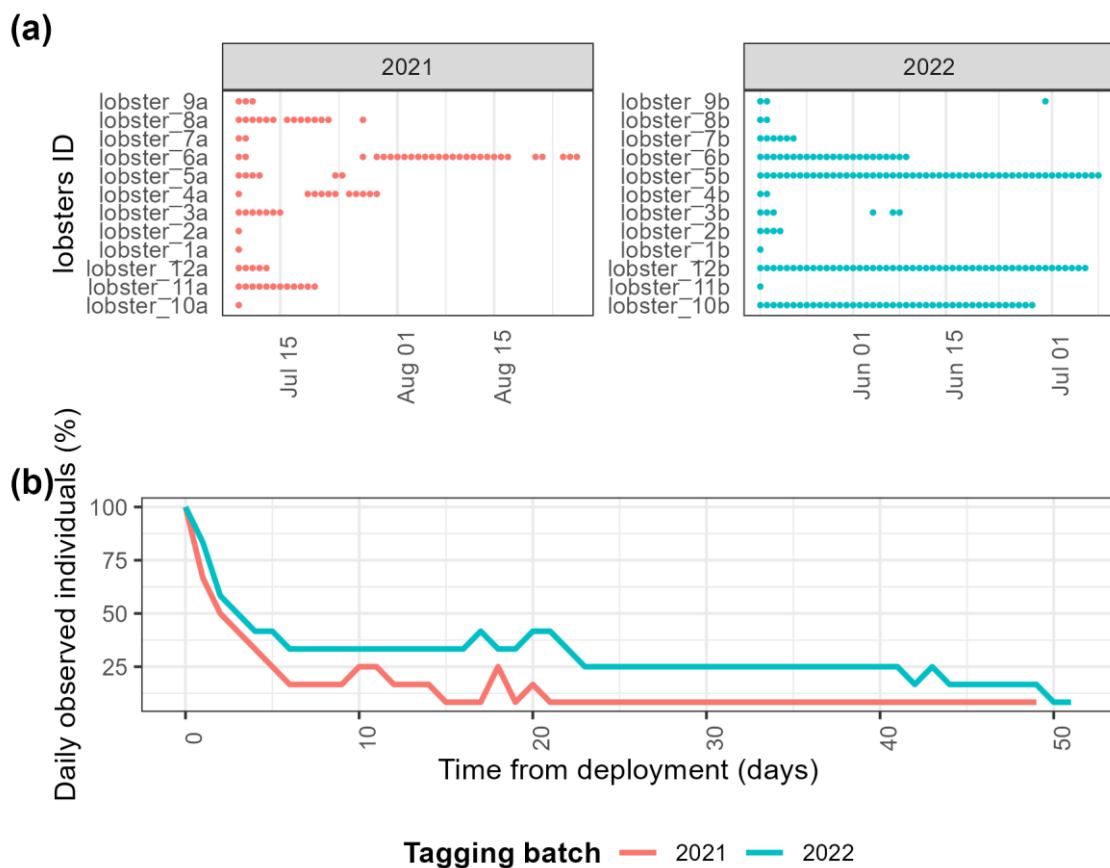

Figure 4-5: *tag overview. (a) Overview of tag detections. (b) Tag decay.*

The area utilization by the lobsters was investigated through a home range analysis. More specifically, UD95 kernels were computed daily for each animal. Home range polygons together with TDOA are shown in Figure 4-6. It is important to note that only 13 individuals exemplified behaviours that led to consistent daily home range (Figure 4-6). The calculations of daily home ranges are constrained by 1) the clustering of the TDOA positions, 2) a minimum of 5 positions within the polygon, 3) the TDOA positions within the home range polygon spanning a minimum of 2 hours. Only a few individuals complied to this filtering and exemplified at least 1 home range polygon (4 for the 2021 batch, 5 for the 2022 batch). These home range polygons are further associated with the different structure in the study

area to determine site visiting (Figure 4-7). Like the results for residency (Figure 4-5(a)), the number of home range polygons is particularly low for the 2021 batch whilst there is more consistency with the animals released in 2022. The location of the home range polygons varied between different individuals for both data sets. Whilst the artificial reefs remained the most visited, the animals also settled around the turbine and acoustic receivers. In addition, the lobsters sometime resided at other locations with perhaps unidentified hard substrates (Figure 4-6 and Figure 4-7).
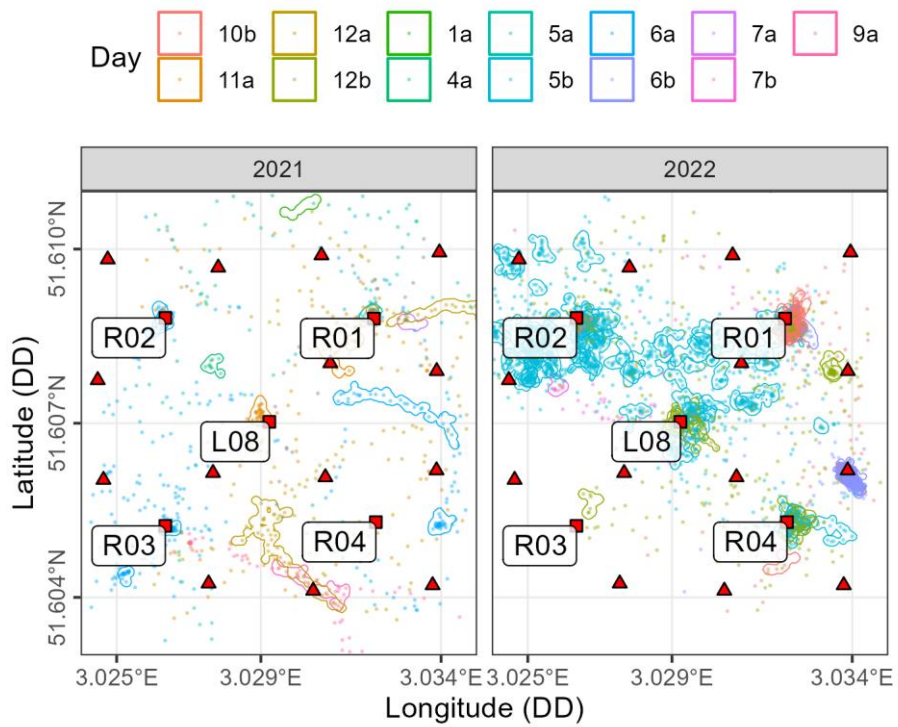

Figure 4-6: *home range polygons and TDOA positions per animal ID (colour).*
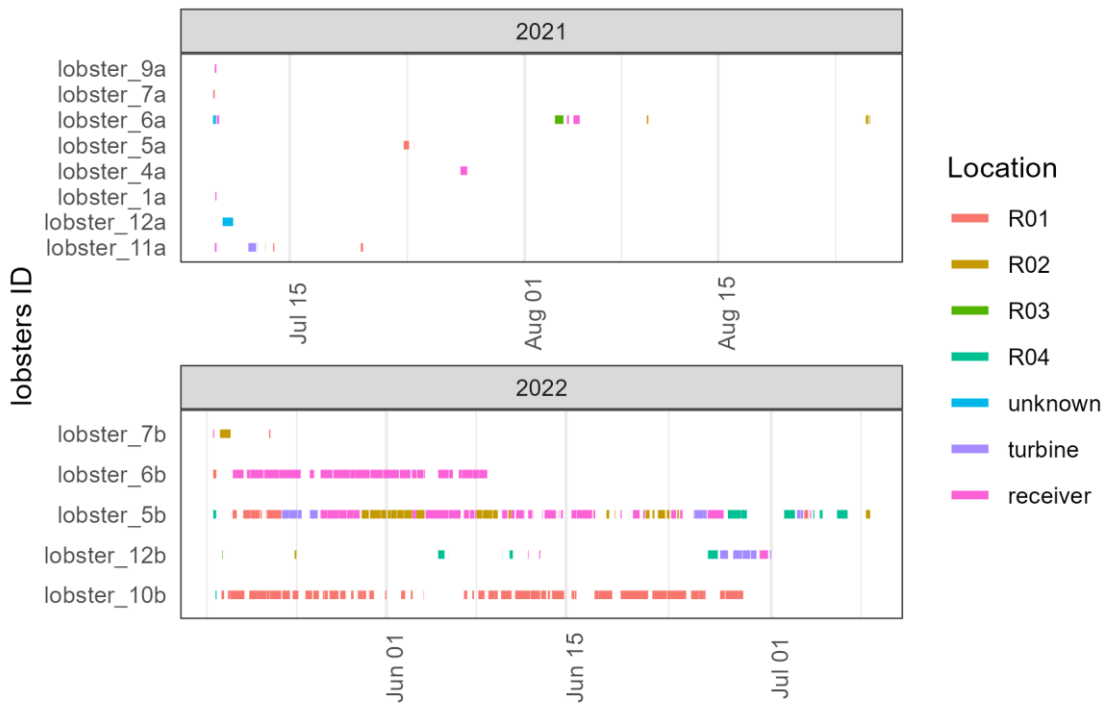
Figure 4-7: *site visiting. Time series of tagged lobsters at different locations based on UD95. Only individuals exemplifying home range areas are displayed.*

The area of all home range polygon (UD95) is computed (in m^2) and yields a time series for each lobster (Figure 4-8). As exemplified in Figure 4-7, the animals tagged in 2021 did not demonstrate consistent home range areas. This is likely due to the animals being unsettled when released. In comparison, three animals released in 2022 exemplified consistent home range behaviour (Figure 4-7, lobster 6b, 5b and 10b). Out of these individuals, lobster 6b and 10b consistently stayed at R01 and at a SW acoustic receiver respectively (Figure 4-6). They also exemplified similar trends in home range area (Figure 4-8, dark green and purple lines) with a large home range at the time of release followed by a decrease with time. In contrast, the range of sites visited by lobster 5b was much more varied, resulting in home range area characterised by large variations and large values (Figure 4-8, green line), which could be interpreted as characteristic of a poor settlement.
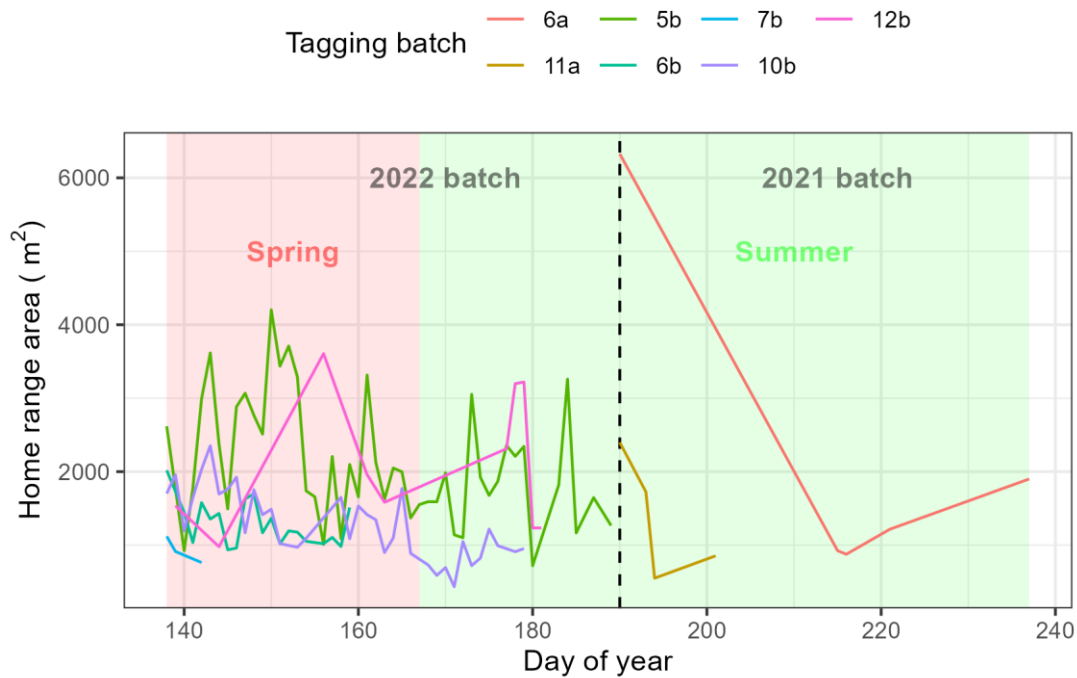
(a)

Figure 4-8: *daily home range area (m². The results are displayed for each lobster ID (colours). The 2021 batch (190-237 day of year) and 2022 batch (138-189 day of year) are separated by the vertical dashed line.*

To compare the area utilization around the different sites, home range area and fidelity are combined across lobster individuals for each year and displayed as boxplots (Figure 4-9, left panels). For the 2021 data set, the amount of data was very limited which hampered any comparison between sites. For the 2022 data set though it is concentrated on three individuals (Figure 4-7) which are of focus in the rightmost panels of Figure 4-9. For these lobsters, the fidelity is >0.5 at R01, R02 and at acoustic receivers (where lobster 5b and 6b resided for extended periods of time). Fidelity at R04 and at the turbine was lower. The home range area is particularly low at R01, a trend that is induced by lobster 10b. **Table 3-1** gives the area utilisation of European lobster as found in this study compared to results from other studies. The actual comparison of the findings of this report with the other authors will be discussed in Section 5.3. The lobsters on the artificial reefs had UD95s ranging from 433 m² to 4203 m². The lobsters near the monopile and on its anti-scouring had UD95s ranging from 731 m² to 3259 m². The lobsters using the structure supporting the acoustic receivers and the sandy sediments surrounding had UD95s ranging from 731 m² to 3259 m². Given the low number and the short residence time no further attention was given to statistical refinement.

Fidelity and home range area are metrics of area utilization. They may vary with time, especially as the animals released on site in this study were caught at another geographical location and needed to settle in the area. To identify the settlement effect, the home range area and fidelity are plotted against the settlement time at site (Figure 4-10). As the animals settle on site, home range area decreases whilst the fidelity increases.

When considering all the data available, there is weak settlement in the area which led to poor residency and fidelity. In addition, despite three individuals (lobster 6b, 5b and 10b) exemplifying a consistent stay in the area, it remains difficult to draw conclusions because it does not lead to enough replication. Especially, there is a large contrast in area utilization and fidelity between these individuals, likely due to individual random effect and potential differences in the level of settlement in the area.
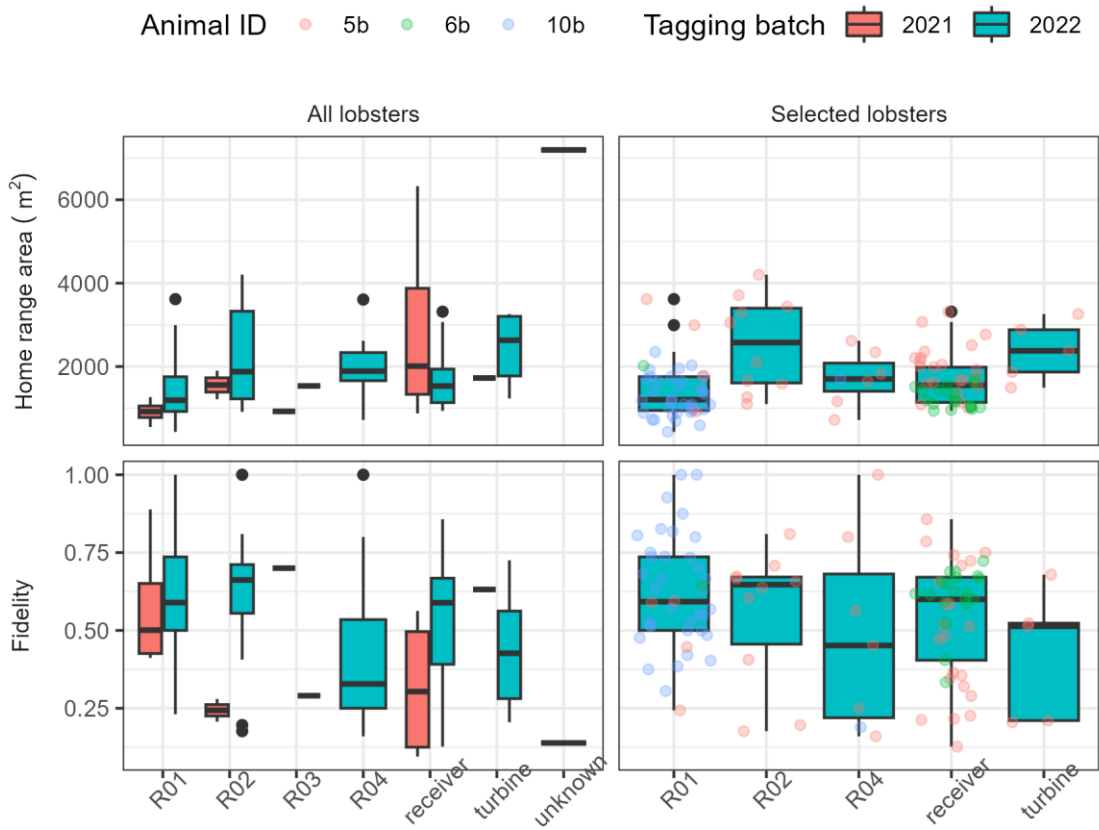
Figure 4-9: *Statistics on home range area (top panels) and fidelity (bottom panels) at different locations. Results are displayed for all animals (left panels) and a selection of individuals (right panels). The individual lobsters focused upon are those that exemplify the most consistent stay in the monitoring area (Figure 4-7).*
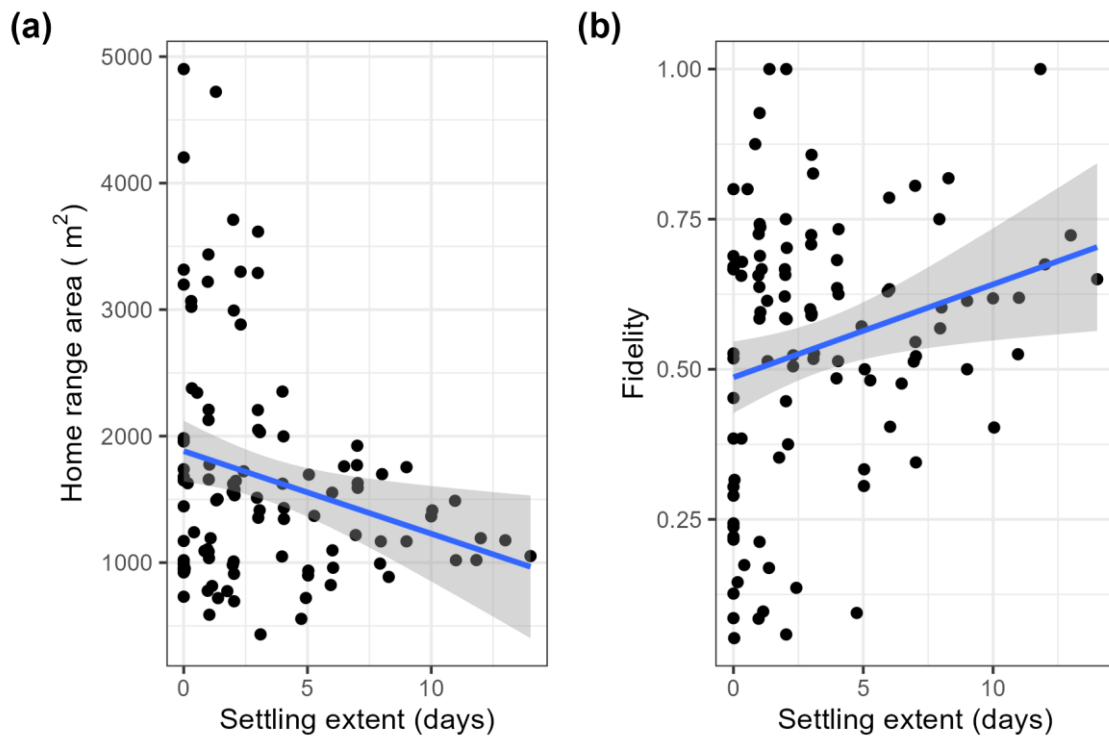
Figure 4-10: *relationship between time at site and fidelity and home range area.*

4.2.2 Behavioural states and hiding in structures

The behaviour of the lobsters in the monitoring area is captured using a spatial HMM. The best model fit was found with the following covariates (Table 4-2): individual ID, sea surface temperature, Current speed, Hour of day and closest distance to reef. The resulting states from the optimal model are shown in Figure 4-11 and given in Table 4-3. The behavioural states are well defined as follows:

- <u>Locally inactive</u>: state associated with low mean and low sd for step length and a close to 360 degrees mean turning angle. The interpretation of this state is reduced local movement with regular change in movement direction.
- <u>Locally active</u>: state associated with moderate mean and moderate sd for step length and a close to 360 degrees mean turning angle. The interpretation of this state is moderate local movement with regular change in movement direction.
- <u>Transit</u>: state associated with large mean and large sd for step length and a close to 0 degree mean turning angle. The interpretation of this state is large and directional movements, associated with e.g. travelling across the monitoring area.
-

As for the area utilization, there is large variation between individuals. This is exemplified in the stationary state probabilities for each lobster (Figure 4-12). Only lobsters 5b, 6b and 10b have large probabilities for the locally active and locally inactive states. This is in line with the fact that only these individuals displayed consistent residency in the monitoring area (Figure 4-7).
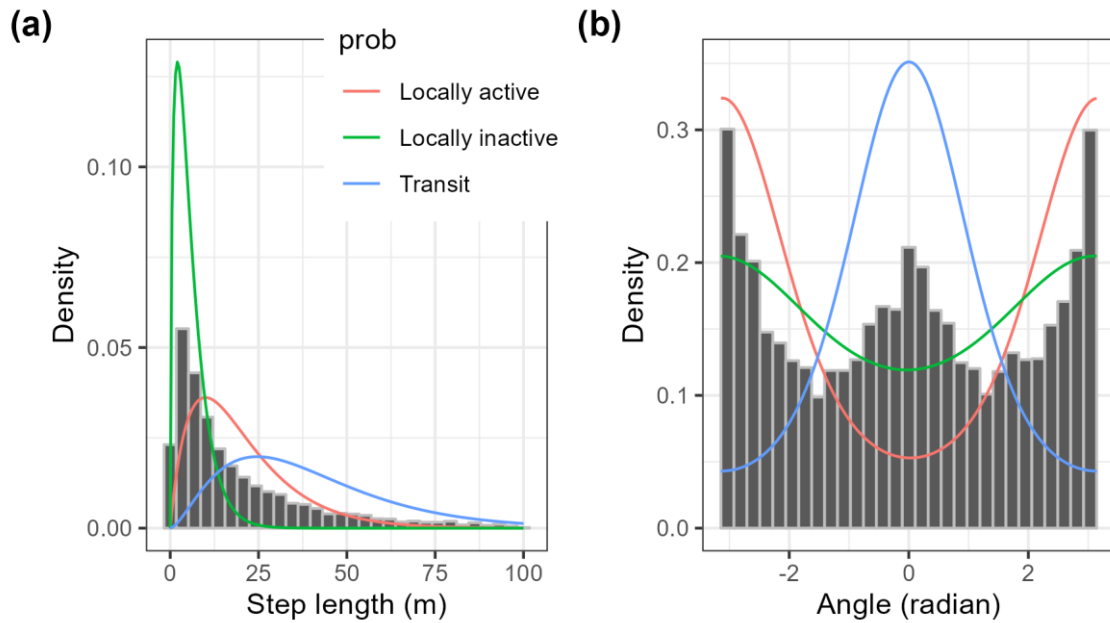
Figure 4-11: *definition of Hidden Markov Model (HMM) behavioural states. The data streams used for the model are step length (a) and turning angle (b). Step length was modelled using a gamma distribution parametrized with mean and standard deviation. Turning angle was parametrized using a von Mises distribution parametrized with mean and concentration.*

Table 4-2: *Model selection of the spatial HMM. The different models are parametrized similarly but include different covariates. The models are ranked and ordered based on the delta Akaike Index Criteria (ΔAIC).*

Covariate formula	AIC	dAIC
~ID + SST + Current speed + Hour of day + Distance to reef	69076.8	0.0
~ID + SST + Current speed + Tag extent + Distance to reef	69039.6	3.2
~ID + Current speed + Hour of day + Tag extent + Distance to reef	69080.5	3.6
~ID + SST + Current speed + Hour of day+ Tag extent + Distance to reef	69129.5	12.2
~ID + Distance to reef	68978.6	63.4
~ID + SST + Hour of day + timeTag + Distance to reef	69149.7	72.9
~ID + Tag extent	69021.5	106.3
~ID + SST + Current speed + Hour of day + timeTag	69204.4	127.6
~ID + Hour of day	69089.8	134.2
~ID	69009.7	134.9
~ID + SST	69053.1	137.9
~ID + Current speed	69074.6	159.5
~1	68680.9	250.7

Table 4-3: *behaviour HMM data streams estimated parameters: step length in m and turning angle in radians.*

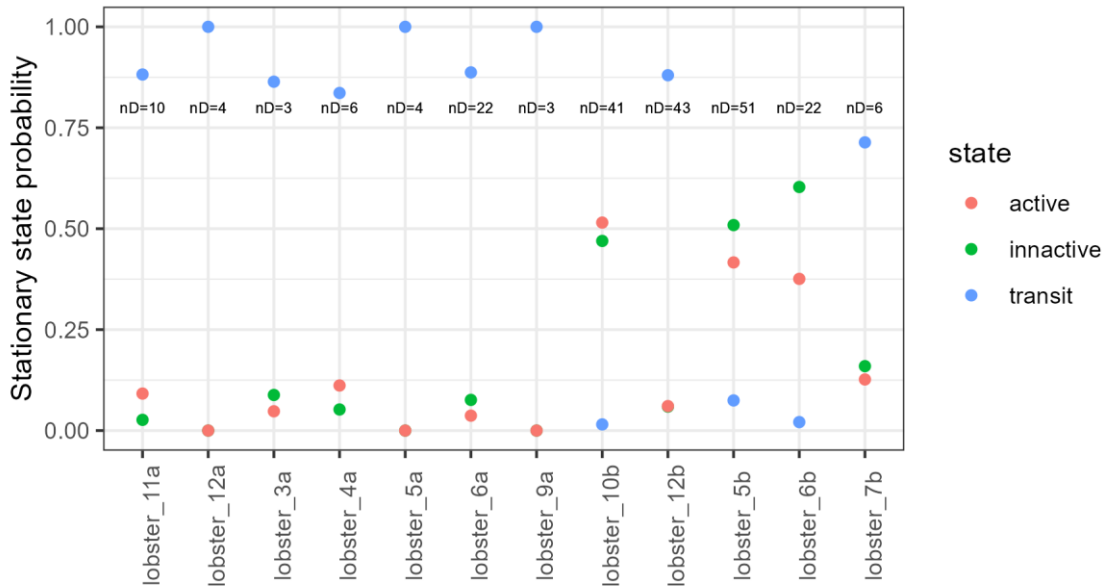| Behavioural state	Step length mean (m)	Step length sd (m)	turning angle mean (radian)	turning angle sd (radian)
BS1: locally inactive	5.60	4.45	3.11	0.27
BS2: locally active	20.30	14.47	-3.12	0.91
BS3: transit	39.58	24.31	0.00	1.05

Figure 4-12: *HMM stationary states probabilities for each individual lobster and each behavioural state. The number days each animal was observed is indicated at the top of the graph.*

A non-spatial HMM (configured with four states and three data streams) was used to infer hiding in the artificial structures. The optimal model was found with the following covariates (Table 4-4): individual ID, sea surface temperature, Current speed, Hour of day and time tag extent. The resulting definition of the states are shown in Figure 4-13. The parameters for each data stream and state are further given in Table 4-5. Of importance here is the hiding state which corresponds to the time of hiding in structures.

The stationary state probabilities for each individual lobster are given in Figure 4-14. The results reflect contrasting hiding patterns, with no hiding found for the individuals that did not visit the artificial reefs (e.g. lobster 9a and 6b), and large probabilities of hiding found for those residing at the reefs consistently (e.g. lobster 7b and 10b). From these results, the individuals that visited the artificial reefs exemplified substantial hiding in the concrete pipes.
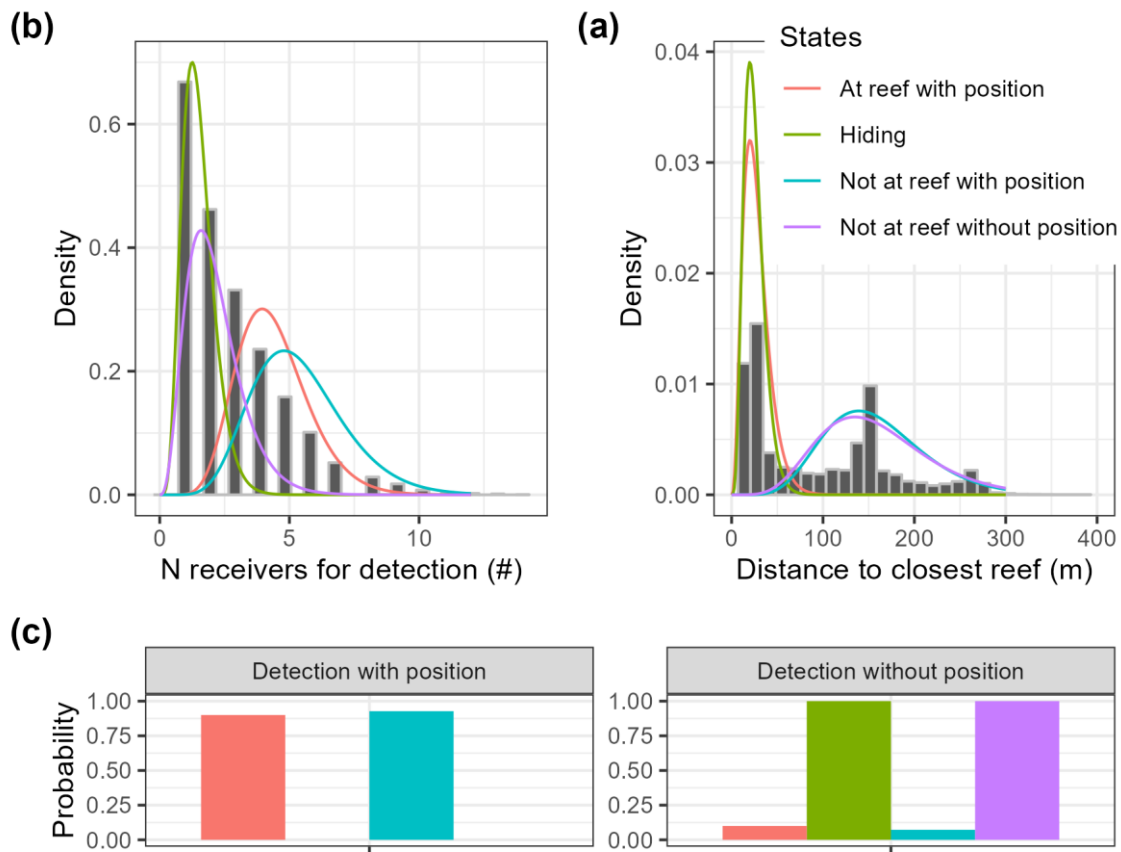
Figure 4-13: *definition of the states for the non-spatial HMM used to infer hiding in artificial reefs. The data streams used for the number of unique receivers in 10-minutes periods (a) the mean distance to the closest reef (b) and whether at least one position exist within the 10-minutes period (c). The number of acoustic receivers and the distance to the closest reef were modelled using a gamma distribution parametrized with mean and standard deviation. The presence of a position was modelled using a Bernoulli distribution parametrized with probability.*

Table 4-4: *Model selection of the non-spatial HMM used to infer hiding in the artificial structures. The different models are parametrized similarly but include different covariates. The models are ranked and ordered based on the delta Akaike Index Criteria (ΔAIC).*

Covariate formula	AIC	dAIC
~ID + SST + Current speed + Hour of day + Tag extent	288693.1	0.0
~ID + Current speed + Hour of day + Tag extent	288715.3	22.2
~ID + SST + Current speed + Hour of day	288724.4	31.3
~ID + SST + Current speed + Tag extent	288732.1	39.0
~ID + Current speed	288763.5	70.4
~ID + WaterTemp0001 + Hour of day + Tag extent	288803.5	110.4
~ID + Hour of day	288836.0	142.9
~ID + Tag extent	288856.7	163.6
~ID + SST	288872.3	179.2
~ID	288876.3	183.2
~1	289891.0	1197.9

Table 4-5: *non-spatial HMM data streams estimated parameters: step length in m and turning angle in radians.*

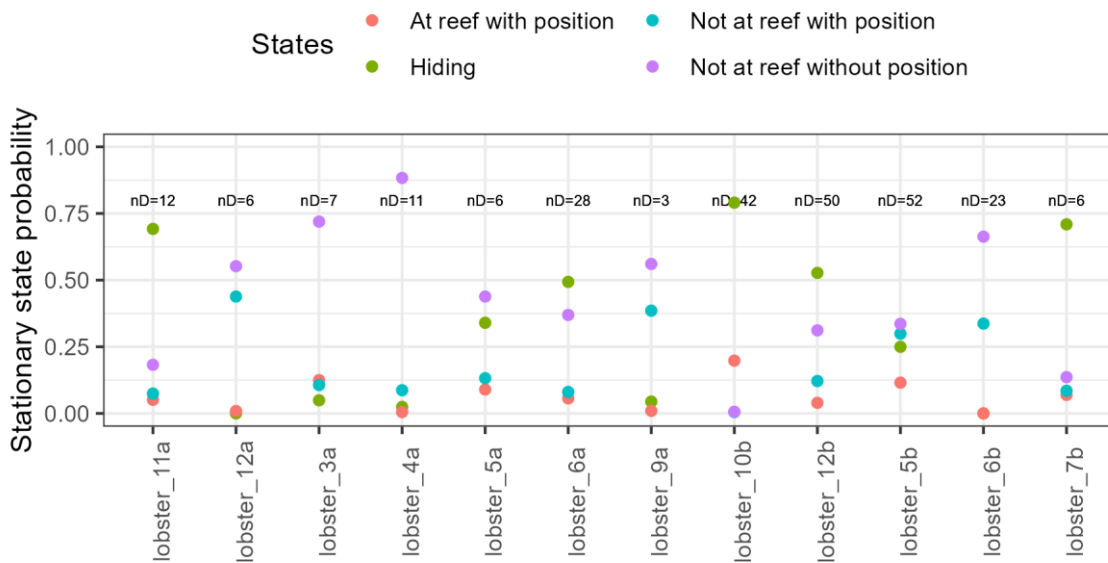| HMM states	number of receivers mean (#)	number of receivers sd (#)	Distance to reef mean (m)	Distance to reef sd (m)	Probability of position
Hiding	1.50	0.61	24.99	11.20	<0.001
At reef with position	4.40	1.40	27.74	14.46	0.9
Not at reef with position	5.38	1.80	159.40	54.87	0.93
Not at reef without position	2.11	1.04	158.23	60.58	<0.001

Figure 4-14: *stationary states for each individual lobster and each behavioural state for non-spatial HMM used to infer hiding in artificial reefs. The number days each animal was observed is indicated at the top of the graph.*

4.2.3 Temporal and spatial patterns

Using the modelling presented above, the spatial distribution of the states is first presented in Figure 4-15. Expectedly, the transit BS is widespread across the monitoring area. In contrast, the locally active and locally inactive states are more concentrated, especially in the northern section, an effect that is partly due to the lower acoustic receiver coverage (Figure 4-1(c)). For the local state, the high concentration around R01 and at a southeastern acoustic receiver is due to the specific site visiting of lobster 10b and 6b (Figure 4-7). Despite the high concentration around R01, the density around the reefs and the turbine is not particularly high, which reflects the poor residency and settling of the animals in the monitoring area.
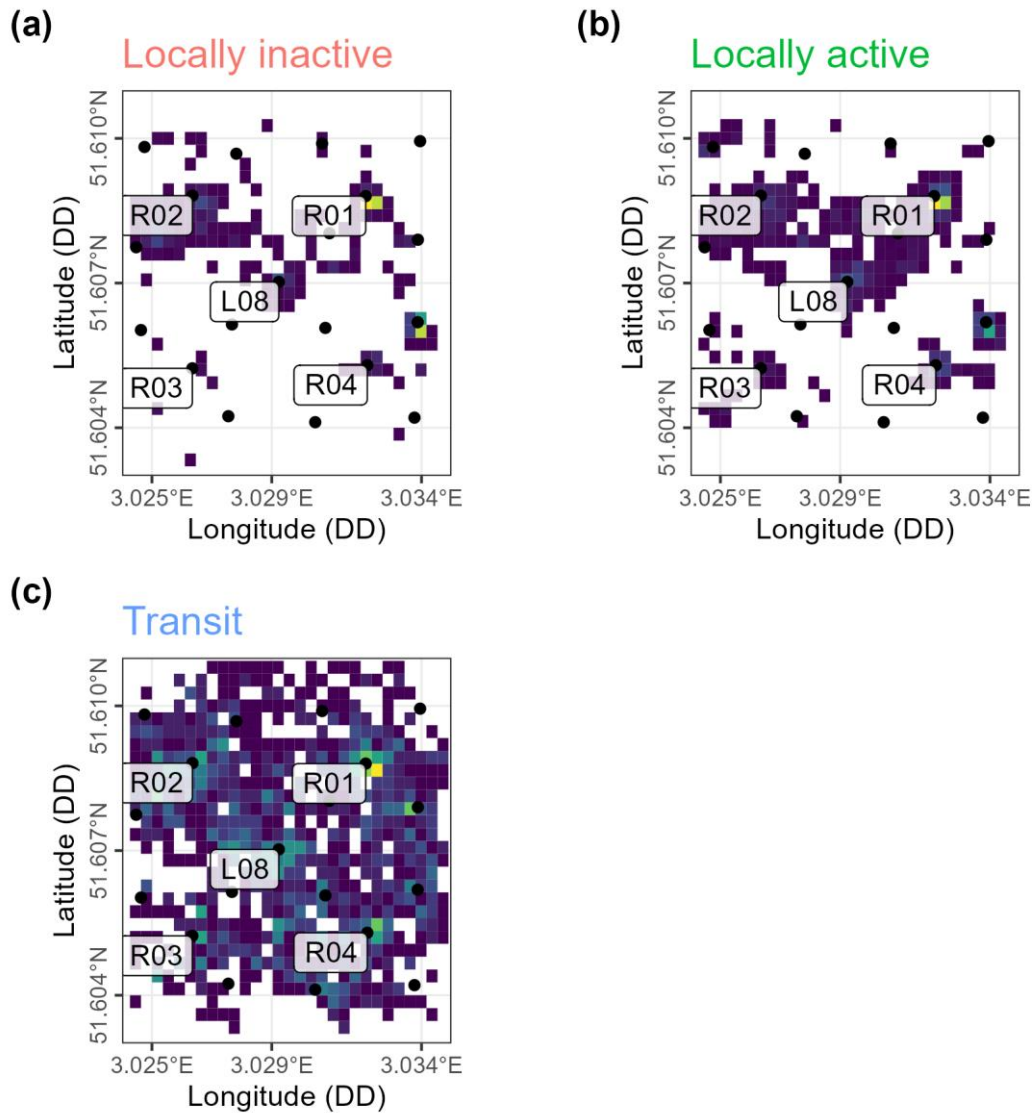
Figure 4-15: *spatial distribution of behavioural states. (a): Spatial distribution of the locally inactive state. (b): Spatial distribution of the locally active state. (c): Spatial distribution of the transit state.*

Behavioural states as estimated by the HMM can further be used to investigate temporal patterns in distance travelled Figure 4-16. The mean values and standard deviations across the time series are given in Table 4-6. Whilst the cumulative distance travelled can be investigated as a whole (e.g. in Skerrit et al., 2015), breaking it down by behavioural states allows one to associate this metrics with local and non-local behaviours. For the hereby study, it is particularly important as the animals released are not resident in the area, therefore exemplifying a range of local and non-local behaviours. The largest daily distance travelled is expectedly associated with the transit state (Figure 4-16, 3rd row). In contrast, the cumulative distance for the locally inactive and active states is lower with mean values of 118.5 m/day and 252.3 m/day respectively. The mean value of distance travelled whilst in the inactive state was 53% lower than for the distance travelled in the active state, though the standard deviation is much higher for the active state (Table 4-6). In addition, the locally inactive state is associated with artificial reefs (e.g. lobster 10b) and other structures that do not provide as much sheltering, such as the frames supporting the acoustic receivers (e.g. lobster 6b). For the latter, because of the lack of sheltering, the distance travelled is larger.
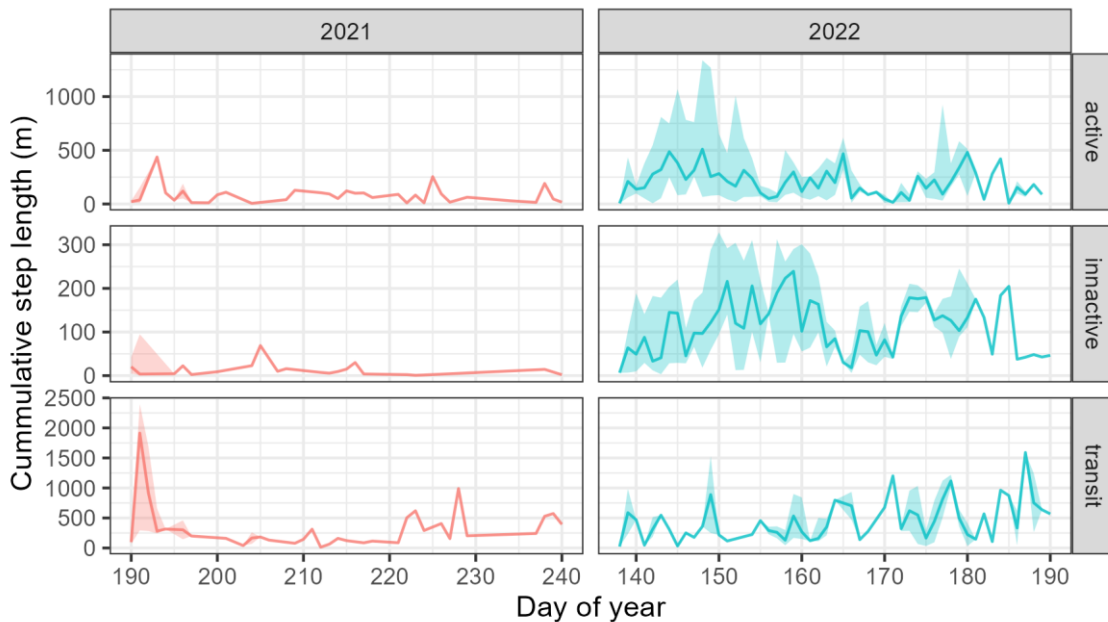
Figure 4-16: *daily distance travelled against day of year for the different behavioural states (locally active, locally inactive and transit) for the 2021 and 2022 data sets. Summary statistics over all individual lobsters are displayed with median values (solid lines) and 25th-75th quantiles (shaded areas).*

Table 4-6: *mean and standard deviation (sd) of daily distance travelled for the different behavioural states and data sets.*

	2021 batch		2022 batch	
Behavioural state	Mean (m)	Sd (m)	Mean (m)	Sd (m)
BS1: locally inactive	17.1	23.9	118.5	89.7
BS2: locally active	78.9	83.9	252.3	268.8
BS3: transit	476.9	607.9	452.9	388.0

Stationary state probabilities as estimated by the HMM are the link between the behavioural states and the covariates. The optimal HMM included the following covariates (Table 4-2): individual ID, current speed, hour of day, sea surface temperature and distance to the closest reef. Because of the large variations between individuals (Figure 4-12), the covariates other than individual ID are scoped separately for lobsters exemplifying a residency of more than 20 days (Figure 4-17).

First, diurnal patterns (Figure 4-17, 3rd column) for the local states are captured by the model for lobsters 10b, 5b and 6b which are the individuals exemplifying settlement in the monitoring area (Figure 4-7). These animals are most active at daytime (10:00AM-06:00PM) with a peak at ~02:00PM. In contrast, local inactivity is highest at night-time with highest levels reached at 03:00AM. Lobsters 6a and 12b have much higher stationary state probabilities for the transit state than for the locally active and inactive states and do no exemplify strong patterns. Second, there is a clear effect of the artificial reefs on the occurrence of the locally active and inactive states with an increase of the stationary state probabilities at ~50m from the reefs for lobsters 10b, 12b and 6a which are the animals that visited the artificial reefs consistently (Figure 4-17, 2nd column). Third, there are observable trends with sea surface temperature (Figure 4-17, 4th column) and current speed (Figure 4-17, 1st column). The lobsters exemplify an increase in activity with increased current speed and the local activity decreases with increasing temperature. The link with current speed seems a shift from transit BS to a more localised BS. High activity at high current speeds is contrary to expectations from an energy expenditure point of view, with lower activity level with increased current speed. However, it is important to point out that the range of current speed captured here is limited. In addition, the locally active state is near the structures so movements could have been made in the lee side of the structures.
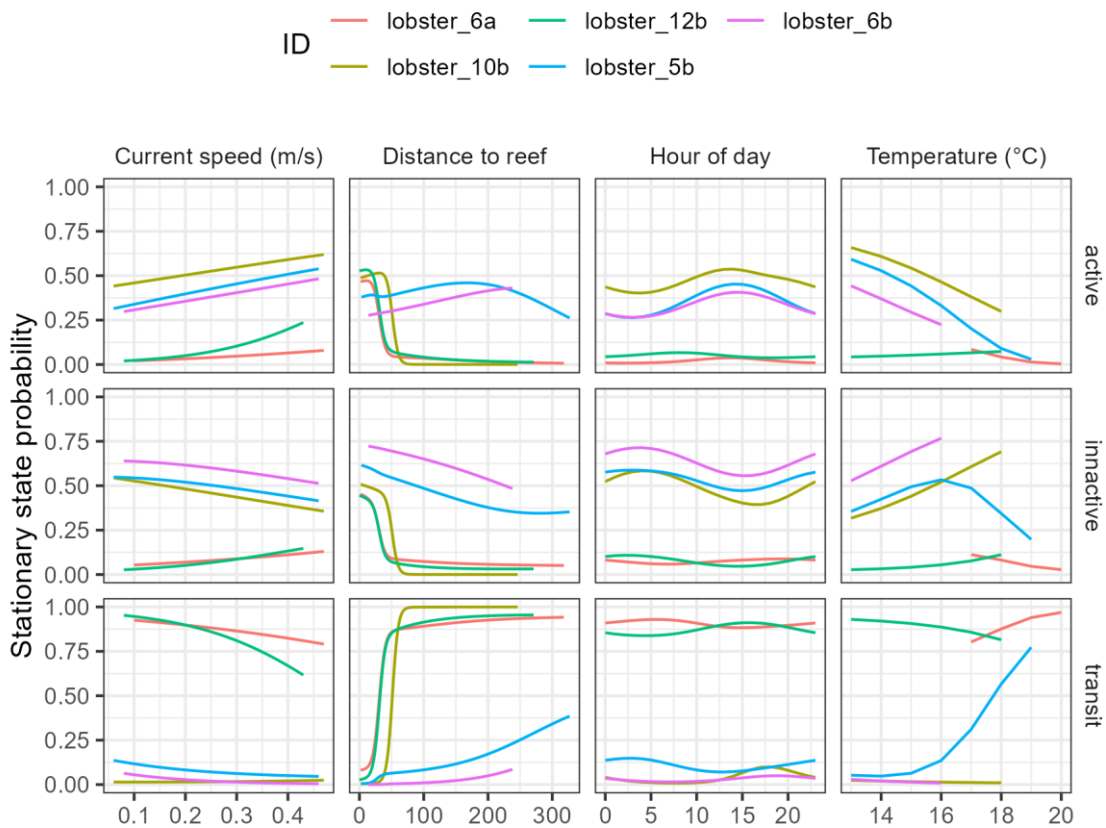
Figure 4-17: *Stationary state probabilities for the spatial HMM used to infer behavioural states. Results are shown for individual lobsters (colours) exemplifying a residency of more than 20 days. Model covariates other than individual lobsters are current speed (m/s), distance to reef (m), hour of day, and sea surface temperature (°C).*

Alongside the estimation of behavioural states, a dedicated non-spatial HMM was devised to infer hiding in the artificial structures. For this model, a range of covariates to transition probabilities were included and are used to investigate the effect of these on the different states. The resulting stationary state probabilities are shown in Figure 4-18 for the hiding state and the current speed, hour of day, sea surface temperature and tag extent covariates. For lobster 6b, the stationary state probabilities were 0 because the animal did not visit any reef (Figure 4-7). An increasing trend with current speed and sea surface temperature can be observed, i.e. the animals had the tendency to hide in the structure as the current conditions became more adverse and sea water temperature increased. To encapsulate diurnal patterns induced by drivers other than current speed, hour of day was included as a covariate to the model and clear diurnal patterns (independent from current speed) are observable. As a function of the hour of day covariate, hiding occurring at daytime. More specifically, the peak of the stationary state probability is reached at 07:30AM for lobster 6a and late morning for lobsters 10b and 12b. last, though it was found that time extent improved the model (Table 4-4), there is no clear trends with this covariate.

Further to the results presented so far, the two HMMs are combined to complement the estimation of behavioural states at times when acoustic detection did not allow fine scale positioning. The resulting time series are shown in Figure 4-19 for lobsters 6a, 5b, 6b, 10b and 12b which are the animals that resided in the monitoring area for more than 20 days. The temporal trends are contrasted between individuals, reflecting very different settling in the monitoring area. Lobster 5b, 12b and 10b visited the reef structures whilst lobsters 6b and 6a only visited the reefs marginally (Figure 4-7). For lobster 12b, no consistent home range could be inferred from the positioning data but the time series in Figure 4-19 reveals that this is probably due to the animal hiding in the structures. For lobster 10b which settled

consistently at R01 for an extended period, a consistent sequency of states was observed (Figure 4-19): Local behaviour is substantial at the start of the time series (17-05-2022 to 29-05-2022), followed by days characterised with hiding in the structure (30-05-2022 to 04-06-2022). The second part of the time series consists of an increase in local behaviours (04-06-2022 to 18-06-2022) followed by a further increase in local behaviours together with a reduction in hiding (19-06-2022 onward), which could be behaviour typically for prior to leaving the monitoring area.

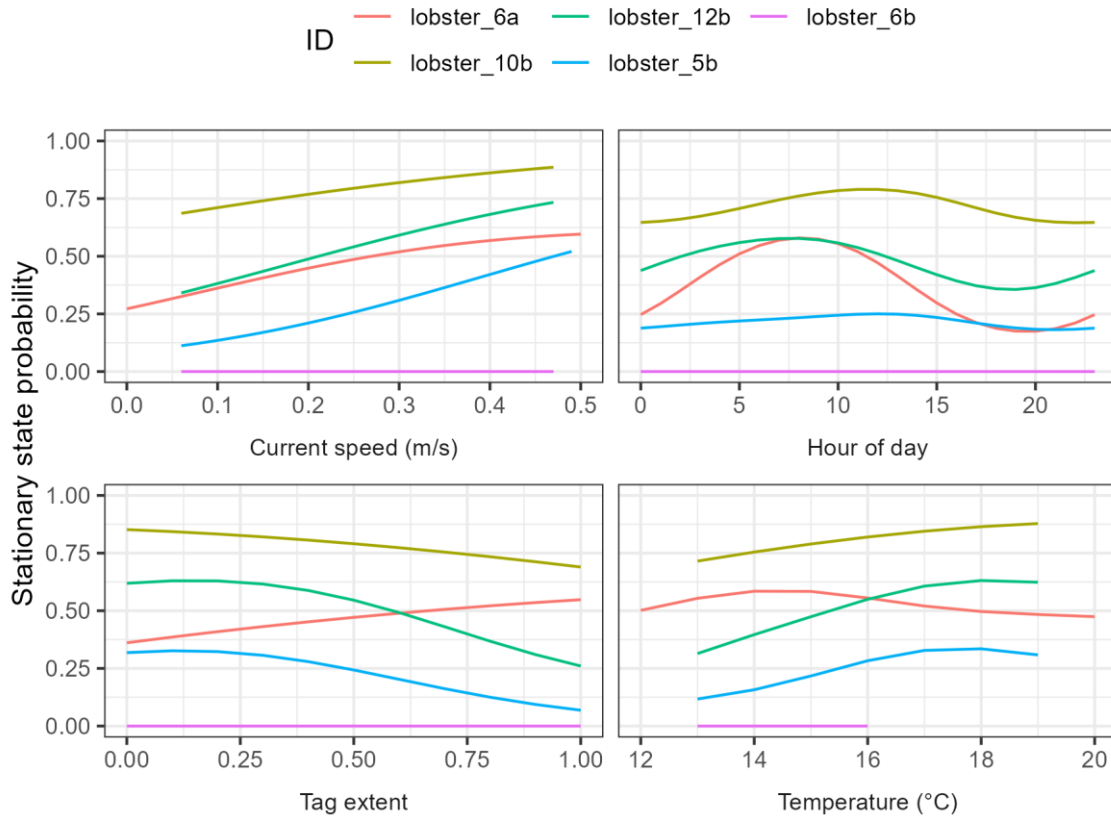**Figure 4-18:** *non-spatial HMM hidden state stationary state probabilities, which represent the relationship between the hiding state and the model covariates. Only the hiding state is presented. Results are shown for individual lobsters (colours) exemplifying a residency of more than 20 days. Model covariates other than individual lobsters are current speed (m/s), hour of day, and tag extent (0 at release, 1 at last detection).*

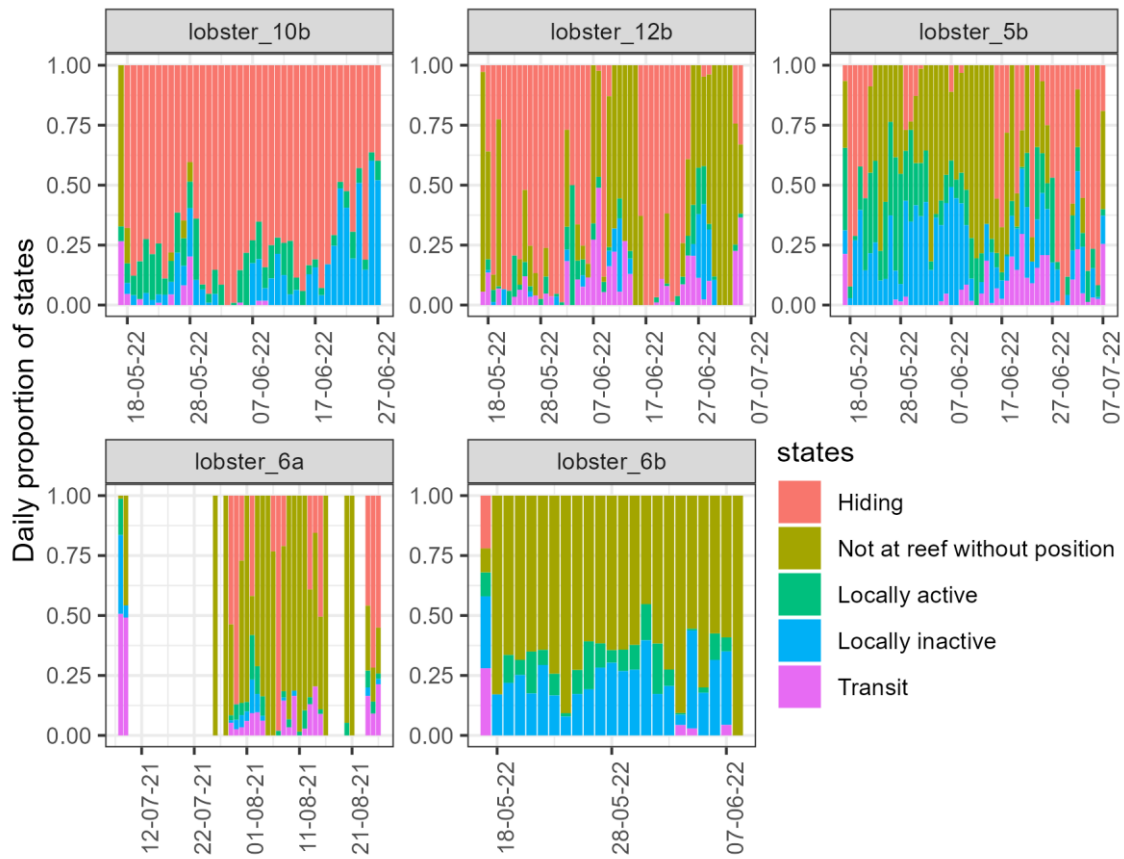**Figure 4-19:** daily proportions *of states, combining the spatial HMM used to infer behavioural states and the non-spatial HMM used to infer hiding in the artificial structures. The proportion of states is based on the decoding of states using the Viterbi algorithm (McClintock & Michelot, 2018). Results are shown for individual lobsters (colours) exemplifying a residency of more than 20 days.*

5 Discussion

In this study European lobsters were translocated from other origins to four artificial reefs in Borssele II offshore wind farm (OWF) in order to gain information on European lobster behaviour as a measure for (artificial) reef functioning. The European lobsters did not settle for prolonged times (Figure 4-5). Still home ranges could be determined and differences in behaviour as well.
After treating the data quality, the aspects of not settling, area usage and behaviour will be treated next.

5.1 Methodological considerations

More than 50% of the registrations consisted of detections recorded by less than three receivers simultaneously (and). Several causes could be thought of:
1. The European lobster were often in the concrete artificial reefs and other shelters (Figure 4-13). The concrete walls most likely blocked or shaded the acoustic signals. This phenomenon has been seen before (Van der Meeren, 1997, Umani et al., 2005). The receivers were at ~125 m from the reef. Given the amount of concrete adding an extra antenna, nearby the reefs will most likely not increase detection numbers.
2. The acoustic receivers were mounted on customised frames with the receiver placed on top of a 1.5 m tall stainless-steel tripod. One can imagine this is a low position to detect small seabed bound European lobsters with high fidelity. They served well to detect the demersal and pelagic tagged cod in the parallel running test (Berges et al., 2023). Most authors had higher positions to monitor the acoustic signals (Van der Meeren, 1997, Moland et al., 2011a, Skerrit et al., 2015, Wiig et al., 2013, Moland et al., 2019). Alike these authors, higher tripods could increase detection numbers. However higher tripods would make the antennas more vulnerable for currents by tumbling them over. Antennas could be moored with an anchor and buoy. This offers the possibilities to hang the antennas high in the water column in an ample overviewing position (Skerrit et al., 2015, Wiig et al., 2013, Moland et al., 2019). This would increase the processing time since the calculated positions would need to be corrected for the movements of the antennas in time and space due to tides, currents and waves.
3. Due to circumstances some receivers were lost reducing the possibilities to have three simultaneously confirmed detections. More regular read-out trips could reduce the effect of receiver loss.

Overall, the poor settlement and short stays resulted in low number of replications. This low number limited the statistical power of the results presented here. Only few individuals exemplify settling in the area. European lobsters are quite individualistic in their behaviour (Skerrit et al., 2015, Wiig et al., 2013, Moland et al., 2011a, 2019, Thatcher et al., 2023, Figure 4-17). Larger numbers of data are needed to really analyse patterns of behaviour. Therefore it was decided to restrain from in depth statistical analysis.

5.2 Potential causes for lack of residency

Both in 2021 and 2022 more than 50% of the European lobsters had left the arena of receivers within five days (Figure 4-5). Potential causes could be:
1. Shock of the translocation and experimental handling.
2. Strong longing to the original homing ground combined with high demands on new homing grounds (Chapter 3, Van der Meeren, 1997).
3. Local European lobsters present.

4. Lack of sufficient food due to the young age and community of the artificial reefs (possibly illustrated by the differences between 2021 and 2022 data?).
5. Lack of suitable crevices (Jensen et al., 2000).

5.2.1 Shock of the translocation and experimental handling

The animals were taken from the laboratory early in the morning and transported to the site in wet rugs. All together it took maximally 8 hours before the animals were released. In addition there was the pre-handling of minimally three weeks in the aquaria of the laboratory. This could have caused serious unrest in these animals that have a strong urge for a crevice and territory.

Moland et al. (2011b a data storage tag) and Skerrit et al. (2015, Vemco tag) and Lees et al. (2018, 2020) tagged European lobsters with on board and released directly just after capture ,b, 2019) Moland et al. (2011a) and Thatcher et al. (2023) took the European lobsters on land to attach the Vemco tag. The handling time was not given. In all cases the animals were released at the site of capture. Most remained at the site of release. So European lobsters can withstand some handling even being brought to land for at least several hours. The big difference with our set up is the release in their home ground whereas in this experiment the animals were released in a completely new area. Lag effects of the handling cannot be excluded still the lack of territory seemed more important.

5.2.2 Longing for their original home

Strong site fidelity to home ranges of origin, i.e. translocated lobsters were used, combined with high demands on newly encountered habitats could have caused a lack of settling. More or less 30% of the translocated European lobsters settled in the area of the reefs. On average they spent ~five days either to leave or to remain on a site (Figure 4-10). Van der Meeren (1997) showed that an European lobster released near its shelter returned in a straight line to its shelter. A second European lobster transplanted less than a km headed immediately towards its original site. Two translocated European lobsters from further distance took up residence in the lagoon after less than 5 hours of roaming. Picciulin et al. (2005) transplanted four European lobsters of which three roamed a while before settling or leaving. Five of the total of six the transplanted European lobsters (over the both studies) did not settle for long (20 days maximum). The sixth lobster was still in the area when the measurements stopped (Van der Meeren, 1997). Various studies have shown that European lobsters have a strong homing and site fidelity (Smith et al., 1998, 2001, Agnalt et al., 2007, Moland et al., 2011a, 2019, Wiig et al., 2013, Huserbråten et al., 2013, Skerrit et al., 2015, Thorbjørnsen et al., 2018, Lees et al., 2020, Thatcher et al., 2023). They know their territory thoroughly, traveling long distances with the crevices out of sight and still returning (Van der Meeren, 1997, Skerrit et al., 2015, Lees et al., 2018, 2020) either by sight and / or more likely by chemoreception (Atema, & Voigt, 1995),
Figure 4-16 seems to suggest that towards the end of the resident period, the European lobsters use less of their shelter and start to roam around.

In Poole Bay, Dorset (UK) newly installed artificial reefs were colonised by passing European lobsters within three weeks (Collins et al., 1991, Jenssen et al., 1994). But here also some settled European lobsters left suggesting temporal residence. European lobsters can be washed away by the currents far off their home grounds, next wandering around looking for some hard substrate to take shelter. E.g. the densities of wandering European lobsters on Dutch NCP soft sediments were roughly estimated at 2 lobsters km^{-2} (Rozemeijer & van de Wolfshaar, 2019) This seems a voluntary settlement process where European lobsters encountered the crevices and shelter they prefer (Rozemeijer & van de Wolfshaar, 2019).

Apparently European lobsters have a strong sense of home. It could be that the transplanted lobsters needed time to settle for a new place as is suggested by Figure 4-10. Clues for finding habitats suitable for settlement could be food availability (scent) and shelter. Meanwhile roaming, >50% of the animals wandered outside the area of detection and > 60% after 10 days (Figure 4-5).

The European lobsters from 2021 came from Ireland. They took less temporary residence than the 2022 European lobsters landed by Dutch fishermen. It could be that the ecological shock was larger for the European lobsters from Ireland (very different water and substrate). But differences between the two study years in hydrology, temperature, history and succession stage of the reefs, cannot be ruled out as potential causes for this as well.

5.2.3 Local European lobsters present.

It could be that local European lobsters were present by migration (Collins et al., 1991, Jenssen et al., 1994). However ROV video footage (at least 24 minutes of each reef) of February 2022 showed no European lobsters. Brown crab was observed only once. Also limited video footage in 2022 and 2023 showed no European lobsters. On the other hand 8 European lobsters were caught by a total of 405 baited pots in 2022 at 500-1000 m distance to the scour stones, indicating both that European lobsters are present and on the other hand densities seemed very low (Rozemeijer et al., 2023). Given the lack of any European lobster in the video footage of 2022, it seems not likely that there was a fierce concurrence for territory and crevices, although it cannot be excluded.

5.2.4 Lack of sufficient food

A lack of sufficient food due to the young age (placed in July 2020 so 1-2 years old) and community of the artificial reefs could be another cause why the transplanted European lobsters did not settle. European lobsters eat a wild variety of prey items: algae, hydrozoans, jellyfish' fish, tunicates, polychaetes, shell fish and other molluscs, echinoderms, and crustaceans. They can be described as generalist predators and scavengers likely to feed opportunistically by consuming items mostly based on availability (Hallbäck & Warén, 1972, Leiknes, 2023).

The reefs were not scientifically monitored during this period. The video footage of February 2022 showed especially plumose anemones (*Metridium* spec) on the inside of current exposed sewer pipes. Less exposed parts could have coverage on the outside. Most conspicuously there was hardly epibenthos visible. The number of other crabs was also low. Older OWFs can have well developed epibenthic communities on the scour layers, providing ample food supply (Ter Hofstede et al., 2020).

Other studies on wind turbines, steel, concrete tripod foundations and anti-scouring can give some indications. Kerckhove et al. (2019) studied succession on the wind turbines and anti-scouring of neighbouring Belgian OWFs. The only long-term (10-year) study identified three distinct succession stages (Figure 2): a relatively short pioneer stage (0–2 years) was followed by a more diverse, intermediate stage (3–5 years) characterized by large numbers of several suspension feeding invertebrates, and a third "climax" stage (6+ years) co-dominated by plumose anemones (*Metridium senile*) and blue mussels (*Mytilus edulis*). After one and two years the potential food for European lobster is available but not in such abundance as later in the succession (Kerckhove et al., 2012, 2019, Jenssen et al., 1994). Bouma & Lengkeek (2012, 2013) also showed potential prey species in their inventory of OWF Egmond aan Zee (OWEZ) after two years. They also demonstrated an increase in species number two years later (maturing of the community).

So it is very possible the food availability was still low on these reefs one and two years after deployment. The hypothesis that food availability determined lobster presence cannot be excluded. In fact it is quite likely.

5.2.5 Lack of suitable crevices

The lack of suitable crevices could also be a cause for emigration out of the study area. Jensen et al. (2000) stated a reef should have crevices for all sizes of lobsters. Preferably they use existing crevices in a rocky environment than dig a burrow themselves (Dybern, 1973). Important aspects for a crevice are den length, entrance size, the presence of multi-openings that function as escape routes, and internal aspect ratio of the shelter necessary for sufficient manoeuvring space. Crevices should have the right length and also be tight fitting (not too broad in order to be able to defend the entrance. Ideally the crevices have sufficient water exchange to prevent accumulation of metabolic waste

products (Jensen et al., 2000, Verdonk, 2021). Jensen et al. (1994) stated a new reef had more of the larger European lobster because the new reefs had more suitable crevices available. The reefs consisted of large (as compared to the European lobster) concrete tubes (**Figure 4-1**). Figure 4-10 suggested the European lobsters have been using the concrete pipes but the dimensions apparently did not meet the requirements as defined in Jensen et al. (2000) and Verdonk (2021). European lobsters prefer a tight fitting crevices (Jensen et al. 2000). The smallest concrete pipes had a radius of 25 cm. With most European lobsters sat maximum 14 cm CL (**Figure 4-4**), they would have needed a crevice with an entrance radius of < 16 cm (Barry & Wickins, 1992).

The scour-bed has typically crevices of 6*6*6 cm (Rozemeijer & van de Wolfshaar, 2019). Given the large size of the European lobsters (CL > 10.5 cm, **Figure 4-4**) these crevices are not suitable.

Thus, lack of suitable crevice can be a potential cause explaining the migration of the transplanted European lobsters. And it is as plausible as lack of food.

5.3 Area utilization

The averaged UD95 ranged from 1,524 m^2 to 2,009 m^2 (**Table 3-1**). This was low as compared to other studies: ranging from 2,068 m^2 to 173,053 m^2. Skerrit et al. (2015) also estimated an UD95 of 455 m^2 but this was in autumn period when European lobsters start to reduce their activities (Smith et al., 1998, Skerrit et al., 2015, Moland et al., 2011a). The 173,053 m^2 (Wiig et al., 2013 Moland et al., 2019) represented a very large UD95 as compared to other studies (**Table 3-1**). The second largest is 19,879 m^2 (Moland et al., 2011a); ~11% of 173,053 m^2. The authors thought that difference in measuring method, low population densities or higher water temperatures could have caused the larger UD95 (Wiig et al., 2013, Moland et al., 2011b, 2019).

5.4 Biological relevance of the different behavioural states

The behaviour and area of the European lobsters was described using different behavioural states. Four behavioural states were defined (Figure 4-11):
- A locally inactive state with low mean step length and a regular change in movement direction. This behavioural state is closer associated to the settlement locations than the other two (Figure 4-15).
- A locally active state associated with moderate mean step length with regular change in movement direction. This behavioural state is closely associated to the settlement locations than the transit state but not as close as the locally inactive state (Figure 4-15).
- Transit state associated with large mean step length and large and directional movements, associated with e.g. travelling across the monitoring area at larger distances from the settlement locations.
  Hiding: being either in the concrete tubes or nearby and thereby in the sound shadow of the artificial reef.

The local inactive state could be interpreted as foraging or being inactive. This seems more resting type of behaviour (given also the low step length, Table 4-3). Given the larger distances from the settlement objects (Figure 4-15), the locally active state could mean intensive searching and foraging behaviour (Skerrit et al., 2015, Martin et al., 2009). Skerrit et al. (2015) associated moderate mean step length with regular change in movement direction to the hard substrate. The irregular hard substrate would force the European lobster to move with large turning angles and low speeds. In our case this behaviour occurred on both the scour bed as well as the soft substrate so it could mean both. According to Martin et al. (2009) and Skerrit et al. (2015) increased speed and directionality (transit state) could stand for exploratory behaviour while at the same time reducing the risk for predation by e.g. seals.

The issue of the hiding and thereby the signal being obstructed has occurred in other researches as well. Van der Meeren (1997) and Picciulin et al. (2003) mentioned the obstruction of the acoustic

signal. Skerrit et al. (2015) had only 24-28% of possible animal tag transmissions detected on at least 3 receivers, which is lower than our situation (closer to 50%, Figure 4-13). Thatcher et al. (2023) saw European lobsters hiding in the scour bed of an OWF for periods from 2 to 187 h, with a mean duration of 6.66 ±0.53 h SE across all sites. This seems shorter than the hiding is this study which can be explained by the differences in substrates. A scour bed is made of small rocks and not suitable to host the large European lobsters Thatcher et al. (2023) used (Rozemeijer & van der Wolfshaar, 2019). So the hiding is both obstruction of the acoustic signal by the concrete pipes and it is actual hiding in a crevice presumably in or between the concrete pipes.

5.5 Correlations with abiotics

A tentative analysis was made correlating the different behavioural states with abiotic factors (Figure 4-17). Current speed, distance to the reef, hour of the day and temperature were all significant variables (Table 4-2). Since the animals showed very heterogenic (opposing) behaviour in relation to the variables it was decided not to generalise the observations but to show the individual behaviour (Figure 4-17).

5.5.1   Current speed

With increasing current speed the behaviour seemed to shift from transit behavioural states to more localised behavioural states. The locally active state is near the structures so movements could have been made in the lee side of the structures (conform Howard, 1988). High activity at high current speeds is contrary to expectations from an energy expenditure point of view. In addition, Howard (1988) showed European lobster get unstable at current speed >0.3 m/s and are washed away at current speeds > 0.4 m/s. Because of the sensitivity for high current speed Howard (1988) showed a high dependency with the tidal cycle. Less transit behaviour and more local behaviour on the anti-scouring or near and in the shelter is conform these observations. Observed current speeds (0 – ~0.5 m/s, Figure 4-17) seem still acceptable for prolonged periods during the tidal cycle for the European lobsters ate the Borssele II reefs.

5.5.2   Distance to the reef

At larger distances from the reefs and shelter the behavioural states changed from small steps, a lot of turns to transit behaviour with increased speed and directionality. This is conform Skerrit et al. (2015) and can be explained as an active switch to explorative behaviour. Usually the males are more explorative (e.g. Skerrit et al., 2015). Three out of 5 European lobsters had their local inactive and active states very close to the artificial reefs. Two other European lobsters exhibited also local inactive and active states further from the artificial reefs. This demonstrates the individualistic behaviour (Figure 4-17). In comparison to Skerrit et al. (2015) and Lees et al. (2018, 2020), the European lobsters of this study seemed to explore more over larger distances (transit behavioural state, Figure 4-15)

5.5.3   Hour of the day

In most cases authors have shown an emphasis on nocturnal behaviour with potentially increased intensity during dawn and dusk (Smith et al., 1998, Skerrit et al., 2015, Lees et al., 2020, section 3.3) Unlike these authors no clear nocturnal behaviour was seen, rather the opposite. Loss of nocturnal behaviour was associated with autumn and winter when light is reduced (Smith et al., 1998, Skerrit et al., 2015, section 3.3). This is not the case in the experimental periods: spring and summer. No clear explanation is at hand other than a sign the animals had not settled yet.

5.5.4   Temperature

Behavioural states shifted to more transit behavioural state with increasing temperature. Metabolism and activity rise with temperature as like all poikilotherm animals (Rozemeijer & van de Wolfshaar., 2019). This is also reflected in larger territories in summer as compared to autumn and winter (Skerrit

et al., 2015, Moland et al., 2019). It could be that with increasing temperature more searching behaviour is initiated in order to obtain more food. That need for more food and at the same time absence of food might also be the reason for moving out when not enough food is encountered. On the other hand, the increased transit activity could be a sign of the not homing an preparing for departure. Both are intertwined.

5.6 Mobility in relation to fisheries and maintenance zone

For the transit behavioural state the highest daily distances were found in 2021 (477 m ± 608 m). Moland et al. (2019) measured a cumulative daily distance of 75 m (± 38 m) which is much less whereas their UD 95 was much larger on average (**Table 3-2**). Skerrit et al. (2015) estimated a cumulative step length of 260 m in spring and 348 m in autumn (no SE given). This is more in the range with current findings.

For fisheries the daily step length seems long enough to get away from the reefs and anti-scouring and out of the maintenance zone of the OWF where fisheries cannot enter. The catch pots need to be placed at least 250 m from the scour bed and the infield cables (maintenance zone) Ministerie van Binnenlandse zaken, 2020). In principle the dynamics of the European lobster (477 m) are large enough to come near the catch pots.

6 Conclusions and recommendations

6.1 Concluding remarks

Only a small proportion of tagged European lobster released at artificial reefs with and without scour-bed in an OWF showed attraction and longer residency to these new hard substrate structures. Most individuals moved out of the study area quickly after release, or after moving around in the study area. E.g. 75 % of the 2022 batch had left after 20 days. Some causes have been postulated from which strong sense of original home, lack of sufficient food and/or lack of suitable crevices seem most plausible.

In this context, the research questions stated at the start of the study are addressed below:

(1) *What are the ranges of movement, habitat use and territories of European lobster? What does this imply for fisheries with pots at 250m from the preferred habitat?*
For the few tagged European lobsters that remained longer in the study area, the European lobsters seemed to move both on and around the artificial reefs and anti-scouring (hard substrates) and the soft sediment. The territories around objects (artificial reefs, monopile, receiver) ranged from 1,524 m^2 (±817 m^2) to 2009 m^2 (±949 m^2). The territory sizes were small as compared to literature (**Table 3-1**).

Three behaviour states were defined: locally inactive, locally active and transit state. The local states were more associated to the hard structures. The transit states (with higher speeds and more unidirectional) were more associated with the soft substrates. The results indicate that for some individuals hard substrates were used, but not exclusively. Also the soft sediments around the structures were used during transit, and temporarily within the home ranges of the few tagged lobsters that remained in the study area for longer periods.

In the local behavioural states the daily distances covered ranged from 17 m (±24 m, locally inactive) to 252 m (±269 m, locally active). When in transit the minimum daily distance was 453 (±388 m). Since the maintenance zone around the OWF objects is 250 m at either side, this could imply that European lobster have sufficient daily movement to come close enough to the baited pots.

(2) *How do the hard substrate of artificial reef and the anti-scouring protection of the reefs and wind turbine influence European lobster home-ranges and movements?*
The European lobsters that remained in the receiver arena had strong associations with the artificial reefs and monopile. Even an receiver was used as crevice for a while (see **Table 3-1**, Table 4-6 and Figure 4-15).

(3) How do sex and size of the animals influence space-utilization and movement distances?
The lobsters used in this study were mostly males due to availability. Not enough data were obtained to test this research question, nor indications for differences were found.

(4) How do seasons and diel cycles influence movement and space-use?
All of the European lobsters had migrated out of the receivers area after 50 days. Therefore only the spring/summer periods could be observed in two consecutive years. Analysing the limited amount of data indicated that the activity seems to shift with increasing temperature from locally active and inactive behavioural state to a transit behavioural state.
Contrary to usual findings the released European lobsters at Borssele II seemed to exhibit more activity during daylight rather than during night time.
Given the low numbers of lobsters taking residence, their individualistic behaviour and the short stays, it is not possible to be conclusive.

The review showed that The European lobster is a large, long-lived decapod crustacean of ecological and commercial importance, distributed from the north of Norway to Morocco in North Africa. Longevity potentially span several decades. The species is considered a nocturnal animal, where light hours are generally spent solitary inside shelters on rocky bottoms. European lobsters rarely move more than a few kilometres for periods up to years. Instead they have a territory around their shelters which they know thoroughly. Territories were found between 1,728 m^2 and 173,053 m^2. The daily mobility ranged from 75 m to 477 m.

The encountered daily mobility is long enough that an European lobster can leave the no-usage maintenance zone assigned to offshore wind industry assets. It can encounter a fishing lobster pot on a daily exploratory stroll.

Using the hiding behavioural state is innovative. Only Thatcher et al. (2023) used it before. As compared we have used an HMM whereas Thatcher et al. (2023) used proximity of the final three receivers position prior to an absence period. More than 50% of the detections was registered by less than three receivers, which did not allow positioning. Hiding in the hard structures, which block the acoustic signal, was likely to play an important role in this. Maintenance frequency should be increased to increase likeliness of receiver retrieval. Still the resulting available high frequency registration of successful movement enabled sufficient quality monitoring in the area, validating the design put in place. As became apparent from Figure 4-17 European lobsters exhibited individualistic behaviour. Combing heterogeneity in behaviour with the low number of replicates the prevented generalisations by correlations with abiotic variables.

A successful framework was developed to capture spatio-temporal trends, infer behaviour and identify hiding in structures by using detections that did not allow positioning as well. The latter is an innovative approach that could also be used in other positioning studies.

Within this study using translocated European lobsters only for a small proportion of the individuals settlement for prolonged times was found. Potential causes could be:
1. Strong longing to the original homing ground combined with high demands on new homing grounds.
2. Lack of sufficient food due to the young age of the artificial reefs and subsequent short period of colonization and development of communities.
3. Lack of suitable crevices.

6.2 Recommendations

Understanding artificial reef functioning is of major importance at this moment since newly placed OWFs need to improve biodiversity and apply biodiversity improving measures. In order to assure effectiveness of measures like artificial reefs, enhanced understanding is necessary.

European lobster are in principle good target species to study reef functioning: they are home bound and can influence their environment by their high energy need (= need for food). But also other reef associated species are of interest like cod and brown crab (*Cancer pagurus*).

Research is needed to reef functioning using animal behaviour (acoustic telemetry) and trophic relation studies (by stable isotope ratios) as a basis. The environment should be manipulated by adding extra reef structures with a diversity of crevices. For future studies the animals should be caught at the location. Given the fast colonisation of the concrete, biomass and biodiversity should already be higher enabling more mobile communities to feed on it. Visual surveys with cameras could be performed to check if lobsters are already present before intensive efforts to catch locally present lobsters for follow-up telemetry studies are carried out.

Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

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Justification

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The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

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Date: 29 February 2024

With knowledge, independent scientific research and advice, **Wageningen Marine Research** substantially contributes to more sustainable and more careful management, use and protection of natural riches in marine, coastal and freshwater areas.

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