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Lesser Sandeel (Ammodytes Marinus) in the Tana River Delta; Temporal Variation in Abundance, Habitat Use and Demography

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Master of Science in General Ecology

Lesser sandeel (*Ammodytes marinus*) in the Tana river delta; temporal variation in abundance, habitat use and demography

Photo Credit: Veronica Nguka Sevedzem. Location: Tana river delta

Preface

This master thesis was made possible in connection with the environmental impact assessment for the proposed dredging project in Leirpollen, Tana, Finnmark. Fieldwork was a collaboration between NaturRestaurering AS and Multiconsult, on behalf of the Norwegian Coastal Administration Troms & Finnmark with the purpose of gaining a deeper understanding of sandeel habitat use and preferences in the Tana estuary.

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This dissertation would not have been possible without the crucial help and support of many people.

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Thank you Relindis and Emmanuel, for all your encouragement and proof-reading of this thesis.

Abstract

Lesser sandeel (*Ammodytes marinus*, Raitt, 1934, sandeel for short) is a keystone species of the Barents Sea ecosystem. However, little is known about the distribution of this species in the Tana fjord or Tana river delta system. This study examines the physical characteristics of sandeel habitat in an attempt to predictand its habitat use and preferences, as well as age and size at maturation, spawning season and individual variation in habitat use. The characteristics of sandeel habitat use were described from grab sampling and depth recordings.

Sandeels avoided areas with substrate content <0.1 mm. Zero-inflated Poisson analyses of the variation in sandeel density across different habitat types revealed abundance to peak at depths between 10 and 20 m for substrate grain sizes in the 1-5 mm range. Sandeel abundance in bottom habitats in the Tana delta, with high abundance in the spring and winter and less in the summer. Habitat preference analyses showed non-random grain-size selection amongst the sandeel individuals with the highest preference for grain-sizes around 0.7 mm and 20 mm. Analyses of the maturation pattern yielded 50 % maturation probability at length 120.8±1.9 mm and at age 0.92±0.05 years) were major determinants for maturation probability. The analysis of sandeel habitat use showed matching characteristics with the depths and habitat characteristics of the area planned for dredging. To maintain sandeel habitat in light of the planned dredging in their optimal habitat, some recommendation have been proposed as well as additional studies that ought to include echo sounding to gain further knowledge on the open water habitat use of this key species.

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1. Introduction

Lesser sandeel (*Ammodytes*), hereafter “sandeel”, is a keystonespecies in the Barents Sea. They feed on plankton and thus form an important mid-trophic link between plankton production and a variety of top predators such as larger fish, sea mammals and seabirds (Greenstreet et al., 1998, Wanless et al., 2005). Sandeels are small fish species belonging to the sand lance family *Ammodytidae*. Equipped with a pointed snout, they are capable of burrowing rapidly into bottom sediments to avoid predators (Christensen et al., 2008, Eleftheriou and Robertson, 1992). They often swim in large shoals during summer (June/July-September) while feeding and will burrow into the sand and remain performantly dormant to escape predators during nigh-time and most of the colder seasons between September to April (Robards et al., 1999). They are also known to be distributed patchily around the seabed (Macer, 1966a)

The delta area between the mouth of the Tana River is an ecologically important area for sandeels The presence of a sandy bottom and a large number of copepods makes this area conducive for sandeels to thrive (Macer, 1966). The tide current between the bay of Leirpollen the rest of the Tana River delta makes the sand form fluctuating dunes which makes it easy for the sandeels to use as shelter/cover. For the Tana delta, sandeels are a major food source for many species of fish, such as cod (*Gradus morhua*), saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*) and flatfish species, particularly plaice (*Pleuronectes platessa*) (Høines et al., 1995), marine mammals and birds such as the IUCN red listed species (VU) Atlantic puffin (*Fratercula arctica*). Sandeels play an important role in the Tana estuary in that they support a large amount of goosander (*Mergus merganser*). The sandeel population here might be a major ecological driving force behind one of the world’s most productive Atlantic salmon (*Salmo salar*) rivers, the Tana River. If the sandeel stocks in this area decline, it could affect the total salmon production in the Tana river because goosander could switch to eat salmon smolt instead of sandeels during spring and early summer (Svenning et al., 2005). Svenning et al., (2005) reported that although thousands of goosanders, which are known from elsewhere to feed on Atlantic salmon smolt, concentrate in the Tana River through which 20 % of all Norwegian Atlantic salmon smolt migrate, goosander predation was negligible in the 2 years of this study, 1981 and 2000. This appears to a large extent to be the result of the presence of vast numbers of readily available sandeel and, early in the season also capelin in the estuary, forming an alternative and important prey source. As the numbers of sandeel probably fluctuate greatly in Finnmark estuaries, it is, however, conceivable that goosander predation on smolt is more important in years with a much lower sandeel population than in normal years. A study was also carried out in the North Sea revealing that five predatory fish species, including three of high commercial value, had better body condition in areas or years with high densities of sandeel (Engelhard et al., 2013). Therefore, changes in sandeel productivity are reflected in the populations of many other species, particularly in breeding birds (WWF, 2006), and in the Tana fjord, possibly also anadromous fish species.

The channel to the inner Leirpollen is becoming too shallow for among others, ships that transport aggregates from the (Quartzite) mine inside the channel at the inner, south-eastern section of the Tana estuary (Figure 1). There is, therefore, a need for dredging this area, and thus, concern has been raised for the sandeel population known by local fishermen to inhabit the Tana delta and estuary. The main focus of this study was to explain the distribution of sandeels and their habitat use and preferences in the Tana river delta.

A method of investigating sandeel habitat use and preferences is through grab sampling that samples species occurrences relative to environmental characteristics. The study of a species' relationship to its environment can reveal the characteristics of the environment that determine the specie distribution (Heglund, 2002). The pattern of distribution of sandeels is determined by biotic, abiotic relationships and life history. Therefore, sandeel abundance, habitat use and habitat preferences can provide insight into the ecology of sandeels and how this may be affected by the planned dredging. Information on habitat requirements, habitat use, habitat selection/preferences, recruitment success (spawning season), age and size at maturation, seasonal variation and density for sandeels in the Tana river delta is lacking.

Sandeels have been shown to have specific habitat requirements in other parts of the world. This includes sediments, salinity, currents, depth and temperature. Sandeels are morphologically adapted for burying into bottom sediments and spend a considerable part of the year buried in the sand, demonstrating a high habitat specificity. Sediment grain size together with the strength of currents over the seabed will affect aeration of the sediment and consequently the supply of oxygen to buried fish. This will influence the distribution and density of sandeels, because of these habitat requirements, adult sandeels are restricted to appropriate areas of the seabed (Reay, 1970, Wright et al., 2000). Depth is also an important general factor, with few sandeels found below 70 m, probably due to the decline in water movement with increasing depth (Wright et al., 2000). Sandeels inhabit a narrow range of 'sand' sediment compositions therefore, by analysing seabed characteristics, it should be possible to predict where sandeels are found (or not) in the Tana river delta (Wright at al., 2000). Substrates used by sandeels have been consistently characterized as well washed, drained, and unpacked and typically contain coarse sands with little or no mud and silt (e.g. (Dick, 1982, Meyer et al., 1979). However, we know very little about sandeel habitat preference and what drives this within the Tana river delta.

Sandeels are known to show size-specific habitat use, where larger sandeels inhabit coarse sand, while immature sandeels use fine to medium sand grains. This was confirmed in a study carried out by Holland et al., 2005. A possible explanation for this relationship could be the ease of penetration into the sediment. However, shear-stress experiments indicated that penetrability should not prevent sand eels from entering fine sand, coarse sand, gravel or silt (Pinto et al., 1984). Alternatively, oxygen requirements may once again underpin this relationship. Larger sandeels are likely to require more oxygen, which will be more readily available in coarser sediments where interstitial spaces are larger and more readily flushed (Holland et al., 2005). In the Tana delta, little is known about sandeel habitat use.

Sandeels rarely occur in sediments where the silt content (particle size <0.063mm) is greater than 4 %, and they are absent in substrates with a silt content greater than 10 % (Wright et al., 2000, Holland et al., 2005). Greenstreet et al. (2010) adapted sediment categories first proposed by Holland et al. (2005) and defined sandeel suitable substrate in terms of "coarse sands" (with a particle size between 0.25mm to 2mm) and "silt and fine sands" (with particles between 0.002 mm and 0.25mm). The greater the percentage of "coarse sands" relative to the percentage of ''silt and fine sands'' the greater the potential for the substrate in a given area to constitute a preferred sandeel habitat (Anonymous, 2014). Sandeels also tend to occupy areas on the sloping edges of sandbanks (Greenstreet et al., 2010). With difficult bottom substrates such as large rocks or where the bottom has a significant slope, it could be difficult to obtain samples.

Human activity is an increasingly important factor influencing the ecological state of the marine environment (Halpern et al., 2008, Syvitski et al., 2005). Developments along coastal shorelines, such as dredgings and other coastline modifications may temporarily or permanently remove suitable habitats for species using these areas (Wen et al., 2010). In this context, there is a need to study the species living in areas influenced by tidal flow and human developments in order to understand the organism's responses to the alterations and the impact the developments might have on them.

The area planned for dredging in the Tana river delta is perhaps the most important known area for sandeels inhabiting this area (pers. comm. Jon Inge Guttormsen), and a disturbance of this area seems unfortunate. Dredging of this area will change the tidal flow, seabed slope and how the sand will settle in time after a possible dredging. In the case of a dredging, any sandeels lying in the sand might also be lost.

The purpose of this thesis was to quantify habitat use and preferences of sandeels in terms of sediment types and depth. In order to quantify sandeel habitat use and preferences, this thesis investigated the habitat requirements and the areas where the sandeel inhabit the seabed within the sampled areas. I also investigated age and size at maturation, seasonal and individual variation in habitat use and growth rates. Finally, this thesis discusses management implications of sandeels in the sampled area in connection with anthropogenic impacts, such as the proposed dredging.

2. Methods and materials

2.1 Study area

The study area was located in the delta of the Tana River, mainly in the shipping route between Tanafjorden and Leirpollen (70.53N, 28.40E), at the inner, south-eastern section of the Tanafjord, Finnmark county, Norway (Figure 1).

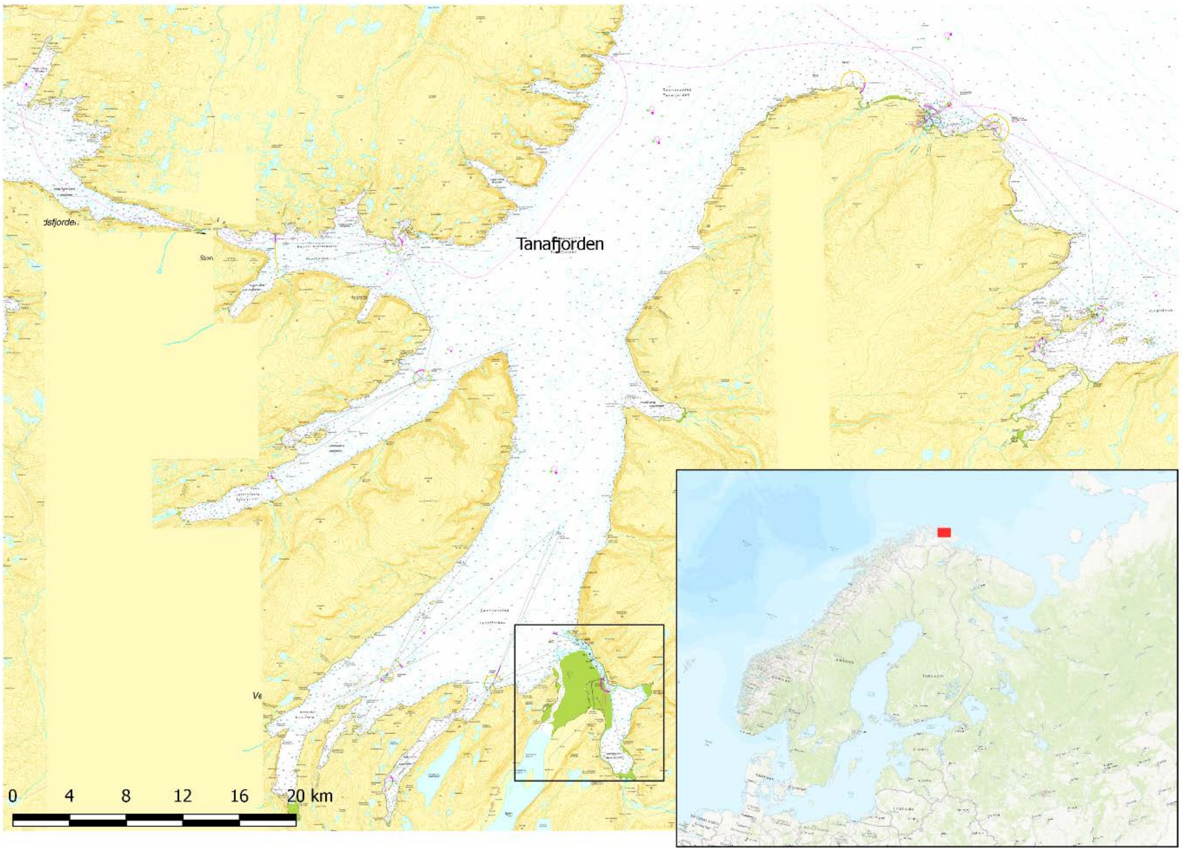


Figure 1. The study area (within black rectangle) and its location in Norway (red rectangle). See figure 2 for actual sampling points. Map Source: The Norwegian Mapping Authority 2018 (WMS).

Sampling of biological data consisted of two consecutive steps: first sampling in the field and then measurements, classification and dissection in the lab. Fieldwork was conducted using a local fishing boat and a captain familiar with this area, during nine sampling rounds (Table 1).

Table 1. Details of the sampling schedule for nine sampling rounds indicating dates, time of day and total number of sandeels sampled per sampling round.

Sampling Round	**Date**	**Start time of day**	**Total number of sandeels**
1	6. March, 2017	05.00	186
2	5. April, 2017	05.00	97
3	27. April, 2017	06.00	193
4	31. May, 2017	06.00	4
5	13. June, 2017	23.00	37
6	30. June, 2017	10.30	26
7	10-11. January, 2018	09.00	140
8	15-16. March, 2018	09.00	189
9	27. November, 2018	09.00	646

All the sampling rounds were divided into areas shallower and deeper than 10 m in field, but due to large deviations from the sea chart depths and complications on board regarding safety (waves, wind, ship traffic, visibility), plans got changed along the way making it difficult to follow the initial plan for depths on the grab shots. All the grab stations were then mapped with a predefined GPS-based plot, together with charts and employing past experiences to pinpoint sampling stations.

From March to June 2017, six successive sampling rounds of sandeels and sediments were carried out at the Tana estuary (March to June) and in 2018, three sampling rounds were carried out in January, March and November in the same area. Divisions of the sampling area into dredge zones and control zones was planned and carried out as a result of an already determined dredging area and proposed landfill area for the proposed dredging project. Four zones were planned in the dredging zones (area of influence) (M1, M2, M3 and M4; Figure 2) and four in the control zone (K1, K2, K3 and K4; Figure 2) which were considered outside the dredging zone. The control zone resembled the dredging zone in depth and by the fact that they were also close to the mouth of the Tana river. It was therefore assumed that the bottom conditions were relatively similar. In addition to these predetermined stations, a few random stations were also sampled inside Leirpollen. In 2018, five additional control zones were added to the study area (NY1, NY2, NY3, NY4 and NY5;Figure 2) at the request of the Norwegian Coastal Administration.

Grab shots were carried out in a total of 13 different zones. Of the 13 zones, eight (M1-M4 and K1-K4) were in rounds 1-6 and five additional (NY1– NY5) in rounds 7-9.

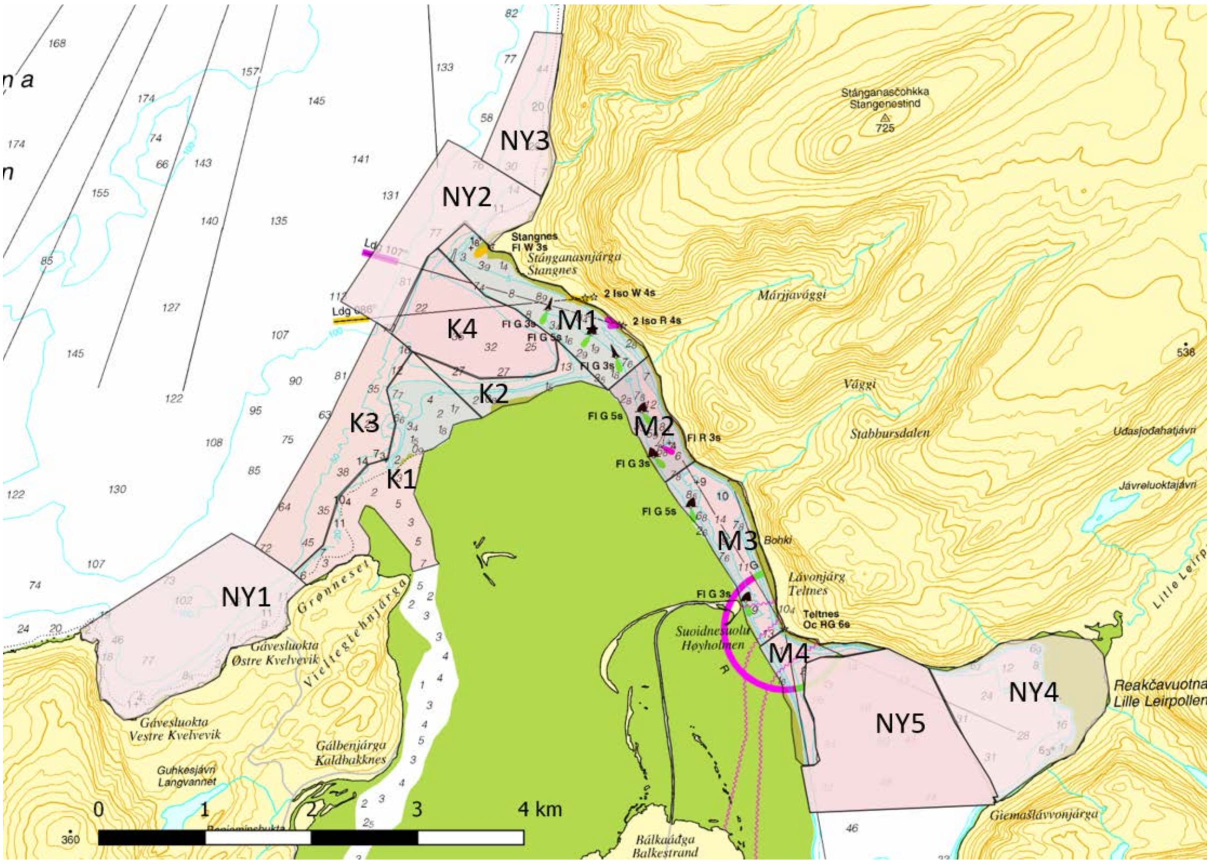


Figure 2. Dredging and control zones. M1, M2, M3 and M4 represent the dredging zones. K1-K4 and NY1-NY5 are control zones. Green areas are sand dunes in the tidal zone that can be above or below water varying from year to year, and between seasons. Map Source: The Norwegian Mapping Authority 2018 (WMS).

For each sampling round, the following were recorded; time, depth, positioning (GPS location), number of sandeel per grab shot, and the grab's fill level (percentage). Other variables noted were a description of the sediments (general impression and dominating grain size) (Table 2). In the annual samplings from January to June 2017, the catches vary between seasons and zone type. Of the 8 zones in 2017, sandeels were caught in 5. In all 5 zones, there was an element of sandy bottom. Because sandeels occur in shoals, the average catch at a given station can easily be affected by a single catch. Considering additional zones in 2018 (rounds 7, 8, 9) it appears that the highest occurrences were in late November (early winter) while the catches were average in January and March of that same year. The indication of relatively high catches in November should be given much consideration due to many traits such as maturation and spawning.

We conducted a total of 241 grab shots combined for the 9 sampling rounds distributed among the 13 different zones, including some grab shots inside the actual Leipollen on the first round Figure A1. 1.

2.2 Sample collection and handling

To sample sandeels and sediments, a Van Veen grab was used. A Van Veen grab is an instrument used to sample sediments in an aquatic environment. It is a clamshell-, bucket-like tool made of stainless steel with dimensions of L x W x H equals 136 x 36 x 35 cm (Figure 3). The grab samples by "biting" over an area of 0.1 m^2, and 8-12 cm into the sediments, so that it can sample a maximum of 24 dm^3 (litres) of sediment. Owing to the fact that the sediments contain less oxygen in sediment layers deeper than 8 cm (Lohse et al. 1996), the deeper sediments outside the reach of the grab have low suitability for sandeels (Girsa and Danilov, 1976). At the first grab deployment at each station, the grab was lowered slowly to the seabed to prevent it from being released too early. While letting the grab down into the water by a cable winch, the two levers with buckets at their ends are spread like an open scissor or a mouth. The levers are locked in this position by a little hook. When hitting the seabed, the hook will unlock the levers. The Van Veen grab has long arms attached to each bucket, thus providing better leverage during closure when the cable is pulled upward Figure 3.

Figure 3. Sampling was conducted using a Van Veen grab deployed with a wire-winch from the boat at between 3 and 5 times at each sapling station (5 times in the M-zones).

A power block was used to wind up the grab to the surface, whereby an adequate sample was obtained at each station. On recovery of the grab, the content of the grab was released into a plastic tub. A water hose was used to flush the samples into a colander whereby sandeels were manually collected and isolated from the sediments (Figure 4). Sandeels were often observed with their heads sticking out between the closed jaws of the grab. These were probably fish caught while fleeing downwards into the sand. The sandeel is well adapted for rapid movement in the sand and some were probably quick enough to avoid the grab. When empty grabs (indicating hard sediment and/or seabed) were recovered, an additional sample was attempted to verify that no sampling error had occurred. The collected sandeels were then counted and put into labelled plastic zipper bags that were later (4-6 hours) frozen for further analysis in the laboratory.

Figure 4. Sampling of sandeels and sediment in the field. Top left: Flushing of sand with a water hose through a sieve to separate the sandeels from sediments. Top right: sandeels and sediment samples are put in zipper bags marked with grab station name for later analysis. Picture at the bottom left: sandeel with its characteristic extensible mouth. Bottom right: sandeels of different sizes.

From March to June 2017, six successive sampling rounds of sandeels and sediments were carried out in the Tana delta. In 2018, three sampling rounds were carried out on January, March and November in the same area. A total of 1518 sandeels were collected for all rounds combined. The number of samples collected per round is shown in Table 1. Within the age range of 0–4 years sampled during nine sampling rounds, total length ranged from 60 to 188 mm.

The number of samples taken at each station and the number of stations sampled per round varied due to wind and waves, ice conditions and unforeseeable damage to the grab or other equipment. Technical problems, such as twisting of the wire, led to rejected grab samples and less successful samples with shallow or no "bite". The grab was deployed at different depths to know what depths were preferred by sandeels.

In each grab station from rounds one to six, the grab was deployed up to three times in order to obtain a single valid grab sample. Exceptions were zones M1 and M2, the planned dredging area, where five grab shots were carried out. We wanted the best possible knowledge base in these proposed impact zones. This was expected not to affect the fish density estimate other than increase the precision.

The first sampling round was made early in the morning until daytime to be able to cover the time of the day the sandeel should be active. When we discovered the large decline in catch in round 4, we chose to change subsequent rounds to the night. Our aim was then to investigate high or low densities of sandeels in the sand at night. On the other hand, we also had low densities of sandeels during rounds 5 and 6, even though these were done at night. The sandeel is probably far more active throughout the day in the Arctic where there is midnight sun, but still during the day, there should be less sandeels in the sand in the late spring/summer. In subsequent sampling rounds 7, 8 and 9, some additional control zones (NY1- NY5) were added. This was to further investigate the control zones compared to the impacted zones. In the majority of the deeper areas (the areas furthest away from land in NY1, NY2, NY3, K3 and K4), it was difficult to retrieve grab samples due to the angle of the sea floor or the size/composition of the substrate in all rounds considering they prefer depths of 5 – 15 m down in the sand. The sandeel grab density data provided an index of the abundance of sandeels buried in the sediments at specific times of year and day.

Sandeel larvae were sampled using a modified plankton net haul (65 µm, Ø=80 cm; Figure A1. 2) that was pulled after the boat for 50 m at two different locations in all the sampling rounds, that is, the control zones and the dredge zone, respectively. The hauls were made at different depths, but as close to the bottom as possible. The main features were drawn approximately 50 meters after the boat before pulling aboard (Figure A1. 2). This was done both in an attempt to sample sandeel larvae, and to sample and investigate the dominating zooplankton at the time. The sample from the bottom container of the plankton net was collected and preserved on 70% ethanol for later laboratory analysis.

All targeted grab stations were sampled on the same day on each of the first six rounds, with a total of eight grab stations, whilst round 7, (10-11 January 2018) and round 8 (15-16 March 2018 and beachfront, 13-14 March 2018) needed two days for sampling. This was because they both had a larger area to sample from i.e. five additional control zones (NY). The beach sampling was done with a shovel on low tide, flipping out the sand to a depth of about 30 cm and checking for sandeels. This was done for 350 places along the shoreline and further within the estuary (figure A1. 4) Round 9 was sampled during the same day through to the night.

2.3 Laboratory characterization of samples

2.3.1 Length, age and maturation determination

In the lab, I measured the total lengths (anterior tip of maxillae to tip of caudal fin) of the fish to the nearest millimetre (mm). Half fish (head/tail) were not included in the total sandeel count.

Age determination was conducted following the International Council for the Exploration of the Sea (ICES) protocols on the seasonal appearance of translucent and opaque zones in sandeel otoliths. The otoliths were extracted and put in a glycerol solution which was then mounted on a microscope to read the opaque and transparent zones (Anonymous, 1995) (Figure 5). The winter zones on the otolith appeared translucent and the summer growth zones appeared opaque. It is these zones which were counted to determine sandeel age according to (Macer, 1966b) and base on the appearance of opaque otolith centres and the seasonal changes in the material on the outer rim, i.e. where it was transparent or opaque. This assumption is done to estimate the start of the growing season. The translucent zones indicate the period of the year at which there was little or no growth rate. Whereas, the opaque indicates the period of the year at which sandeel growth rate was rapid. By counting the number of opaque and transluscent rings, the ages 0+, 1+, 2+, 3+ and 4 were determined.

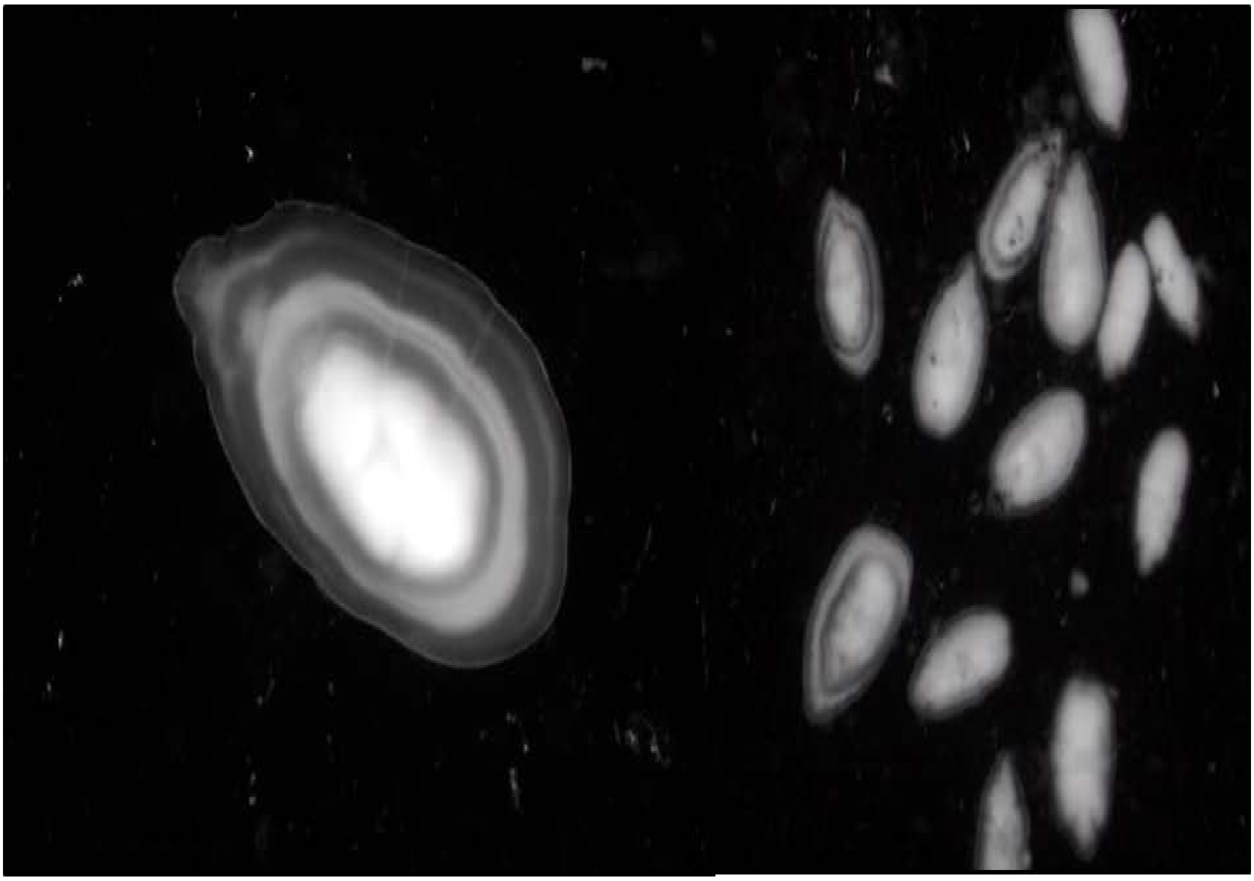


Figure 5. Laboratory analysis of otoliths (over). The otolith on the left is elderly three-year old individual, caught during round 9, which was then at the end of its third winter (winter zone = transparent/dark zone). The opaque zones are growth zones. To the right, we see a selection of otoliths from different ages. The smallest otoliths are from individuals that just experienced their first winter.

For most sandeels, all otoliths were read. In stations with many samples (rounds 7, 8 and 9), a subsample was selected (mostly the larger individuals) for otolith reading and dissection, and the remaining smaller sandeels were only measured for length. The smaller individuals were aged with length measurement considering that all individual ≤110 mm were 0+ years old (sandeels starting their growing season). Although there could be exemptions in the above assumptions.

Due to low numbers of fish, all individuals from rounds 4, 5 and 6 were examined for maturation stage and the other rounds were subsampled for maturation stage (again, larger individuals were chosen for dissection). Stage of maturity was determined by score of visual inspection of the gonads (Figure A1. 6). As noted by Macer (1966), it proved difficult to see gonads / sex in younger individuals (round 1-8), and older individuals after the fish have spawned. Sandeels will begin the development of gonads in the fall, until spawning in mid-winter. All analyses of maturity at age and size were therefore based on data from the ninth round in late November 2018. All individuals for which maturation stage was indeterminate were considered immature and all mature fish of both sexes were in late maturation at the time of sampling. The gonads growth rate starts in September -October and spawning takes place in November -January. The Norwegian Institute of Marine Research's guide to sampling of fish and crustaceans was used as a sampled guide (Mjanger et al. 2017).

2.3.3 Stomach content

The stomach content was checked for zooplankton, and possible sand, upon dissection. Identification of the dominating stomach content (copepods *Calanus finnmarchicus*) or other zooplankton was done under a microscope. A total of 50-70% of individual stomach content was checked for copepod from all the sampling rounds. The percentage of empty stomachs in the investigated individuals varied between 70-100%. 13% of the total catch from all the sample rounds lacked head and / or tail or bowels due to the way the grab caught the fish, and these fish were counted, but not dissected.

2.3.4 Sediment analysis

Sediment samples from each grab recovery was collected and checked to determine grain size, and this was used to evaluate habitat characteristics. Once at the surface, the grab was emptied and cleaned for the next sample (Figure 4). The dominating grain size category was assigned in situ and later the average grain size was derived from the size category by geometric mean and the size categories of the sediment were combined to fit the Wentworth grade classification (Wentworth, 1922). Based on laboratory assessments and combinations of these grain-size classes, mean grain size was yielded according to Table 2.

The sediments inside the Leirpollen were found to be technical impossible for approved grab shots (more than 15 failed grab shots per zone due to hard and tightly packed substrate). This meant that sampling inside the Leirpollen was terminated. Difficult natural conditions (depth / slope / bottom substrate) led to zero sandeel catches from zone K4 under round 5 and round 6. In zones K3 and K4, only two fish were caught during all rounds (grab shots 2K4B, round 2). Hard seabed may be the most likely reason for a site to be categorized as unsuitable for sandeel, while sediments with excessively high percentages of silt and fine sand were second (see results section).

Table 2. Sediment category (size range) under the Wentworth scale (1922) with the corresponding diameter.

Sediment size category (mm)	Nomenclature under Wentworth	Mean diameter
>256	Blocks	362.0387
64–256	Stones	128.0000
32–64	Very coarse gravel	45.2548
16–32	Coarse gravel	22.6274
8–16	Medium gravel	11.3137
4–8	Fine gravel	5.6569
2–4	Very fine gravel	2.8284
1–2	Very coarse sand	1.4142
0.5–1	Coarse sand	0.7071
0.25–0.5	Medium sand	0.3536
0.125–0.25	Fine sand	0.1768
0.063–0.125	Very fine sand	0.0884
0.002–0.063	Silt	0.0156
<0.002	Clay	0.0020

Table 3. Proportion of grab shots with coarse sand (best sandeel habitat) distributed on M and K zones

Round	**Proportion of coarse sand M-zones**	**Proportion of coarse sand K-zones**
1	83.0 %	8.3 %
2	68.8 %	16.7 %
3	62.5 %	0 %
4	75 %	16.7%
5	43 %	11.1 %
6	58.3 %	0 %
7	62.5 %	0 %
8	42 %	0 %
9	62.5 %	0 %

2.4 Analysis of sandeel abundance, habitat use and -selection.

All the statistical analyses and plotting were undertaken using the program R, version 3.5.2 (R Developing Core Team 2018) and the results presented using diagrams such as scatter plots, histogram, box plots, prediction plots and tables. Two-way analysis of variance (ANOVA) was used to test if the size/length distribution is different between zone type across sampling rounds

In order to quantify and test if the size/length distribution was different between zone type across sampling rounds, I fitted linear models using zone type (control vs dredging zones) and round as categorical predictor variables and individual length measurements as response.

Analysis of catch count was done by estimating the catch as number of all individual per square meter and adjusting for the grab filling as follows:

$$\frac{\text{Count}}{\text{grab type}} \quad \text{X} \quad \frac{100}{\text{Grab filling}}$$

In order to estimate age and length at maturity (also framed as maturation graph e.g. (Heino et al., 2002), logistic regressions using age or length as univariate predictors and maturity status (mature=1, immature=0) as binomial response were fitted using glm procedure with logit-link function (Hosmer and Lemeshow, 2000). The length-at-maturity (L_α) and age-at-maturity (α) was defined as the length and age, respectively, at which probability of being mature was 0.5 (Stearns, 1992). These metrics were retrieved using the dose.p-function in the MASS-library on the fitted age- and length-specific GLMs.

Distribution of sandeel abundance measurements showed an excess 0 observations compared to the expected Poisson distribution that characterizes count data (McCullagh and Nelder, 1989). When comparing the count distribution with the one obtained when the 0 observations are taken out, I found the non-zero distribution to be normally distributed on the ln-scale (Figure 10). This indicates that the data has a surplus of 0 observations (0 inflation). I therefore decided to analyse sandeel abundance by using zero-inflated Poisson models (ZIP), where the probability of obtaining 0-observation is modelled as a sub-model and non-0 observations are modelled as ordinary Generalised Linear Model (GLM) with log-link (Zeileis et al. 2008, Wagh and Kamalja 2017). Generally, ZIP models can be produced as follows:

$$\Pr(y_j = 0) = \pi + (1 - \pi)e^{-\lambda}$$

$$\Pr(y_j = h_i) = (1 - \pi)\frac{\lambda^{h_i} e^{-\lambda}}{h_i}, \quad h_i \geq 1$$

This is explained in the formula below

$$\Pr(0) = a + bD$$

$$\Pr(0) = a + bD + cD^2$$

Where Pr(0) is the dependent variable, a= slope, *D*=independent variable and b= intercept

D^2 was used to explore the alternative of finding minimum and maximum values.

The response variable y_j can have all non-negative values and λ is the expected Poisson value for that observation. π is the probability of extra 0 values (0 inflation) beyond what one should expect from the Poisson distribution. Both the two sub-models can be modelled as generalized linear models where the 0-model is modelled with logit-link and the number model is modelled as ordinary Poisson model with log-link. The average from the models can be estimated as $(1-\pi)\,\lambda$ and the variance as $\lambda\,(1 - \pi)\,(1 + \pi\lambda)$.

As predictor variables in the various ZIP models, depth and substrate grain diameter were used in different combinations for both the zero and count sub-models. Grain diameter was consistently ln-transformed from the ln-based Wentworth scale. The ZIP models with second degree polynomials were also adapted for both predictor variables as we expected to find optimization values for both (i.e., depth and grain diameter values with the highest sandeel abundance) which were not in any of the extremes of the measured values, but rather toward the middle (Figure 6).

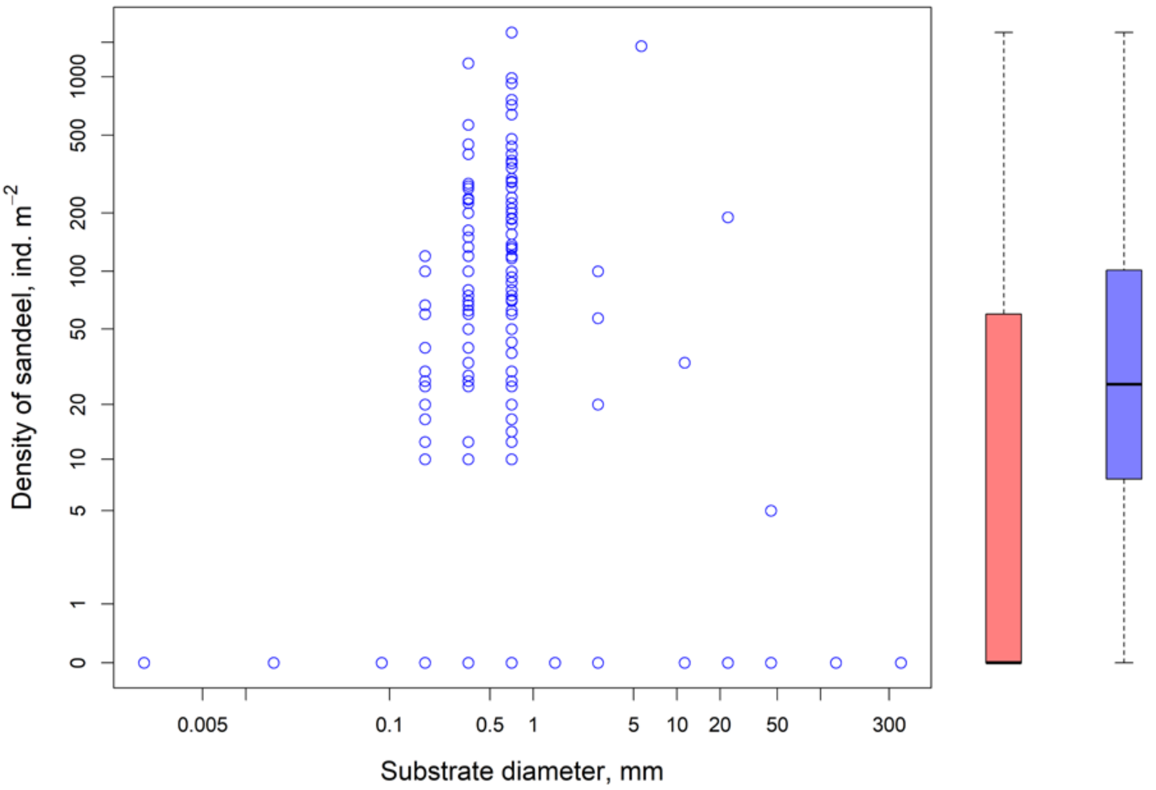


Figure 6. Scatter plot of sandeel densities as a function of substrate diameter per grab from all the 9 sampling rounds 2017 and 2018. To the right are box plots of sandeel density distributions shown for all rounds (light red) and without 0 observations (blue). The boxplots show 10 and 90 percentiles (the outer lines); 50 % of the observations are within the rectangles and the median value is shown as the thick black line inside the rectangles (located at the bottom of the light red). Note that the axes are log-transformed.

The data were strongly skewed with a large proportion of samples containing no sandeels, (zeros) whereas a few samples contained large numbers of sandeels (Figure 7). To justify this, the zero-inflated model was used. When the zeroes were removed, a normal distribution was obtained (Figure 8).

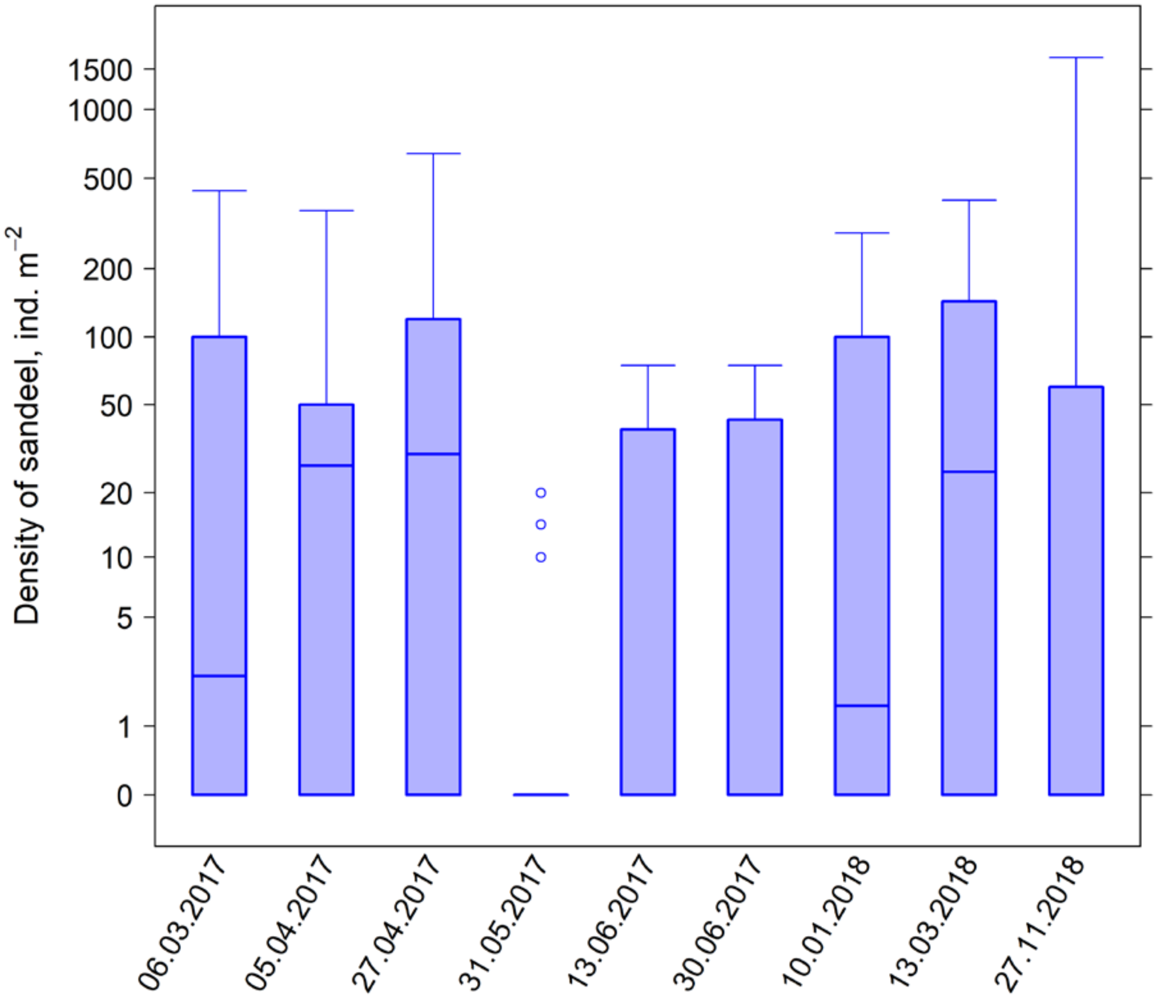


Figure 7. Box plot of sandeel densities for the nine sampling rounds. Note that the y-axis is on a logarithmic scale. The horizontal lines within the boxes represent median values, boxes encompass 50 % of the observations (25 and 75 % percentiles) and whiskers 10 and 90 % percentiles.

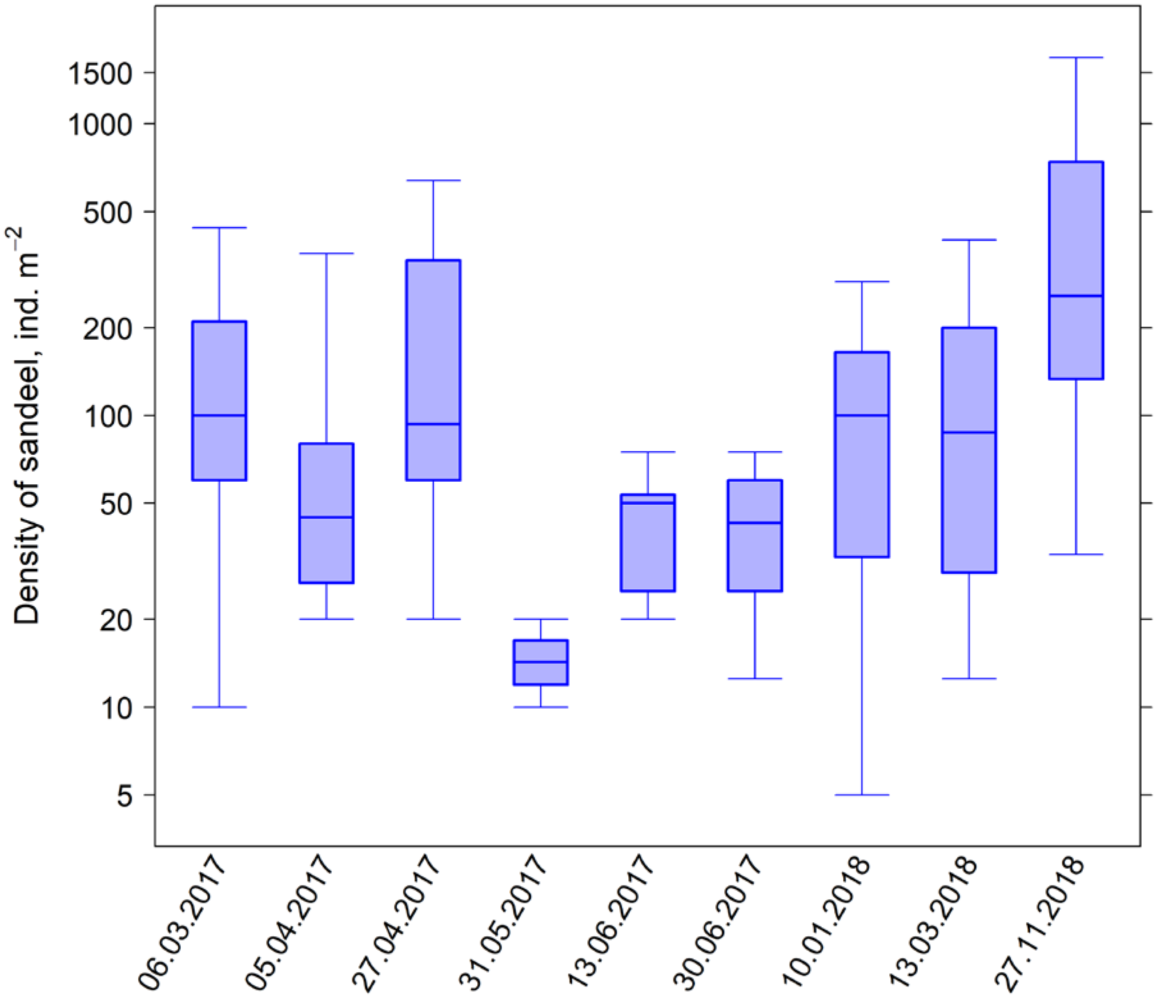


Figure 8. Box plot of count data (no zeroes) for all the sampling rounds. Note that the y-axis is on a logarithmic scale. The horizontal lines within the boxes represent median values, boxes encompass 50 % of the observations (25 and 75 % percentiles) and whiskers 10 and 90 % percentiles.

Model selection was performed using AICc (Burnham and Anderson, 2004), where the model with the lowest AICc is selected as the model that most effectively balances precision in the estimates against bias based on the principle of parsimony; ie the simplest explanation that can explain the data is to be preferred and used to select from competing models that describe a phenomenon (Burnham and Anderson, 2004). In order to define habitat use and habitat availability for sandeels, a habitatHS analysis was done using selection ratio and grain size. Habitat selection was analysed using the AdehabitatHS (Calenge, 2011), Manley 2002 to explore the grain size of various substrates. There was a significant non-random grain size selection amongst the sandeels (X^2 =24832, df=13, p<0.001). Estimates were very precise.

3. Results

3.1 Variation in individual characteristics

3.1.1 Length distribution

In figure below (Figure 9), the length of individual samples collected ranged from 60 mm to 188 mm, with the largest caught in late autumn and winter (27.11.2018 and 10-11.2018) and the smallest sizes in late winter (15-16. 03.2018). The average size of individuals collected for most rounds were between 90 mm and 110 mm. The highest number (646) was recorded in late autumn/early winter (27.11.2018) and the lowest catch in summer (4, 37, 26 for 31.05.17, 13.06.2017, 30.06.2017, respectively). All these results are indicated in (Figure 9)

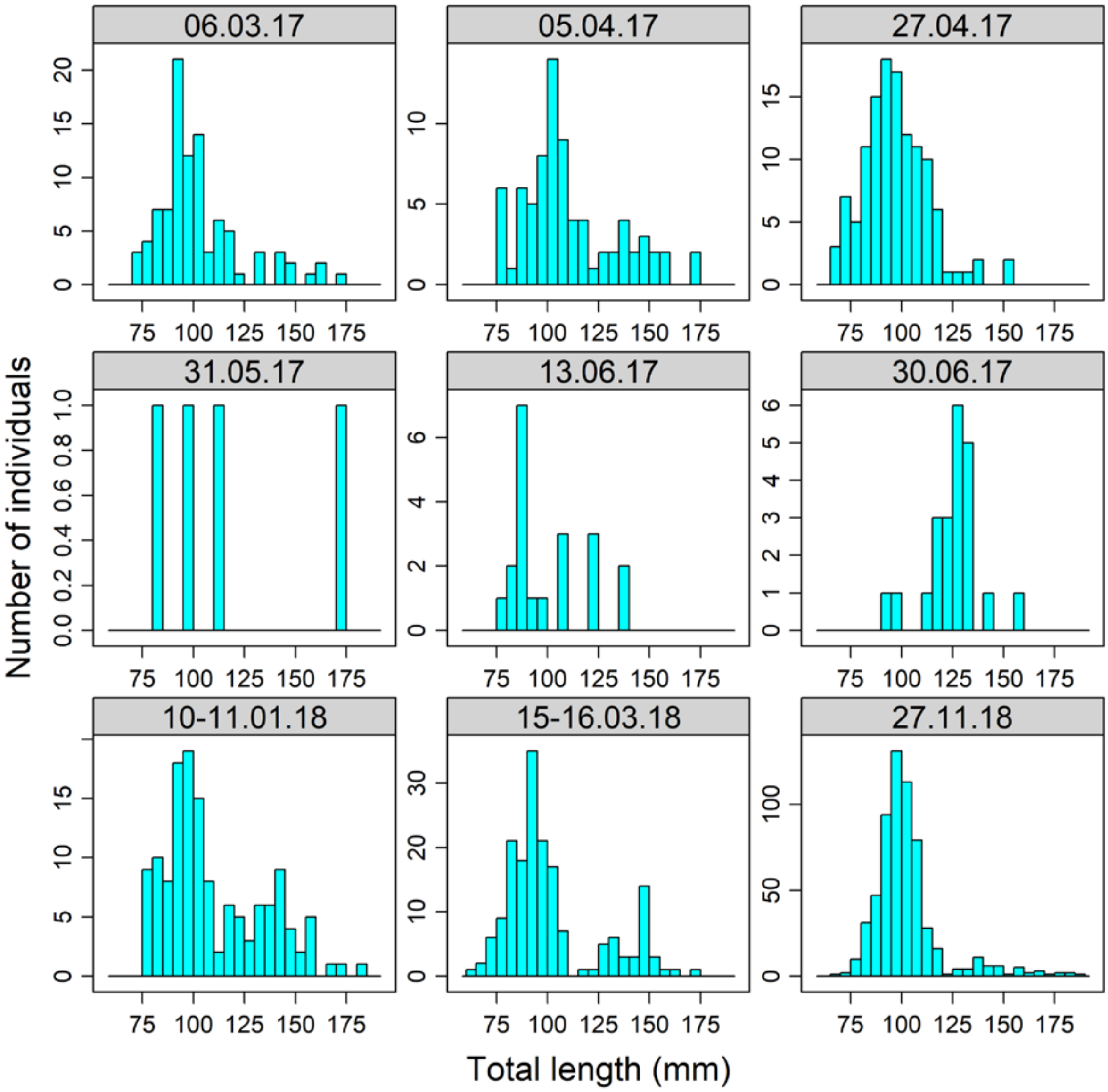


Figure 9. Length distribution of sandeels sampled during rounds one to nine. The different scaling of the y-axes depends on the number of catch- the higher the catch, the higher the interval.

The length distribution varied significantly among sample rounds and zone types (two-way anova: F=6.61, df=5,1158, $p_{round*zone\ type}<0.00001$). Figure 10 shows rounds 1, 4 and 6 having few or no individuals from the control zones, and for most rounds, the length distributions look similar between the zone types. However, during November 2018, large individuals were only found in the dredge zones.

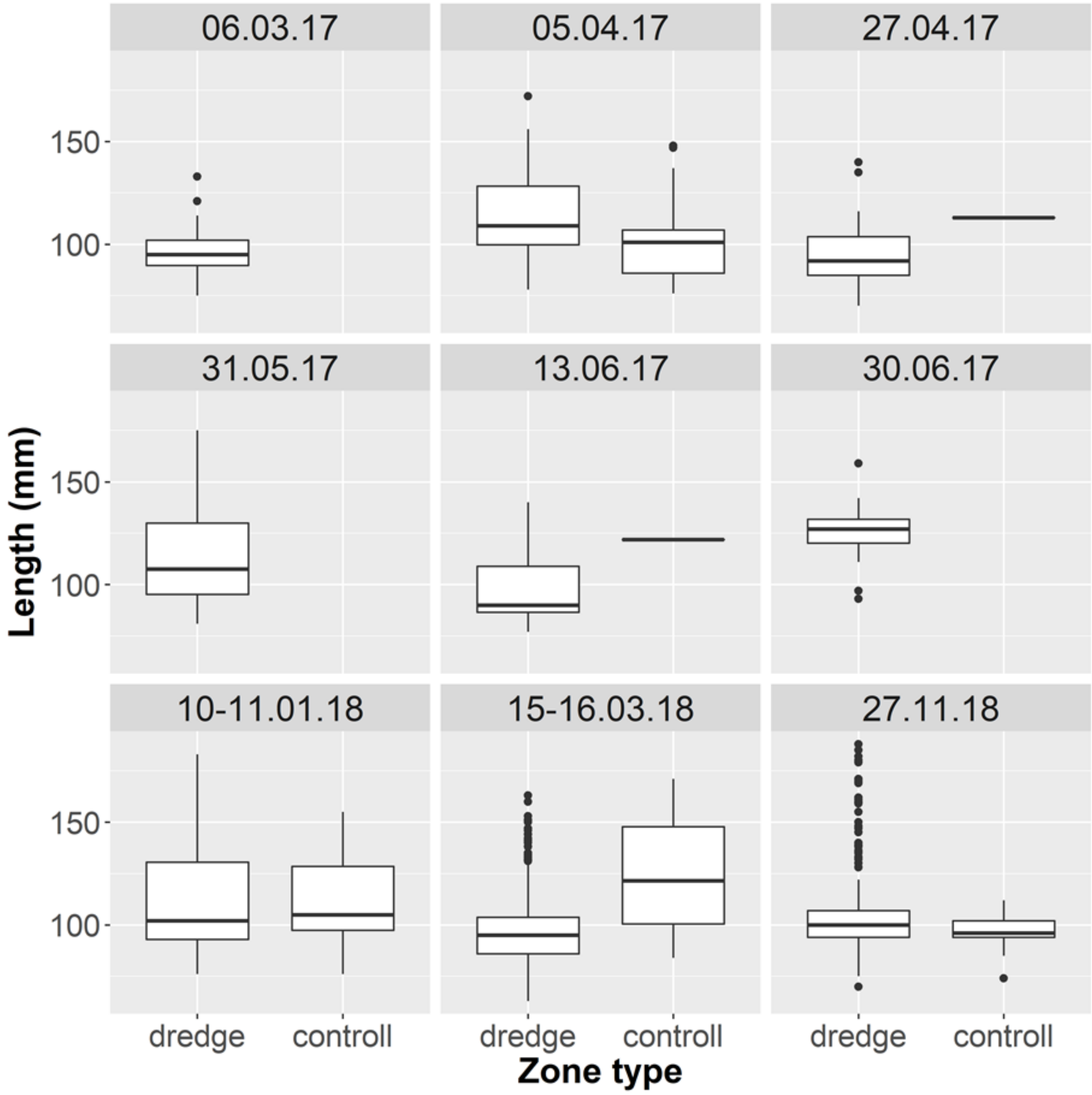


Figure 10. Boxplot of the seasonal variation in length distribution of sandeels in the Tana delta for control and dredging zone. The thick horizontal lines in the boxes represent the median, the boxes include the 25 and the 75 percentiles and the whiskers include the 10 and 90 percentiles.

3.1.2 Age distribution

From figure 11, it is observed that age increases with corresponding increase in length. For instance, in early January, ages 0, 1, and 2 all showed some increase in length, although age 1 shows more spread than the rest. Early March at age 1, there is a high expansion in length, but was less pronounced in mid-March. In early April, ages 1 and 2 have similar increase in length. However, in late April (27th April 2017), age 2 becomes more pronounced and skewed. All individuals at age 0 in early April turn age 1 in late April. This follows that those at age 1 in early April will turn age 2 in late April. This therefore goes with other age classes considering that mid-April was set as the birth date. So, all the age-0 in early April become age-1 individuals in late April, Figure 11.

In late May 2017, age 3 is more spread and less skewed. From the beginning of June, the spread in length is more pronounced at age 1, which reduces significantly toward the end of June. In November 2018, all ages exhibit some spread in length dominated by ages 1, 2 and 3 and least at age 4. Also, most of the distribution for this month is skewed.

Figure 11 shows that many individuals at the age of zero to two years are of length ≤150 mm and few individuals age three to four are of length >150 mm. On average, age 0 were more numerous than age 1 in all the sample rounds, with age 1 being more numerous than age 2. Individuals older than age 2 constituted less than 2% of the stock.

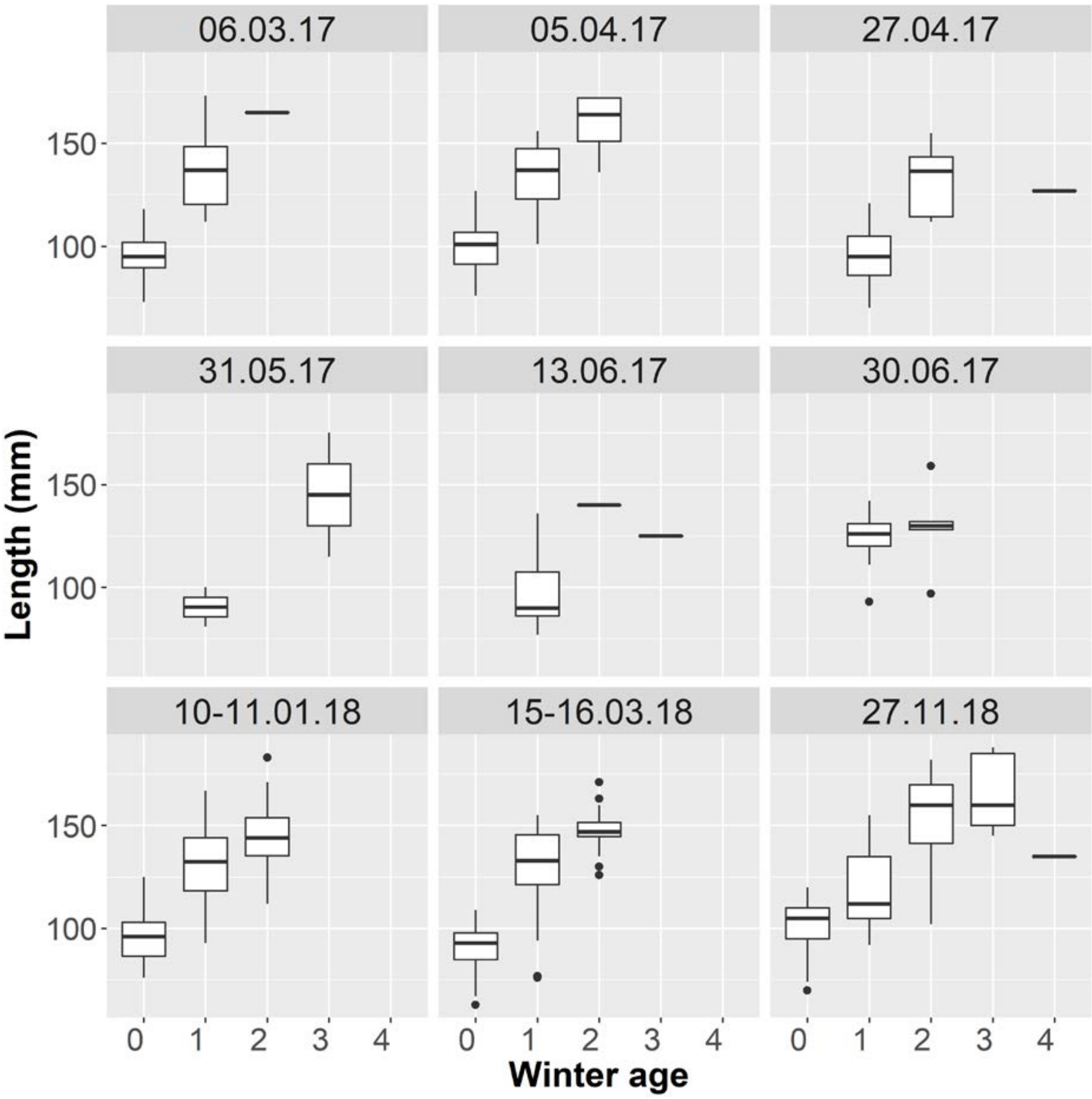


Figure 11. Boxplot of length variation at winter age among sample rounds in the Tana estuary area. The upper and lower quartiles are represented by the boxes, the median by the thick black horizontal line separating the upper and lower quartiles and the whiskers represent the minimum and maximum values

3.1.3 Length- and age at maturation

In order to study maturity by length and age, I restricted the analysis to data from the period immediately prior to and during spawning, i.e. late November. All age 0 individuals were immature Four individuals displayed maturity at age 1 at lengths 101, 102, 105 and 108 mm, respectively, and all fish larger than 120 mm were mature. The proportion of mature fish varied according to zone type and length in all the sample rounds.

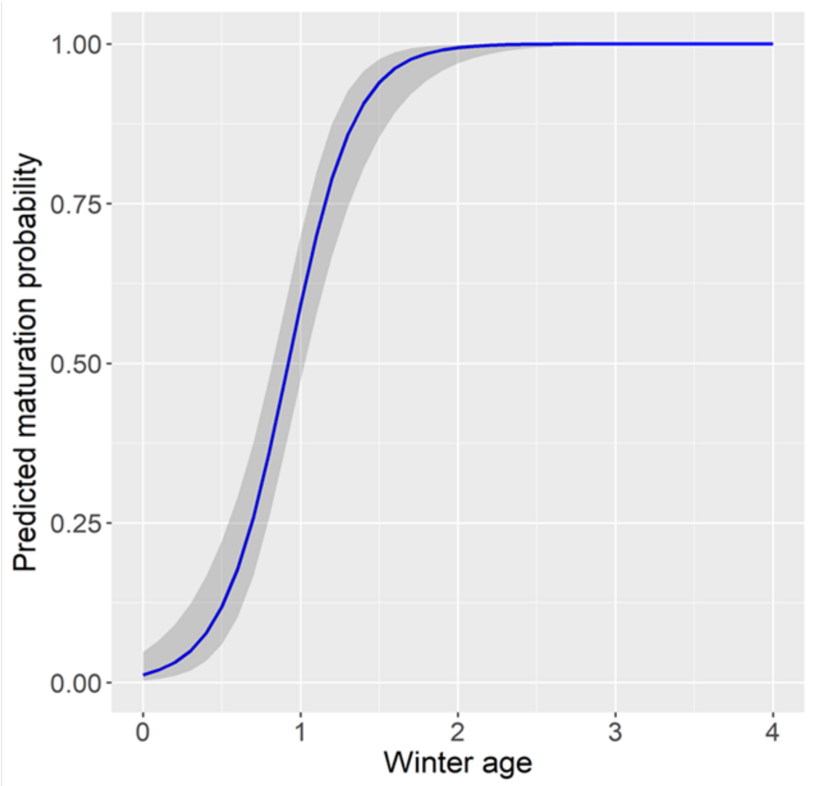
The fitted length-and-age specific maturity GLM-models provided predictions of length and age at maturation Table 4. From the parameter estimates, the length at maturation was estimated to be L_α 120.8±1.9 mm and age at maturation: α=0.92±0.05 years. The maturation analyses revealed maturation to be positively associated with both length and age (Figure 12).

Table 4. logit parameter estimates for the age- and length-specific maturation models fitted to the round 9 data. ***=p<0.00001, Est= estimates, SE= Standard error

Term	Est	SE	p
Intercept	-4.379	0.712	***
Age	4.752	0.742	***
Intercept	-18.503	2.61	***
Length	0.153	0.023	***

At age 0, the maturation probability is zero, and it begins with a gradual increase up until 0.5 winter age, and suddenly increases rapidly until 1. Thereafter, it increases gradually to full maturation at 2.

Maturation probability is 0 until length reaches approximately 90 mm and increases rapidly between 100 mm and 125 mm, then slow increase to full maturity at length >125 mm. At length 150, prediction probability of maturation is 100%



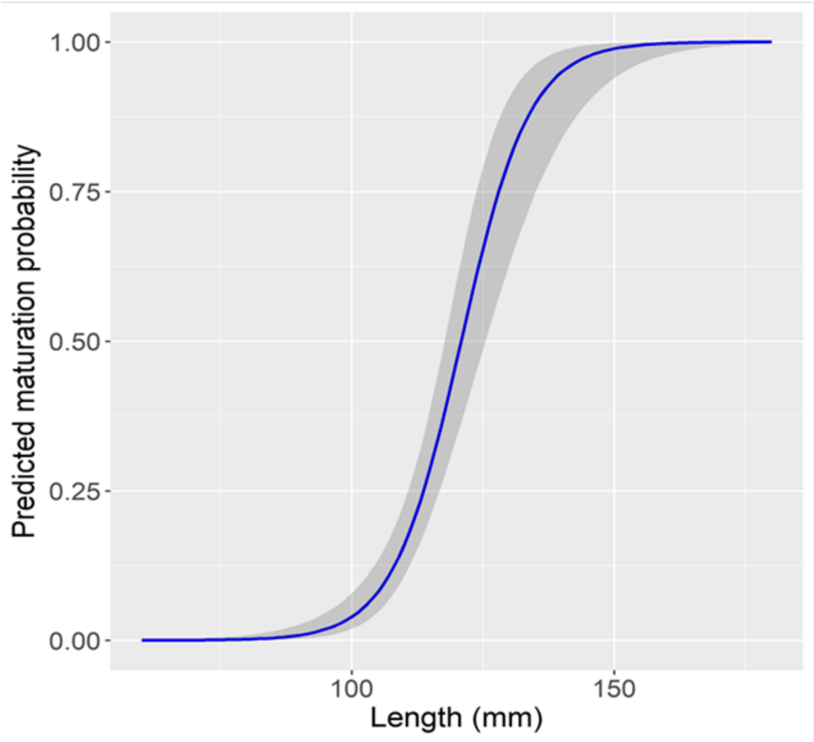


Figure 12. Prediction plot of length (bottom) and age maturation pattern for sandeel individuals in the Tana delta from sampling round 9. Predictions were made from models presented in table 7. Shaded areas represent the 95% confidence interval. The figure shows probability of being mature as function of size and age as predicted from the GLMs.

3.2 Sandeel eggs

Only one sandeel egg was observed in the sediment samples from round 1, while in the sediment samples from round 2, 4-6 and 9, no sandeel eggs were observed. Several sandeel eggs were observed in the sediment samples from rounds 7 and 8 predominantly in the M zones. Round 3 was not analysed for sandeel eggs.

In the lab, subsamples of 50 ml of sediments were placed in a Petri dish and assessed under a microscope to determine the presence/absence of sandeel eggs. Sandeel eggs (0.8-1.0 mm in diameter) could be observed by the eggs having attached to sand grains (Figure A1. 7A). The number of sandeel eggs per sediment subsample was recorded for rounds 7 and 8. In order to verify that the eggs were sandeel eggs, they were opened to examine the larvae morphology.

3.3 Diet

In round one, 32 % of the sandeels examined for gastric contents was dominated with copepods, while green algae were dominant in round 2-6. 43 % had zooplankton other plankton in the stomach, and 25 % had empty stomachs. Of the examined fish from round 7, 40 % had more than 10 % stomach content. This indicates that the fish are also eating in the winter. Between 10 and 20 % per grab and sampling round had individuals with empty stomachs. About 50 % of rounds 8 and 9 were dominated with copepods.

3.4. Horizontal net sampling

Seven of the 18 horizontal net hauls contained sandeel larvae (Table A1. 1). The highest number of sandeel larvae was from net haul 4 on round 2 with a total of five sandeel larvae. The sandeel larvae that were caught in the net hauls were very small (4-8 mm), except for one individual in haul 10, round 5. Net pulls from rounds 7,8 and 9 did not have any sandeel larvae, but rather shrimps and a lot of copepods.

3.5 Habitat use and distribution

The number of sandeels collected depended on how coarse or fine the sediments were; i.e., the coarser the grain, the greater the possibility of having a greater catch and vice versa. In the NY zones (control zone), there was no catch or very few sandeels due to the presence of rocks or fine grain/silt. Although few individuals were caught in fine grain sand. The sandeels that were sampled showed a clear dominance in coarse sand (Figure 14), but it was also observed that sandeels are distributed across medium, coarse gravel and fine sand. No sandeels werefound in the finest substrates (“mud” with high amounts of silt and clay) or in gravel (> 2mm) / stone substrate. Table 2 shows the proportion of coarse sand (0.5-2mm) in K, NY and M zones distributed across the different rounds, with a clear dominance in the M zones.

The relationship of sandeel abundance with depth indicated that the probability of sandeels occurring increased from 5 to 15 m. Their probability of use then declined from 15 to 40 m. However, the number of sandeels per grab ranged from 0 to 100, catches of 0 occurred in depth between 0 -3 m and 40 -80 m

3.6. Habitat use models

Although the number of sandeels in the samples varied widely for 2017 and 2018 sampling, the species occurred regularly enough to tell something about the prevalence. The model's parameter values as presented in Table 5 and a prediction plot shown in Figure 13 showed selected model is very good since as much as 94 % of the variation in sandeel density is explained by this. The model shows that one should expect to find the highest density at depths of 10-13 meters and substrate diameter of 0.1-5 mm.

3.6.1. The ZIP Model - Sandeel density

The sampling rounds 1, 2, 3, 4 were made from early in the morning until the daytime to be able to cover the time of day when the sandeels should be active. A large decline in sandeel catch during round 4 was observed and the subsequent round 5 was changed to night. This was to investigate if there were high occurrences of sandeels in the sand at night. On the other hand, low densities of sandeels were obtained during round 5 and 6, even though these were done at night. Round 2 also had a reduced amount of sandeels in relation to round 1 and 3 (by about 50%). Rounds 7 and 8 had relatively high densities in line with the winter sampling (rounds 1-3 in 2017), whilst round 9 had the highest density of all the surveys; i.e. early winter (27^{th} November 2018) in the M zones (zones earmarked for dredging). Few sandeels were present in the K zones except for round 1, 4 and 6. However, round eight recorded high amounts of fish in the K zones (n=90). The M zones recorded high amounts of fish in all the sampling rounds. The grab percentage indicating the grab’s fill level was as high as 90%.

Overall, 99.5% of sandeels caught were from the M zones. During round 2, 67% of the fish were from the M zones and in round 3 were 98% from the M zones (a total of 4 fish in the K zones). During round 4 and round 6, all the fish were from the M zones. In round 5, 94% of the fish were from the M zones. During round 7 and 8, 85% and 91%, respectively, of all the fish were caught in the M zones. During round 9, 96% of the catch was from the M zone and 4% from the control zone (K zone) and the additional control zones (NY Zones). These ratios are overestimated for the M zones since five grab shots (instead of three) were used in zones M1 and M2.

Table 5. Model selection table for ZIP models that estimate sandeel abundance (y = ant. M-2) as a function of depth and substrate diameter in the study area. The supported models are adapted to the data from all the rounds. General model structure: y = number | Pr (y = 0). K = number of parameters, AICc = corrected Akaike Inforamation criterion, AICc = difference between candidate model and candidate model with created AICc, ModelLik = model probability among supported models, AICcWt = AICc weight (model AICc support), LL = loglikelihood value.

Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
ln(Diam)² * depth² | ln(Diam) + depth	12	26649.77	0	1	1	-13312.4	1
ln(Diam)² * depth | ln(Diam)	8	27779.84	1130.07	4.06E-246	4.06E-246	-13881.7	1
ln(Diam)² * depth | ln(Diam) + depth	9	27781.94	1132.172	1.42E-246	1.42E-246	-13881.7	1
ln(Diam)² * depth | ln(Diam) * depth	10	27784.03	1134.259	5.00E-247	5.00E-247	-13881.7	1
ln(Diam)² * depth | ln(Diam)²	9	27799.15	1149.378	2.60E-250	2.60E-250	-13890.3	1
ln(Diam)² + depth² + ln(Diam):depth | ln(Diam) + depth	9	27821.64	1171.871	3.40E-255	3.40E-255	-13901.5	1
ln(Diam)² + depth² | ln(Diam)	7	28502.13	1852.367	0	0	-14243.9	1
ln(Diam)² + depth² | ln(Diam) + depth	8	28503.93	1854.165	0	0	-14243.7	1
ln(Diam)² + depth² | ln(Diam)² + depth²	10	29891.74	3241.975	0	0	-14935.5	1
ln(Diam)² + depth | ln(Diam) * depth	8	29959.87	3310.098	0	0	-14971.7	1
ln(Diam)² + depth | ln(Diam)	5	30899.52	4249.753	0	0	-15444.7	1
ln(Diam)² + depth | ln(Diam)² + depth	8	31267.95	4618.182	0	0	-15625.8	1
ln(Diam)² | ln(Diam)² + depth	7	31823.66	5173.892	0	0	-15904.7	1
ln(Diam)² + ln(Diam)² | ln(Diam)²	6	32443.98	5794.216	0	0	-16215.9	1
ln(Diam)² + depth | ln(Diam)² + depth	8	31267.95	4618.182	0	0	-15625.8	1

A new analysis was conducted using the immature individual count and it showed the same supported model as in table 5.

Table 6 .Parameter estimates of the most supported ZIP-model selected based on AICc (Burnham and Anderson, 2004) predicting number of sandeel individuals per sqm as function of substrate grain diameter (Diam) and depth. The count-model parameters are on ln-scale and the zero-inflation model parameters are on logit scale. The model had an explanatory rate of 1.00 (R^2_N≈1.00) N= Nagelkerte, SE = standard error.

Count parameter estimates			**Zero- parameter estimates**		
Term	Estimate	SE	Term	Estimate	SE
Intercept	4.621	0.027	Intercept	-0.333	0.184
ln(Diam)	-1.808	0.061	ln(Diam)	-0.615	0.148
ln(Diam)²	-1.621	0.038			
Depth	0.068	0.002			
ln(Diam)*depth	0.178	0.005			
ln(Diam)²*depth	0.12	0.003			

In the figure (13) below, at the substrate diameter of 0.001 to 0.1, there is no presence of sandeel at all depths. From the grain size of 0.1 to 1, there is a high concentration of sandeels at an estimated depth of 5 - 15 m. Nevertheless, the concentration dropped significantly from 15 - 40 m. There is a sparse distribution of the sandeel from a substrate diameter of 1 to 20, found at a depth between 10 and 15 m.

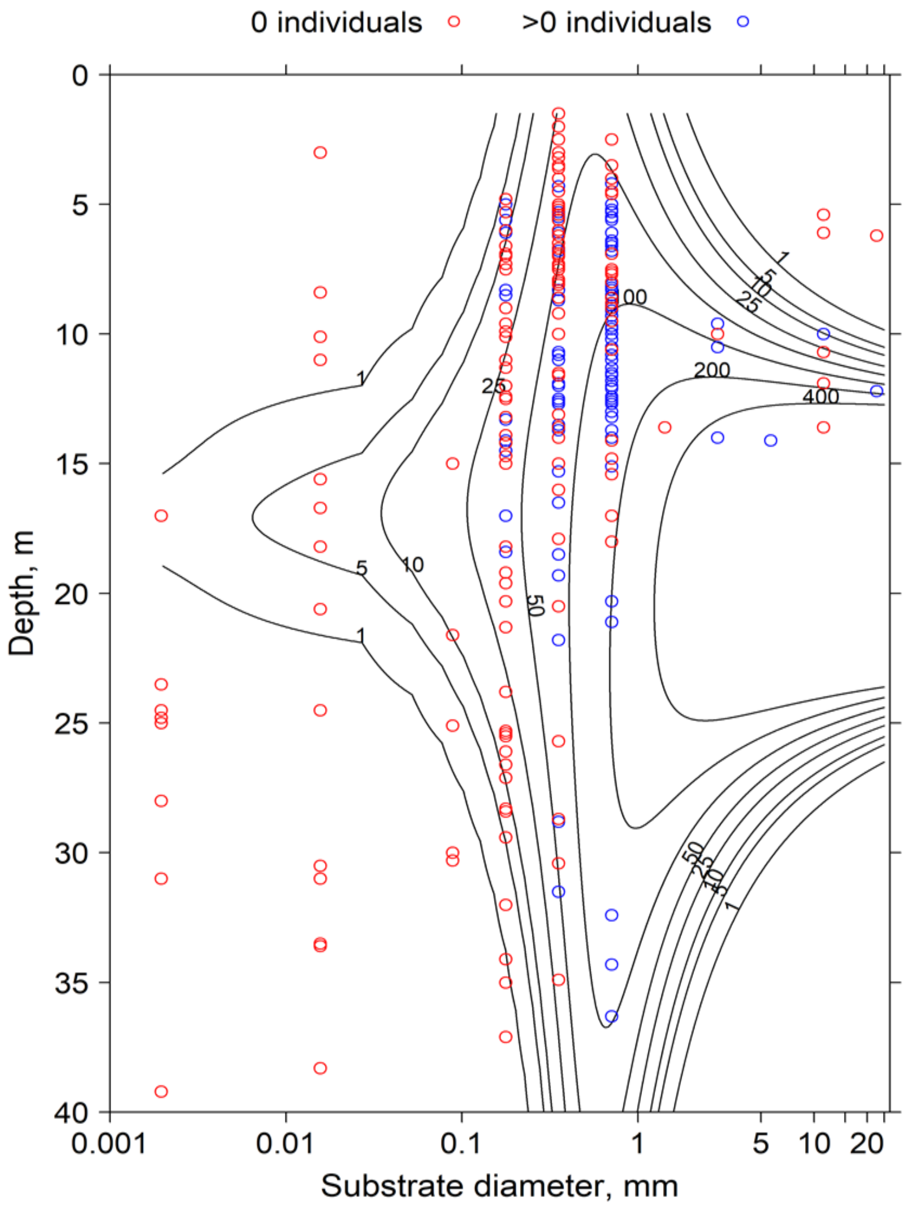


Figure 13. Prediction plot of the ZIP model presented in Table 6. The contours represent estimated sandeel density (individuals per m^2). Single observations from grab shots are shown both for specimens with zero sandeel catch (red) and with sandeel catch (blue).

3.7. Habitat selection

For substrate grain sizes in the 0.002-0.1 mm interval, sandeels showed avoidance of the habitat. At the grain sizes 0.7 and 20 mm, selection ratios were significantly larger than 1, indicating preference for these grain sizes. However, for grain sizes between 0.7 and 20 mm, there was no evidence for positive habitat selection. The sandeels displayed increased avoidance of the habitat from grain size larger than 20 mm (Figure 14).

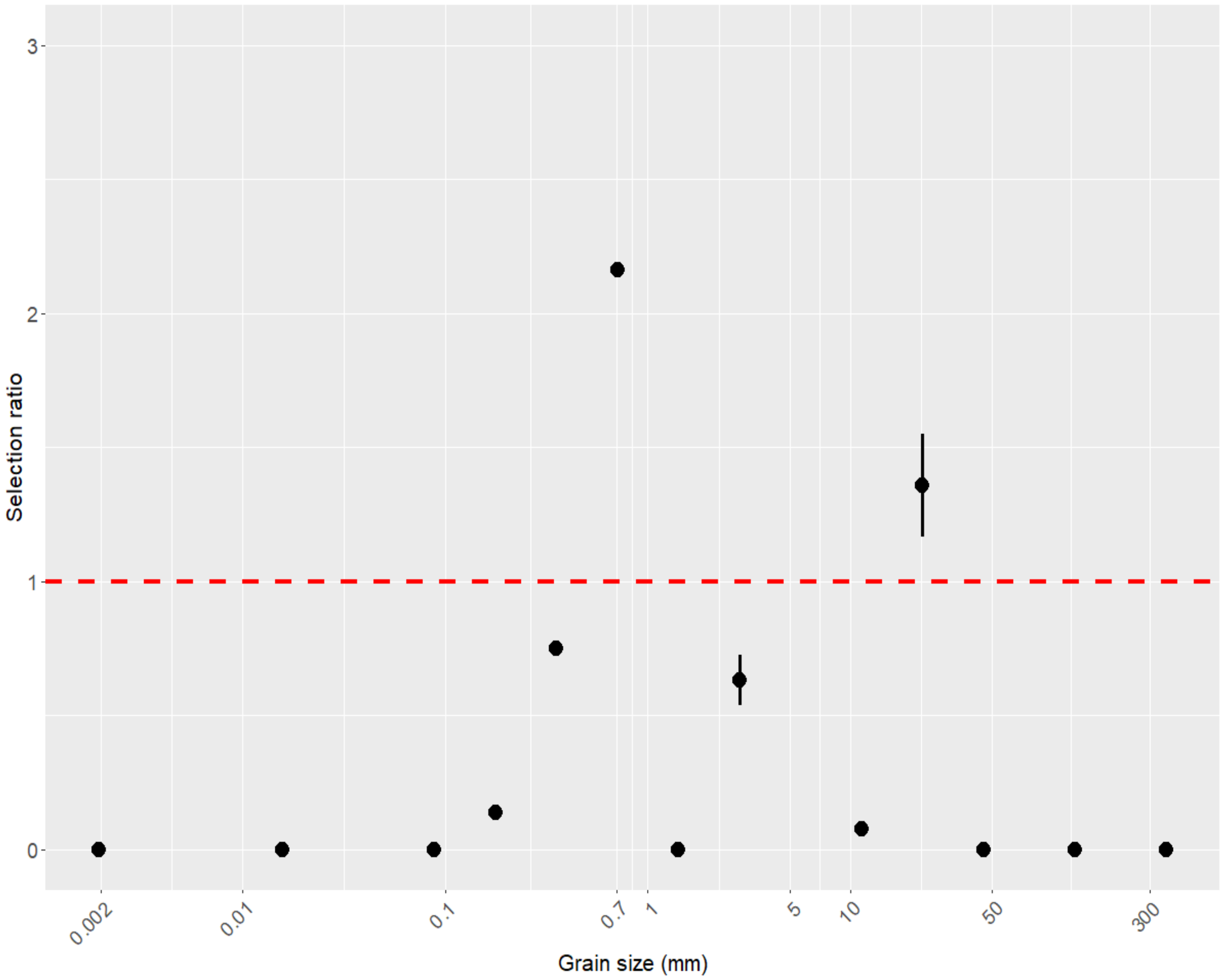


Figure 14. Grain-size selection ratio for sandeel sampled in the Tana estuary during 2017 and 2018. Values above 1 (dashed red line) indicate habitat preference and below 1 represent habitat avoidance. Vertical bars represent 95% confidence interval. Points with no visual CI-bars have very narrow CI-bars.

4. Discussion

The objective of this study was to characterize habitat use and habitat preferences and to describe differences in the demography of sandeels in the Tana river delta using a grab. The variations in the above mentioned varied according to time of day, season and depth into the sand. Sandeels used and preferred sediments with a medium to coarse grain sand which was mostly concentrated in the plan dredging line yet to be done.

4.1. Variation in individual characteristics – Length and age distribution

Variability in individual characteristics is an important trait in sandeels life patterns. This is because, these variations are connected to growth features such as length and age and likely depends on seasonal alterations. This study revealed that length distribution varied significantly among sample rounds and habitat type. Growth in sandeels is very seasonal (Bergstad et al., 2002) and appeared to be density and food dependent. This could be attributed to the burying behaviour of sandeels in the winter and the feeding behaviour in the summer. Strong variations in individual growth in areas outside the Tana river are a result of the fluctuations and trends in nutritional conditions (Bergstad et al., 2002). It is therefore likely larvae (recruitment) variation is the most important cause for length variability on the Tana delta and recruitment success is expected to be related to the occurrence and composition of copepods(van Deurs et al., 2009) during the early larval stage. Expectations as far as sandeel length is concern ranges regionally as shown in literature ((Wright, 1996, Bergstad et al., 2001, Boulcott et al., 2007, Johnsen et al., 2009, Wanless et al., 2004) . For example, this study recorded an individual with the highest length of 188 mm smallest length of 66 mm (figure 11). Strongest growth was observed in the period March to June, but for the age 0+ sandeels, the growing season was until October – November. Length distribution in the Tana delta was not similar to what other studies have found. Estimates of maximum size of sandeels can range widely among areas. Length as great as 270 mm in Berring sea.

Larger sandeels were found to be concentrated in the dredge zones compare to control zones. This may be caused by highly variable growth due to favourable growth conditions in these areas (prey availability, preferred grain size), large differences in local recruitment and mortality rates (caused by movements i.e foraging or hiding between habitat areas) and competition (Nelson and Ross, 1991). Access to food resources influences growth as indicated in (van Deurs et al., 2011) who stated that starvation risk decreases with increasing length of sandeels. In addition, environmental and seasonal cycles that influence zooplankton production are likely to contribute to the observed differences in length (Macer, 1966b).

Earlier studies in length distribution have suggested that sandeels grow faste in length at north-eastern and central locations, at high temperatures and the asymptotic length and condition both increased towards northern sandeel banks (Rindorf et al., 2016), Tana river delta included.

Age distribution varied progressively among sample rounds with respect to length (Boulcott et al., 2006). Changes in age 0 in spring and winter length appeared to be driven by changes in larval growth rate between March 2017 and 2018 winter sampling. Age 0 sandeels maybe the principal prey of many of the seabirds breeding in the vicinity of the study area accounting for their total absence during the summer.

4.1.1. Maturation stage and spawning seasons.

Length and age are major determinants in maturation probability (MacDonald et al., 2019, Boulcott et al., 2006). The results of this study therefore confirmed this with the observation that maturation probability increases with age and length in the Tana delta. Sandeels showed a considerable growth in length ($L\alpha$) and age (α) at maturity with $L\alpha=120.8 \pm 1.9$ and $\alpha= 0.92 \pm 0.05$ respectively. This followed that the maturation analyses positively associated with both length and age.(Bergstad et al., 2001) found that all sandeels over 170 mm were sexually mature and under 115 mm are immature. This, of course, is research from the North Sea, which lies considerably further south than the Tana delta. This can be affected by spawning and hatching time, as well as many other factors that affect life cycle and growth / aging. The sandeels from the study in the North Sea was also generally older than the fish sampled in this study.

The maturation probability graph of this study confirmed sandeels attain full maturation at age two. (O'Connell and Fives, 1995). This was consistent with the ICES stock calculations that assumed the entire population of sandeels will be fully mature at 2-year-olds. However, sandeels from the Firth of Forth and Fisher Banks (offshore waters to the east of Scotland), which recorded a prevalence of maturity of 79 and 58%, respectively, clearly did not conform to this broad assumption (Boulcott et al., 2006). This study observed maturation probability had a slow increase at age 0 to 0.5 winter age. This could be due to overwintering with little or no growth rate and rapid maturation from 0.5-1 winter age. This is attributed to increase feeding and full maturation that is attained at the age of 2. (Gauld and Hutcheon, 1990, Macer, 1966b)

The gonads growth begins in September - October and spawning in this area takes place in November – January (Gauld & Hutcheon, 1990), as supported by the last round at the end of November 2018. Fish that have poor growth conditions tend to have delayed maturation (Berrigan and Charnov, 1994). Mortality may also vary little over time. Eggs and larvae were not widely used in the sediment samples. Few egg and larval findings can be explained by the fact that the grab and net hauls probably did not hit the right place at the right time, since both stages can occur in large quantities after spawning and hatching. The larval stage of the sandeel is planktonic, ie the ocean currents are the main mechanism of movement at this stage.

Spawning has been recorded directly in December and January (Bergstad et al., 2001, Gauld and Hutcheon, 1990, Macer, 1966a, Reay, 1970). During round nine (27.11.2018), sandeels with full grown gonads were caught in the M zone, indicating that M zones are hot spots for spawning. This led to the deduction that sandeels in the Tana delta probably spawn in December-January. Data from round nine also presented sandeels that had recently spawned. With a few sexually mature fish from round nine, it could be established that sandeels that spawned probably burnt a lot of energy and most likely die afterwards. Sandeels can live up to 10 years old, but they are rarely older than 2 years (Bergstad et al., 2001). Older fish may spawn elsewhere further out into the estuary, but where this takes place is uncertain in the Tana fjord. However, it is not known when the spawning time is for sandeels outside the Tana delta. This lack of knowledge, together with the fact that little sandeel larvae were found in this area reinforces the need to find more about the spawning time and areas of the sandeels in Tana fjord as a way of further research**.**

4.2. Habitat use and Distribution.

The determination of sandeel habitat use lies on specific physical characteristics of that site that fill sandeel habitat requirements – depths, sediment types and distribution depend on statistical models used for this study. Putting together the information about substrate diameter and depth variables against sandeel abundance, the results show that the highest densities were between 5 and 15 meters and 0.1-5 mm grain size in the substrate. When these data are adapted to ZIP models, the model selection (Table 3) showed that the most supportive model has an interaction effect between ln (substrate diameter)^2 and depth^2 for the number-part model and additive power between ln (substrate diameter) and depth for the null part model.

Sandeel density = ln (diam) ^{2} * depth^2 | ln (diam) + depth

The models presented indicated that sandeel habitat use were strongly associated with shallow water banks with subtidal activities, depths and coarse sandy substrates. A study conducted by (Ostrand et al., 2005), found that sandeels remain close to areas of sandy sediments. This current study showed that sites lacking coarse sand or contained mainly of rocks had no sandeels. It therefore supports Ostrand et al (2005) assertion.

The results showed the probability of sandeel abundance with depth range increasing from 5 m to 15 m due to the high tides and presence of well aerated substrates. The depth range used by sandeels was relatively smaller than other studies have found; 30-70 m in Wright et al., 2000. Their probability of use then declined from 15 to 80 m, likely due to reduced currents agreeing with previous estimates of sandeels depth distribution (Robards and Piatt, 1999) and substrate selection (Holland et al., 2005). Sandeels selection for shallow depths is consistent with the findings of (Winslade, 1974) that sandeels are visual foragers and sensitive to light while burrowed. Hence, the penetration of light through sand and through water could restrict the depth of burial in the sand and also the maximum depth at which sandeels are found. As mentioned earlier, the aeration of the sediment influences the distribution of sandeels (Reay, 1970) and will also affect the depth to which sandeels can bury depending on the depth of sediment aeration.

The results again showed a significant decline in the probability of finding sandeels in sediments where the sediment fraction was >0.1 mm and median grain diameter >20 mm. The grain size distribution of sites with sandeels present indicated the presence of coarse grain sand and the availability of food. Sites with no sandeel indicated the presence rocks, silt/mud to very fine grain sand. This study was consistent with the laboratory work of Wright et al., 2000 and work in the natural environment of Holland et al (2005), that focused on identifying the sediment characteristics that define the seabed habitat preferred by sandeels. Both approaches produced similar results, indicating that sandeels preferred sediments with a high percentage of medium to coarse grain sand (grain size 0.25–2 mm) and avoided sediment containing 4% silt (grain size 0.063 mm) and 20% fine sand (particle size 0.063–0.25 mm). This gives little oxygen circulation and is probably also hard to dig into the sand. For their dependence on well-oxygenated water, it is likely the sandeels will stay close to the surface of the sediment. They may not go deeper than 8-10 cm into the sediment layers because they respire with the water that is between the sand grains. At these depths, the water flow may be too slow thus reducing oxygen supply and further worsened by increasing silt content. This means that oxygen rich sand will make a good habitat used for sandeels.

Sandbanks could consequently be considered an Essential Ecological Habitat (EEH) because they serve as spawning ground, nursery, feeding, or resting habitat for sandeels. (Rijnsdorp et al., 2009, Petitgas et al., 2013).

The presence of medium to coarse grain sand in the M sampling zones confirmed Pinto et al (1984) that the sediments in this area were preferred sandeel habitat. These M zones maintained their consistency in use as sandeel habitat in all the sampling rounds and therefore, maybe areas where sandeels could be found predictably in each season. This was indicated in all the rounds, but most significantly in round nine.Although there were zones where habitat use was constant, some zones demonstrated variation in habitat use and this implied that sandeels habitat use was restricted to certain sediment types. In effect, sites where sandeel were caught had sandeel presence throughout the sampling seasons in 2017 and 2018 supporting the data that sandeels habitat use remained constant during the sampling rounds (January to June 2017 and Janaury, March and November 2018).

The dominance of sandeels in the M-zones could be attributed to many factors, but preferably the bottom substrate (coarse sand) which was most present in this zone. It could also be due to the sorting processes of the local flow conditions created by the high tides and making this type of sand, which is easy for the flow of water, good oxygenation and ease of penetration into the sediments (Holland et al., 2005)). The sandy bottom conditions and water flow in the dredging zone were special, making it good growing and foraging grounds for sandeels. Due to the high-quality sandeel habitat in the dredging zone, the average density of sandeels in this area was more than twice as high as the average in the entire study. However, none or few sandeels were found in the K zones as a result of the presence of rocks in the seabed, grab failures or very steep areas difficult to sample.

4.3. Seasonal variations.

Seasonal shift in sandeel abundance observed in this study appeared to be a prevalent occurance. Possible reasons could be changes in environmental characteristics such as grazing conditions (nutrient availabilities i.e copepods *Calanus finnmarchicus*, light -increases the primary production and thus the secondary production is the food source sandeels), movements to and from suitable habitats and the occurrence of predators in areas between seasons. There were clear trends in the number of sandeels when comparing the catches from the different sampling rounds. Most species were caught during the winter and late autumn than in spring and summer. This may be linked to overwintering (buried in sediments i.e. the fish went back into the sand and not using the sand as much as in the summer) and feeding in the water columns respectively. Seasonal water temperatures could also affect the abundance of prey available for larvae (Robards et al (1999b) and the development of fish eggs by directly affecting the plankton production (Johnston et al., 1998) influencing seasonal variation in sandeels. (Johnsen and Harbitz, 2009), also carried out a survey in the peak feeding season of sandeel (April-May) showing that the abundance and geographical distribution of sandeels and the density measures are affected by the proportion of sandeel buried in the sand. All these claims were confirmed in the present study.

In the winter and autumn, sandeels remain in hibernation while buried in intertidal and shallow subtidal substrates - overwintering. The overwintering stage may be seen as an adaptation for survival during a period when conditions are unfavourable for feeding and predation risk is high (Winslade, 1974) . This could be the reason more sandeels were caught in the grab during autunm and winter. Contrary to what (Field, 1988) reported about sandeel abundance in preferred habitats from spring to late summer and uncommon during the rest of the year i.e winter and autumn, this study discovered that more sandeels were caught in the grab during the winter and autumn. As the feeding period progressed in the summer, the proportion of the sandeel population active in the water column in this study area declined while the proportion buried in the sediment increased. This resulted to increased catch in the winter and reduced catch in the summer. During summer and early spring where feeding occurs primarily in the water column, most of the sandeels are out of the sediments and move about in the water column in search of prey and plankton, hence, they are not caught with the grab. Poor eating conditions could force sandeels to be more active and thus have an increased probability of not being caught in the grab**.** The sandeels are probably far more active throughout the day in the Arctic where there is midnight sun, but there will still be less sandeels in the sand during day in late spring / summer.

In the spring, shoals of sandeels were observed on the surface, and was told by the captains that it was common to detect shoals of sandeel on the surface, as bird flocks, pursue and dive to eat them. It has been suggested that the high abundance of sandeels provides sufficient prey to prevent predation of salmon smolt by piscivorous fish (Svenning et al., 2005). Though sandeels were prey to fish and sea birds, they are also targeted by marine mammals. As was told after round seven that fishermen had caught a number of cod fish a week before Christmas in 2017 (10-11. January 2018) and found sandeels in their bowels (pers. comm. Captain Jon Inge Guttormsen).

4.4. Habitat preference

Understanding what controls the behaviour of sandeels at different grain sizes can be complicated but is key to understanding habitat availability and habitat use. This study showed a significant non-random grain-size selection among the sandeels (Manley's-χ^2 =24832, df=13, $p<0.001$), selecting positively for grain sizes around 0.7 mm and 20 mm and the other ones selecting against (Figure 14). Positive (or negative) selection for a given habitat may suggest that the habitat is used more (or less) frequently than expected by chance. High levels of habitat use can be associated with negative selection if that habitat is available contrary to low levels of habitat use which can be associated with positive selection if the habitat is unavailable. This study contradicted with 0.25 to 2 mm grain size reported by (Holland et al., 2005), 0.35 to 1.35 mm by Reay (1970) and 0.25 to 2.0 mm by Wright et al (2000). This could be attributed to the presence of medium, coarse sand and coarse gravel present and the ease of penetration into the sediment. These differences in grain sizes may also be attributed to sampling efforts that do not properly quantify sediment properties when trying to predict sandeels habitat preference. This may lead to inaccurate predictions. Further research and detailed training program for scoring sediments in the field which could help in accurate predictions. In these habitats, sandeels may seek resources that are best able to meet their requirements for survival.

4.5. Dredging

During the sampling, it has that sandeels has an important habitat in this particular shipping route as juveniles' fish. When removing large amounts of bottom substrate in the M1 and M2 zones which falls within the depth range planned for the dredging yet to be done, sandeels maybe be adversely affected. It is in these zones that spawning takes place and probably the only significant spawning area in the whole Tana river delta. Dredging expected to be done by a commercial dredging company, on behalf of the Norwegian Coastal Administration Troms & Finnmark may affect the sea-life in this area, change the tidal flow and how sand settles in time after dredging. During the dredging process, any sandeels lying in the sand will likely be lost. When the seabed is cleared off its original sediments, the composition is altered and the existing habitat of creatures and organisms that depend on it may disperse or die due to the unfavourable changes caused. Dredging this area may also change the turbidity of the water leading to the already existing contaminants to spread further into the water-body affecting the marine environment. However, if a dredging of the entrance to Leirpollen turns out to be ecologically sound, it will be very important to know when and how the dredging is carried out. Summer dredging is by far the best for sandeel population. It is also very difficult to estimate the potential effects of dredging on the sandeel stock but a muddy mid-winter dredging in the best sandeel egg habitat will potentially lead to large negative effects on the stock level of sandeels in this area.

4.6. Grab sampling - justifications and limitations

Grab sampling offers a relatively cheap method of assessing local sandeel population and considered as a useful method for investigating sandeel habitat use and preferences. It provides a large number of point estimates of sandeel density. The high number of samples analysed during this study provided information on sediment characteristics of the seabed at each location sampled.

Despite higher catchability, the sampling reliability of the grab is uncertain because stones can prevent the grab mouth from closing completely, as occasionally observed during sampling (Johnsen and Harbitz, 2013). It was likely some sandeels escaped capture, hence the grab probably provides only minimum estimates of sandeel abundance. This is because the grab samples a small area (0.1m^2) (Greenstreet et al., 2010) meaning that even in key sandeel habitats, the grab may occasionally catch no sandeels even though individuals may be present in great numbers nearby. When the grab was retrieved sandeels were often observed with their heads sticking out between the closed jaws of the grab. It is therefore likely that some sandeels escaped during capture (Johnsen and Harbitz, 2013). These were probably fish caught while fleeing downwards into the sand. The sandeel is well adapted for rapid movement in the sand and some were probably quick enough to avoid the grab. This could affect the total estimates of sandeel abundance in this study area by giving only a minimum abundance estimate that are biased low. There is likely a size-bias in the samples as large individuals are more likely to escape the grab than smaller ones. Also, environmental effects may affect catchability as most fish get more mobile as temperature rises – this could also influence part of the seasonal pattern

found in the data. The consequence of catchabilities below 1 (1 would mean catching all available for catch) is density estimates that are biased low.
Whilst sandeel distributions are known at a coarse scale, existing sediment data are not sufficiently high-resolution to provide more detailed knowledge. The diversity and abundance of many sandeels is linked to habitat types, which is characterised by a constant change in this study area, indicating major shift in sandeel habitats over the time period of the data used in this study. A more in-depth behavioural study on sandeel is required to verify the relationships found here.

The study also revealed that estimating the correct sandeel density and determining the sediment type which sandeels use and prefer in the field could be a challenging task with the use of grabs, where it gives an estimate of biased fish density due to equipment limitations and variation in sandeel assembleges which vary vary considerably in the time of the day and in seasons.

4.7. Recommendations

The thesis suggests that if dredging must be carried out, environmental follow-up programs with methodology similar to that presented in this thesis should be implemented. This should be carried out before, during and after the dredging period. In addition, similar studies should be done the same year and preferably once every 3 or 5 years after the dredging has been completed. In this way, one can document any changes in the stock and investigate more into the spawning as well as where the adult individuals and eggs are located throughout the year. In addition, a study using an echo sounder, in parallel with grab sampling, should be conducted to map out the occurrence of sandeels in the entire Tana fjord. This could help determine the relative importance of the Leirpollen area as optimal and limited sandeel habitat and to detect deposits of spawning fish and spawning grounds, during the four seasons.

I would also suggest that future grab sampling and all other sampling equipment (e.g., trawl and echo sounding) be accompanied by measurements of temperature, oxygen and salinity profiles (e.g., using CTD-sounds) as this will allow for higher precision on both estimates of catchability and thus density estimates – plus provide additional dimensions to sandeel niche estimation. Multiple sampling rounds should be conducted to have consistent data which will act as a baseline survey and help the decision-making process around the planned dredge.

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6. Appendix 1

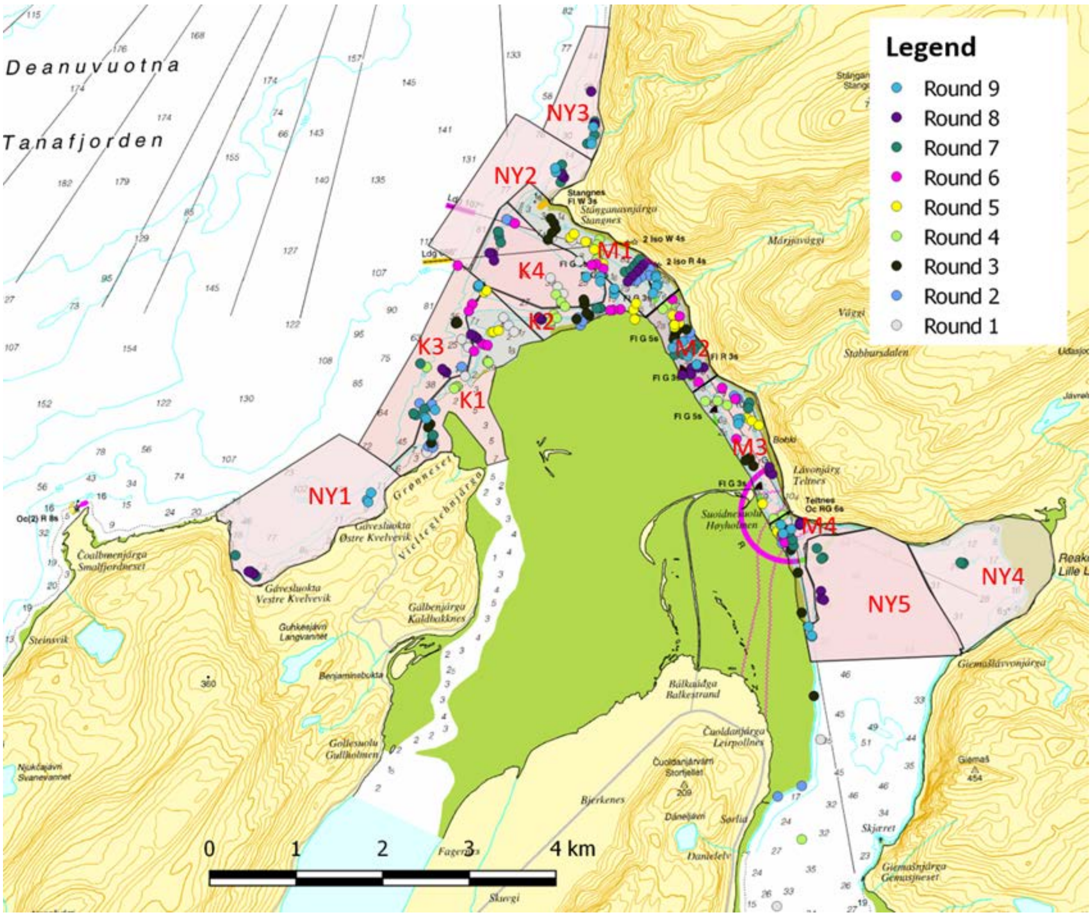

Figure A1. 1. Overview of all grab shots done during rounds 1-9 in the 13 different zones, plus extra sampling in Leirpollen The grab shots for the different rounds have different colours, see the legend.

Figure A1. 2. Sampling of sandeel larvae and zooplankton was conducted using a modified plankton net haul.

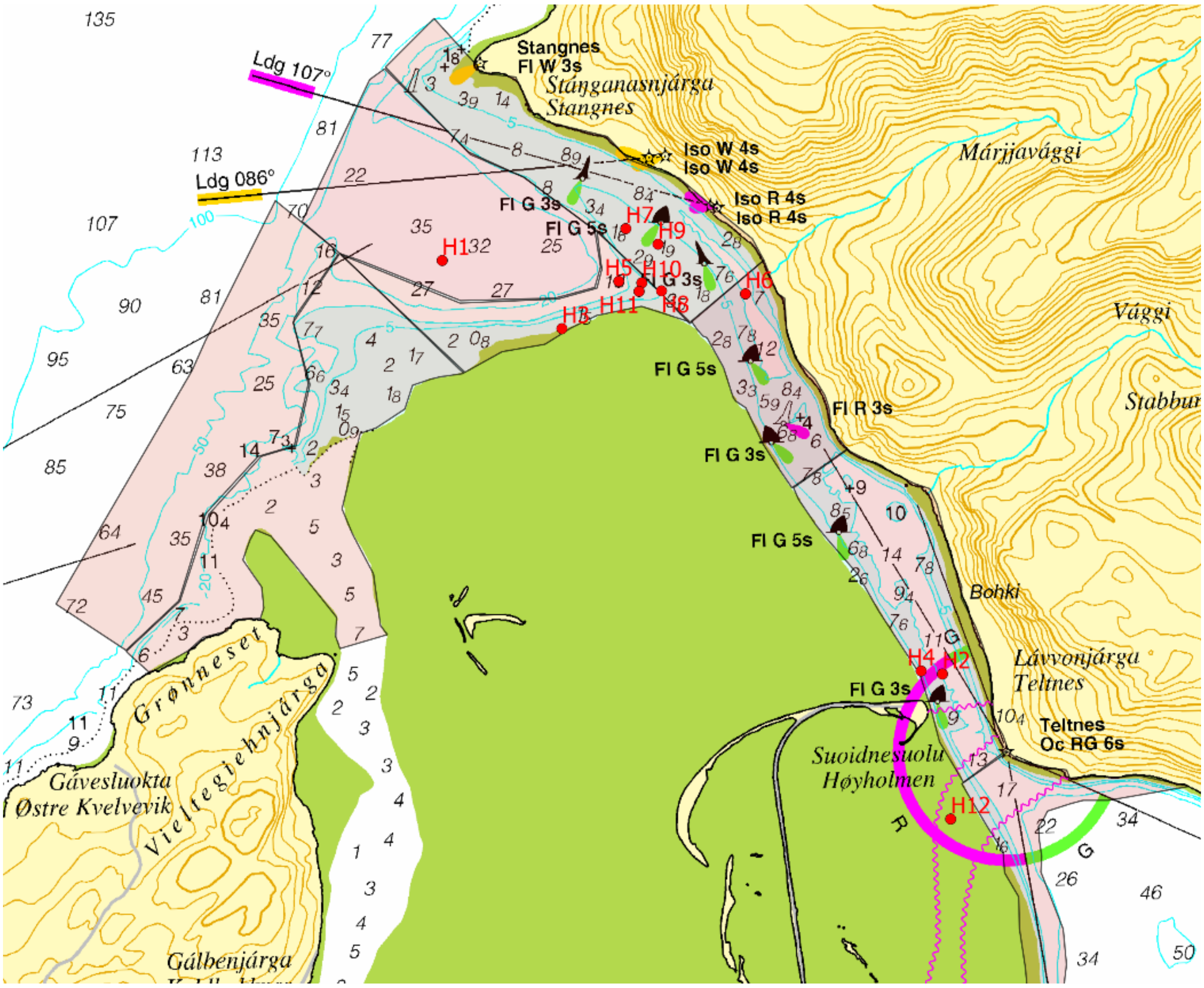

Figure A1. 3. Net pulls H1-18 made in the different zones through pulling. Source map basis: The Mapping Authority 2018, Hydrographic-WMS). Two net pulls in each round. See appendix

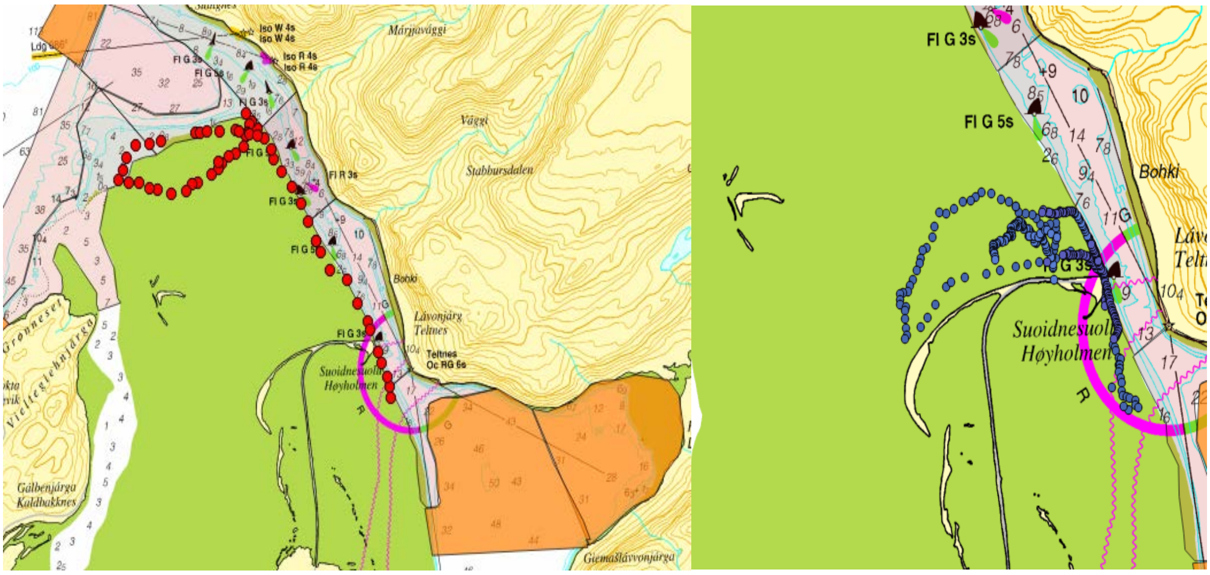

Figure A1. 4.The map on the left shows where the grab shot with a small grab from a boat was carried out on March 14, 2018. These grab shots were made between the littoral zone and down to 5 m deep. The map on the right shows approximately 350 shovel flips in the accessible littoral zone in the tidal zone. The Mapping Authority 2018, Hydrographic-WMS.

Figure A1. 5. Sandeel length measurement.

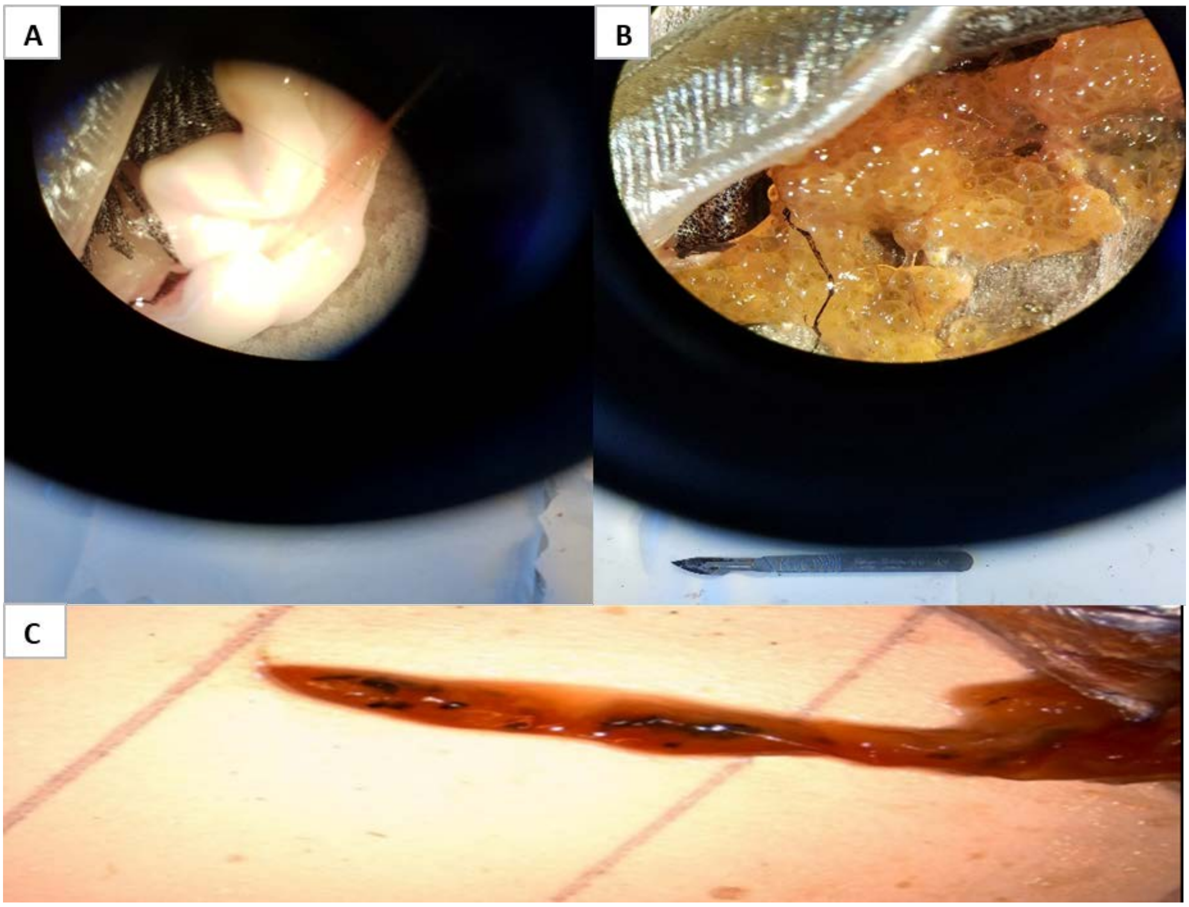

Figure A1. 6. Maturation stage of male and female sandeels. Mature Male (left) and female (right) sandeel gonads. The sandeels were sampled on sapling round 9 in zone M1.

Figure A1. 7. View of sediment samples for sandeel egg and grain size / composition(c). Image at the downright shows a sandeel egg (attached to a grains of sand) and to the left several sandeel eggs with sand grains adhered.

Table A1. 1. Plankton and sandeel larvae from the net haul 1-18 divided by sampling round 1-9, showing content in the water sample as well as depth, position and date of the net hauls.

Round	Date	Depth (m) to bottom	GPS-position	Sandeels larvae	Calanus finmarchicus	other
Net haul 1	6.03.2017	30-35	70.5333N, 28.3882E	3	250	
Net haul 2		13-14	70.5133N, 28.4573E	0	150	
Round 2						
Net haul 3	5.04.2017	4,2-7	70.5300N, 28.4048E	1	10	lots of algae
Net haul 4		8,8-10	70.5135N, 28.4543E	5		lots of algae
Round 3						
Net haul 5	27.04.2017	7-12,5	70.5322N, 28.4130E	1		lots of algae
Net haul 6		11,5-12,8	70.5314N, 28.4308E	0	50	lots of algae
Round 4						
Net haul 7	31.05.2017	04-05 m	70.5346N, 28.4142E	2	50	
Net haul 8		07-08 m	70.5317N, 28.419E	1	100	
Round 5						
Net haul 9	13.06.2017	3,6-4	70.5339N, 28.4187E	0	50	some amfipods
Net haul 10		08-09 m	70.5321N, 28.4163E	1	20	lots of algae
Round 6						
Net Haul 11	30.06.2017	09-10 m	70.5317N, 28.4158E	0	10	lots of organisms from the river
Net Haul 12		10-11 m	70.5065N, 28.458E	0		some organic material
Round 7						
Net Haul 13	10-11.01.2018	12 m	70.535483, 28.420533	0	800-1000	lots of copepods
Net Haul 14		34,8	70.537383, 28.386317	0	8-900	lots of copepods
Round 8						
Net haul 15	15-16.03.2018	36.7 m	70.533333N, 28.387017E	0	700-800	
Net haul 16		8.9 m	70.540367N, 28.391650E	0	600-700	
Round 9						
Net haul 17	27.11.2018	28,1	70.50255N, 28.4728E	0	600	some shrimps
Net haul 18		16,5	70.519567N, 28.448683E	0	500	some shrimps

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