



MSC THESIS MARINE SCIENCES

24 years of red knot numbers and the relation with their prey in the Western Wadden Sea

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ABSTRACT

Food availability and food stock depletion by foraging populations can have substantial effects on the population size. How these aspects combine is rarely studied on long time scales, considering the complexity of ecological systems and the challenges to collect all relevant data. Migratory red knots (*Calidris canutus*) have been studied in the Western Dutch Wadden Sea over 24 years (from 1993 until 2017), and so has their and food availability. Here, we examine the relationships between numbers of red knots and their food in the Western Wadden Sea. First, the relation between red knot population size in the Vlie tidal basin and the availability of edible sizes of the preferred prey species (*Limicola balthica*) and an alternative prey (*Cerastoderma edule*) is considered. The effect of prey quality, defined as the flesh to shell ratio of the prey, on the red knot population size is also taken into account. Furthermore, the relation between red knot numbers and elimination of prey in edible size classes in the Vlie tidal basin is analysed. To validate the relations between red knots and their food, the total available prey biomass and total calculated prey elimination are compared with the theoretical energy requirements of all red knots counted in the Vlie tidal basin each year. The numbers of red knots correlated positively with the amount of preferred prey (*L. balthica*) available, whereas there was no such relationship for the alternative prey (*C. edule*). Moreover, the number of red knots counted yearly correlated positively with mean quality of the preferred prey. This implies that any change in the availability of high-quality *L. balthica* will affect the red knot population. With increasing numbers of red knots, the calculated elimination of the edible size classes of *L. balthica* also increased, whereas there was no relationship with the estimated elimination of the alternative prey. The fraction of *L. balthica* eliminated was constant with the yearly number of red knots in the Vlie tidal basin. The fraction of eliminated prey was higher in edible prey size classes than overall, indicating that the elimination could indeed be caused by red knots. In general, the total prey biomass available and the total eliminated prey biomass in the Vlie tidal basin were of the same magnitude as the estimated energy requirements of all red knots counted in the study area. This work suggests strong causal links between the number of red knots in the Wadden Sea and the population of *L. balthica* both for availability of prey and prey depletion by red knots. This means that when there is insufficient high-quality prey available, a part of the red knot population cannot reside in the Western Wadden Sea.

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INTRODUCTION

The question which factors determine population size in a particular area, is one that has fascinated ecologists for ages (Malthus, 1798; Verhulst, 1847; Verhulst, 1838; Verhulst, 1844; Lotka, 1925; Volterra, 1926; Andrewartha & Birch, 1954; Mcnamara & Houston, 1987). Food supply is one of the primary aspects that regulates changes in population sizes, and can therefore attribute to an estimate of the maximum number of individuals that can be sustained by a system (Dhondt, 1988; Goss-Custard & West, 1997; Sinclair & Krebs, 2002; Nolet *et al.*, 2006). This estimate (often called ‘carrying capacity’) can be an important tool in population management. However, foraging populations can also decrease their prey resources during foraging through food stock depletion (O’Connor & Brown, 1977; Schneider & Harrington, 1981; Zharikov & Skiller, 2003). This elimination of food determines the amount of food still available to a population. Therefore, insight in the effect of both food availability and the depletion of food resources on foraging populations is needed in order to establish if populations are limited by their food. Understanding such relationships on time scales longer than a few years will provide essential knowledge that can be applied in conservation of populations.

The Wadden Sea is a crucial stopover site for many migratory shorebird species within in the East Atlantic Flyway (Engelmoer *et al.*, 2006; van Roomen *et al.*, 2018). The temperate intertidal wetland stretches along the coasts of The Netherlands, Germany and Denmark and has received UNESCO Natural Heritage status in 2009. In spite of this international recognition, many shorebird populations show long-term trends that are more negative than the general trend along the entire flyway (van Roomen *et al.*, 2018). Food availability is considered to be an important factor, although the details are not understood except for a few species (van Roomen *et al.*, 2018). Migratory red knots (*Calidris canutus*) use the Wadden Sea as wintering and stopover site on their migration along the East Atlantic Flyway. The birds have received much scientific attention, especially with respect to their feeding ecology (Piersma, 2012). A wealth of knowledge has been gathered in the course of the years about the red knots as well as their bivalve prey in the Wadden Sea. Their population size (Piersma *et al.*, 1993; van Gils *et al.*, 2006; Kraan *et al.*, 2009; Folmer & Piersma, 2012) and spatial distribution (van Gils *et al.*, 2005; Oudman *et al.*, 2018) clearly depend on food availability. Additionally, red knots have been suggested to use the tidal flats of the Wadden Sea to capacity, therefore any decrease in suitable foraging area would result in a decrease of red knot numbers (Kraan *et al.*, 2009). Although red knots and their foraging have been studied intensively in the western Wadden Sea since the 1980s (as reviewed by Piersma (2012)), the relationship between red knots and their prey on time scales longer than a decade is open to scrutiny in this study.

As red knots visit their wintering areas with tens of thousands of individuals at the same time, they deplete their prey while foraging (van Gils *et al.*, 2003; Ahmedou Salem *et al.*, 2014; Bijleveld *et al.*, 2015). When more red knots are present in the Wadden Sea, they will consume more prey. If prey production is not in the same order of magnitude at the same time, prey depletion will occur. Less prey will therefore be available for the population in the course of winter, the period of non-renewal (Beukema, 1974; Zwarts, 1991; Zwarts *et al.*, 1992). Contrary to the expectation, van der Meer and colleagues (2001) did not find a correlation between production of prey and the energy consumption of locally roosting red knots in the Wadden Sea. Instead they found that the biomass production was too high to be explained by foraging red knots. However, the expectation is that if there is a relation between the red knots and their prey, more prey would result in presence of more red knots and therefore increased prey depletion. Foraging red knots also alter the average prey quality (defined by the shell to flesh ratio) through selective foraging, by selecting high quality prey to eat (Bijleveld *et al.*, 2015). This offers an interesting additional perspective, because there are certain (explorative) individual red knots that prefer high quality prey and actively look for prey with a low relative shell mass (Bijleveld *et al.*, 2014; Oudman *et al.*, 2016). As a result of depletion, the high quality prey will become scarcer and fewer explorative red knots can be accommodated by the prey stock. The expectation is that the giving-up density (prey densities at which a patch is no longer profitable and birds give up foraging there) for these individuals is lower than for non-explorative red knots, because high quality prey are more scarce.

In this study, we investigate the two-way nature of the interaction between the red knot population and their prey in the Western Dutch Wadden Sea on a long timescale. We examined how long-term variation in availability of prey and prey elimination through foraging during the year related to the abundance of red knots. In order to achieve this, monthly red knot roost counts in the “Vlie” tidal basin (Western Dutch Wadden Sea) were analysed over a period of 24 years. Also the availability of the preferred prey species (*Limicola balthica*) and an alternative prey (*Cerastoderma edule*) of edible size classes for red knots was determined yearly. The quality of the prey was determined on the basis of ratio of flesh to shell. Prey availability and prey quality were then linked to the size of the red knot population in the study area. It was then assessed if the total edible prey biomass in the study area was consistent with the calculated energy requirements of all red knots. On the other hand, we evaluated whether the prey that was eliminated over a year related to the red knot population size. We also examined if the total eliminated prey biomass in the study area was consistent with the calculated energy requirements of the total red knot population in the Vlie tidal basin. We expected to find a positive relation between red knot numbers and their prey availability and prey quality. The similarity between the total edible prey biomass in the Vlie tidal basin and the red knot energy requirements was expected to be stronger for the preferred prey (*L. balthica*) than for the alternative prey (*C. edule*). If depletion by red knots is the cause of prey elimination, the amount of prey elimination is expected to correlate to the number of red knots in the Vlie tidal basin. If the red knots were responsible for the elimination of prey, eliminated biomass should be corresponding with the energy that is required by all red knot and the prey elimination is expected to be highest in prey of edible size classes.

MATERIALS AND METHODS

Study area

The study area was the Vlie tidal basin, in the western Dutch Wadden Sea (Figure 1). Two subspecies of red knots (*C. canutus islandica* and *C. canutus canutus*) visit this area. The Siberian-breeding *canutus* subspecies uses the area as a stopover site during their flight to north-west Africa, whereas the Greenland, Iceland or Canadian breeding *islandica* subspecies overwinters in the Wadden Sea (Piersma *et al.*, 1993). There are two high tide roosts in the basin that are used by the red knots to spend the high tide in the Vlie tidal basin; the uninhabited island Griend (53°15'N, 05°15'E) and the sand bank Richel

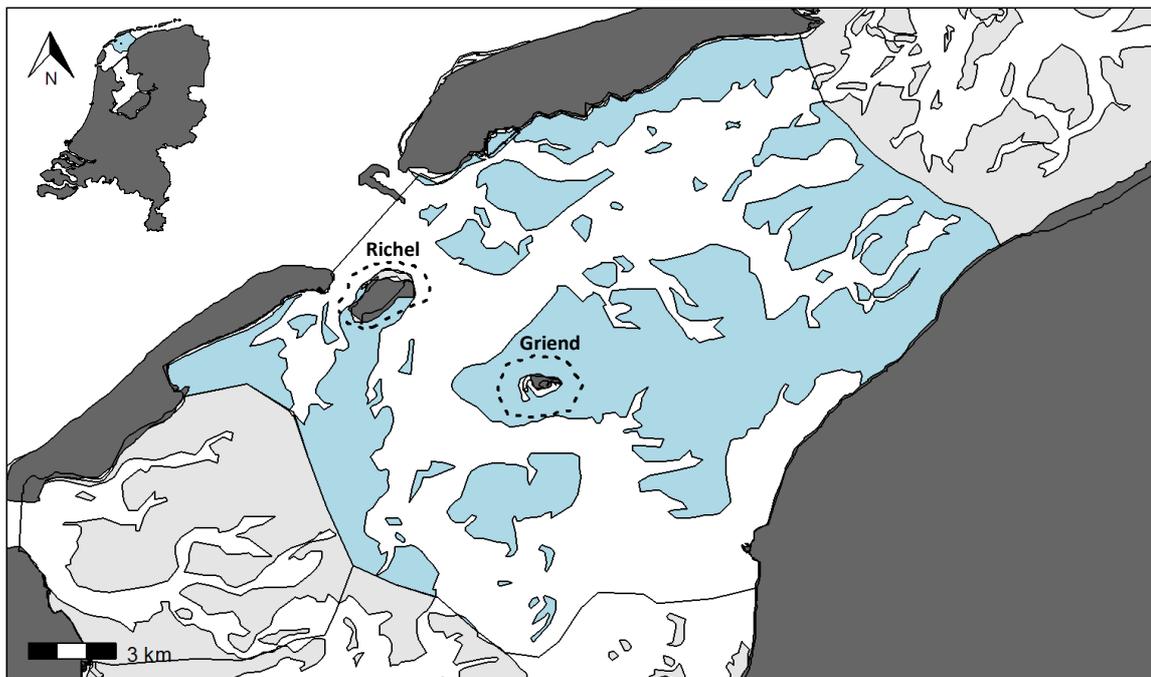


Figure 1: The study area of the research. The mudflats of the Vlie tidal basin, used by the foraging red knots at low tide, are shaded in blue. Griend and Richel are the two islets surrounded by a dotted area. These two areas are where the red knots are counted during high tide. In the upper left corner an overview of the location of the study area within the Netherlands is given.

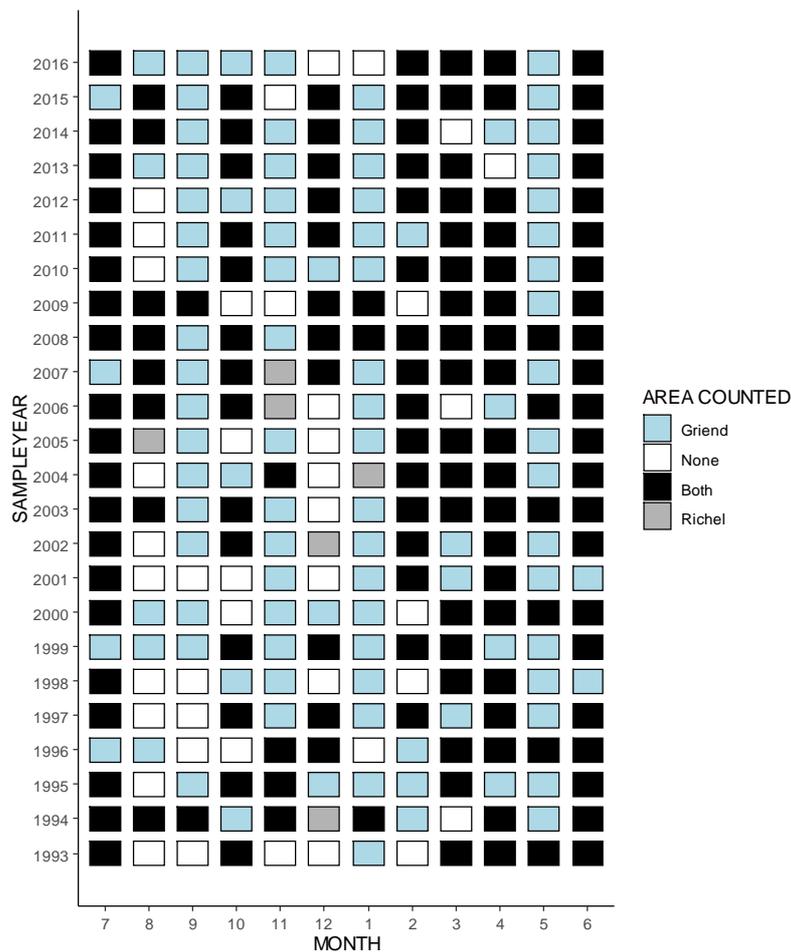


Figure 2: Overview of the monthly high-tide roost counts during the study period. White tiles represent a month that is not counted on either roost, light blue and grey indicate that a roost is counted on Griend or Richel only respectively and black tiles indicate that both roosts were counted that month.

(53°29'N, 05°13'E). During low tide, large flocks of red knots roam the exposed mudflats to forage on hard-shelled mollusc prey. Red knots roosting on Griend and Richel mostly stay within the Vlie tidal basin to forage (Piersma *et al.*, 1993; van Gils *et al.*, 2006).

Red knot counts

Monthly high-tide roost counts were carried out by volunteers coordinated by Sovon (the Dutch Centre for Field Ornithology) on the roosts Richel and Griend between July 1993 and June 2017. Because the red knots counted on Griend and Richel stay within the Vlie tidal basin to forage, the number of red knots counted at high tide represents the number of red knots residing in the Vlie tidal basin every day of that month (Piersma *et al.*, 1993; van Gils *et al.*, 2006). Due to circumstances (e.g. poor visibility, storm) bird counts could not be carried out every month, despite the intention to do so. For months with missing counts on either Richel, Griend or both roosts, the red knot numbers were estimated and imputed by Sovon using the program U-index (Bell, 1995; van Roomen *et al.*, 2002; van Roomen *et al.*, 2006). The estimated number of red knots was based on the combination of the ratio of red knots in the area of interest and surrounding areas (site-effect), the ratio of red knots in the missing month and other months (month-effect) and the ratio of red knots in the missing year and other years (year-effect) (Bell, 1995; Soldaat *et al.*, 2004; Sovon, 2015). It is assumed that the site-effect is stable over years and that the month and year effect are the same for all locations (Soldaat *et al.*, 2004; Soldaat *et al.*, 2007). A complete review of the method is beyond the scope of this report, but please refer to Underhill & Prys-Jones, 1994, Soldaat *et al.*, 2004 and Soldaat *et al.*, 2007. Figure 2 gives an overview of the red knot counts on Richel and Griend. No single month was counted all years or found to be representative for the whole year (Figure 2 & Appendix I). Therefore, all monthly roost counts (including imputed values) of each year were summed to obtain the yearly red knot bird-months counted in the Vlie tidal basin. A bird-month is defined as the amount of months one bird can reside in an area, or the amount of knots that stay in an area for one month. A year in this research is defined relative to the migration of red knots and therefore starts in July when the red knots start arriving in the Wadden Sea.

Red knot prey

Even though red knots have been observed foraging on a variety of bivalves, gastropods and the occasional crustacean, depending on availability and the season, *C. edule* and *L. balthica* form up to 98% of the diet of knots (Zwarts & Blomert, 1992; Dekinga & Piersma, 1993). Therefore, these two species represent the prey for knots in the present research. Of these two prey species, *L. balthica* has been shown to be the preferred prey, because it has a higher prey quality (Zwarts & Blomert, 1992; van Gils *et al.*, 2005). Because red knots swallow their prey whole, there is a maximum size limit to the prey they can ingest. Prey with a maximum shell length of 16 mm for *L. balthica* and 12 mm for *C. edule* is still ingestible, larger prey is not available for red knots to eat (Piersma *et al.*, 1993; Zwarts & Wanink, 1993). Even though the shell length is a single measure of the prey species, it is indicative of the three-dimensional size of prey (Zwarts & Blomert, 1992). Where *C. edule* is always found buried just underneath the surface, *L. balthica* can bury out of reach of the bill of red knots, making the prey buried deeper than 4 cm unavailable (Zwarts & Wanink, 1989; Zwarts & Blomert, 1992; Zwarts *et al.*, 1993). Unfortunately, a measure for prey burial depth was not available for all sample years. The burying depth of *L. balthica* also varies with the season, as they bury deeper in winter (Zwarts & Blomert, 1992). The measure for depth was only available in summer for this research, leading to an unknown overestimation of the fraction of prey in the top layer. As the burying behaviour is also varying between years (Zwarts *et al.*, 1992), we opted not to include burying behaviour in the analysis.

Prey data collection

Benthic surveys were carried out in the Vlie tidal basin each year between July and September in the period from 1993 until 2017. This time period covers several sampling programs and the sampling grid slowly expanded, so not every sampling station has been sampled an equal amount of times (see Figure 3). The area around the island Griend has been sampled for the longest period of time within our study period and the coverage of the sample grid expanded from there. Only sampling stations within the red knots' main foraging were included in the analysis (see Figure 3). There is large variation in prey availability between different tidal mudflats, which could result in an error in analysis and interpretation of results if samples outside of the foraging area are included (Piersma & Bijleveld, personal communication).

The samples were taken on a fixed 500m grid that was complemented by 20% randomly located points placed on the grid lines from 2008 onwards (see Figure 3). The sample sites were found using a handheld

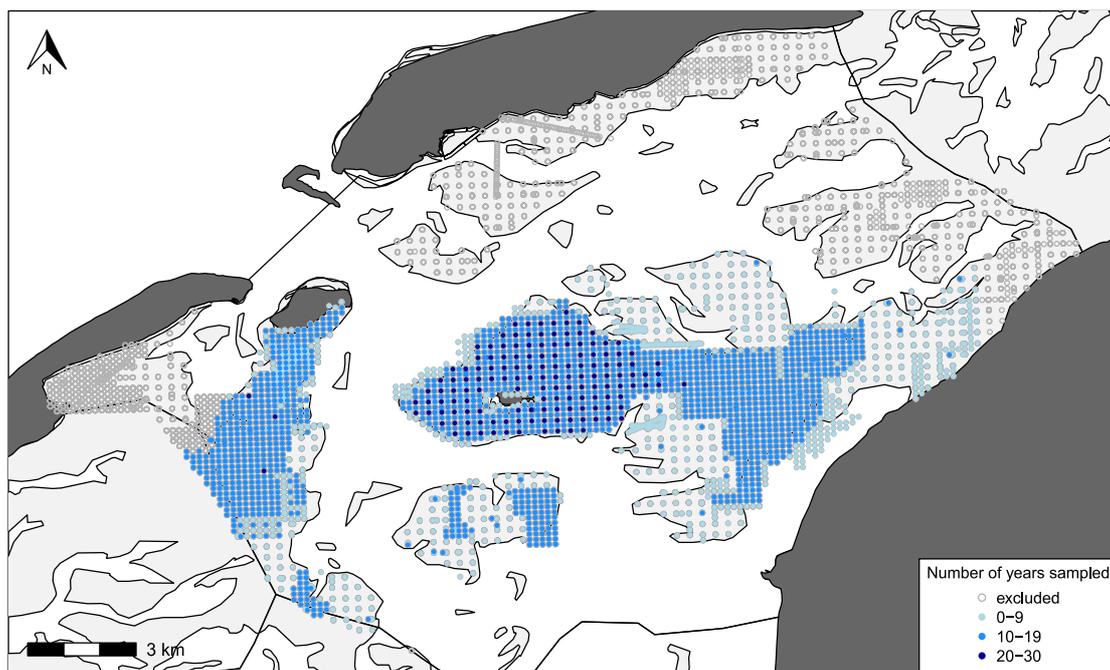


Figure 3: Distribution of the benthic sampling stations on the tidal flats of the Vlie tidal basin. The darker the color of the sample point, the more often a sample point has been sampled. Sampling stations indicated with open grey circles were excluded from the research.

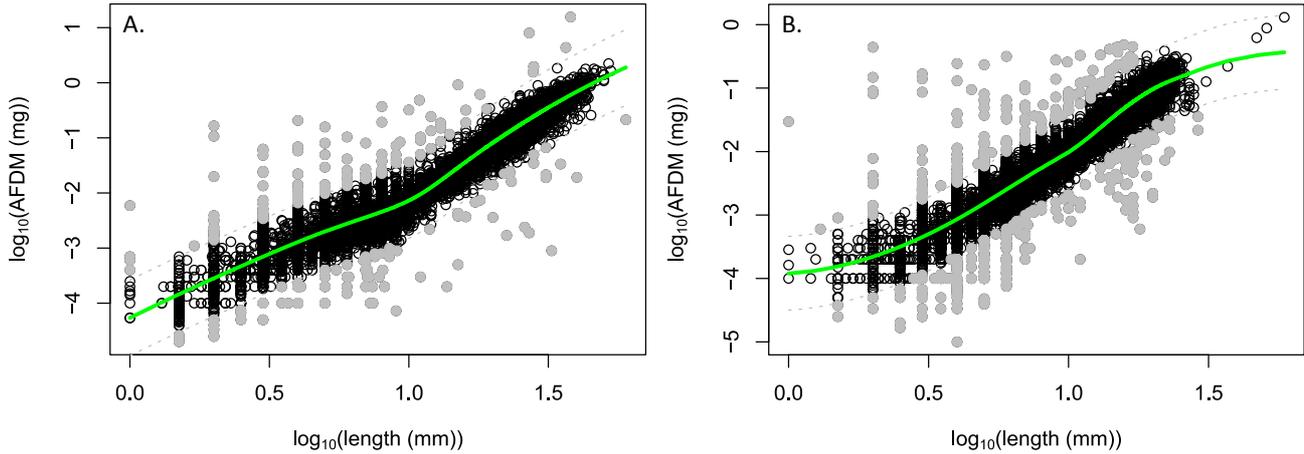


Figure 4: The relation between $\log(\text{Shell length})$ and $\log(\text{AFDM})$ for both prey species. The LOESS regression for $\log(\text{AFDM})$ versus $\log(\text{Shell length})$ is indicated in green. Data is plotted underneath; outliers are plotted in grey. The grey dashed line indicates the outlier envelope.

GPS and reached either by foot (during low tide) or by boat (during high tide). Using a core with a surface of $1/56 \text{ m}^2$, the top 40 cm of the sediment was collected and sieved over a 1 mm mesh size. Large molluscs ($> \pm 8 \text{ mm}$) were separated from the rest of sample and stored in plastic bags in the freezer at -20°C . The rest of the sample was coloured with Bengal Pink and stored on a 4% formaldehyde solution. Bivalves were identified to species level and the shell length was determined to the nearest 0.01 mm in the laboratory. For the large prey species ($> \pm 8 \text{ mm}$), the yearly growth rings on the shell were counted in order to estimate the age of the shell. The shell and flesh of the large bivalves were separated. The flesh of the prey species was incinerated in order to measure the Ash Free Dry Mass of the flesh of each individual prey (AFDM). The large shells were dried separately and the dry mass of the shell was determined.

When a prey individual had been identified to species level and the shell length was measured, but the AFDM could not be weighed, the AFDM was estimated using LOESS regression of the species-specific relation between the shell length and the AFDM (Figure 4). Outliers in measured AFDM (measurements outside 1.5 times the interquartile range) were also identified and the measured AFDM was replaced with the calculated value. There were three sample points with unrealistically high prey densities. These were assumed to be measuring errors and were excluded from further analysis.

The prey abundance and prey biomass per square meter was determined by dividing the respective measurements of the two different prey species per sample by the surface area of the sample. The mean prey density in individuals per square meter and mean biomass density per square meter were calculated by taking the averages of all samples per year. The correlation between the mean prey density and prey biomass per square meter and the number of red knots bird-months counted on Richel and Griend was calculated for each year.

Prey Quality

Prey quality was calculated using:

$$\text{Quality} = \frac{\text{AFDM}_{\text{flesh}}}{\text{Dry Mass}_{\text{shell}}}$$

where a prey individual has a higher quality if it has a higher flesh/shell ratio. The prey quality could only be calculated when both AFDM and the dry mass of the shell were measured. As the prey quality is a fraction where the dry mass of the shell should always be larger than the AFDM the maximum prey quality is 1. Due to measuring errors, sometimes the dry mass of the shell and AFDM were in a same range, resulting in very high prey quality. In these instances, the maximum prey quality is assumed to be 1. The correlation between the mean prey quality and the cumulative numbers of red knots was calculated.

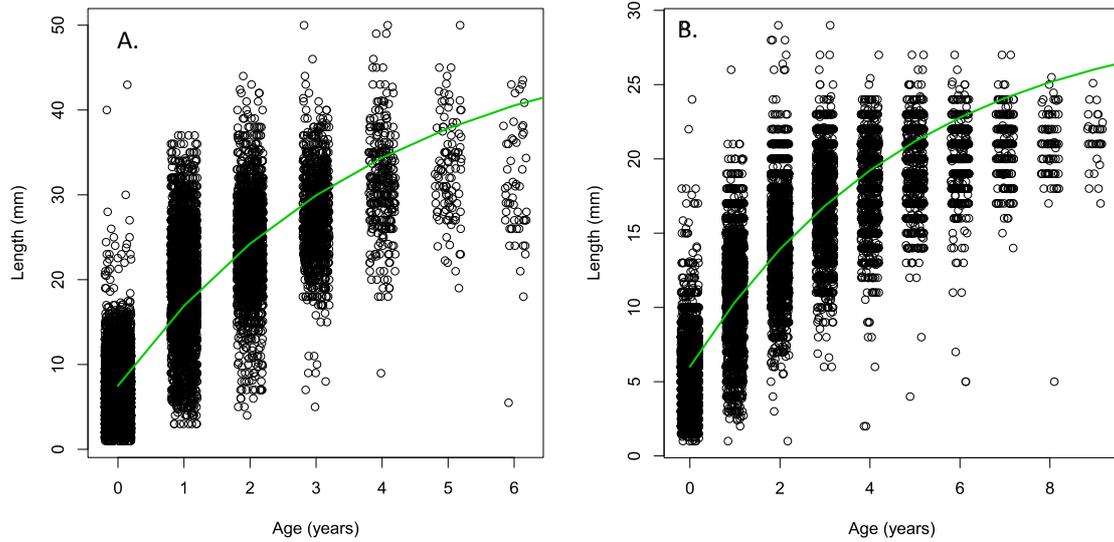


Figure 5: The relation between age and shell length for both prey species. Growth curves showing the average length at each age for both prey species are indicated in green (fitted Von Bertalanffy growth curve). A) *C. edule*. B) *L. balthica*

Prey elimination

In order to estimate the prey depletion by red knots, the prey elimination in edible length classes each year was calculated. Prey availability was predicted based on the growth per year for each length class and this prediction was compared to the observed prey availability each year. When there was more prey predicted than observed, prey was eliminated during the year.

The growth of the prey was calculated using the prevalent Von Bertalanffy growth equation (von Bertalanffy, 1938) where the length (L) at any time (t) is given by:

$$L(t) = Linf * [1 - e^{-K*(t-t_0)}]$$

Where $Linf$ is the asymptote of the length that would be reached by the average individual of infinite age, K is the growth parameter t is the time (in years) and t_0 is the (imaginary) moment in time where the size is zero (sometimes also defined as the moment of hatching). The Von Bertalanffy parameters K and t_0 were fitted based on the observed age-length relation of the shell for both species (Figure 5). The age of the prey was determined by counting the growth rings. In order to calculate the growth curves *C. edule* with ages over 7 years and *L. balthica* older than 10 years were omitted. These were the oldest ages observed in more than 3 different sample years, prey species with older ages that were only observed once or twice could be a miscount of growth rings. For $Linf$, the mean observed length at the maximum age (45 mm for *C. edule*, 25 mm for *L. balthica*) was taken. Varying the values of $Linf$ (between the minimum observed length at the maximum age and the maximum observed length at this age) resulted in similar result patterns. Based on the growth parameters from the fitted Bertalanffy curve, the length-dependent growth over a year was estimated for the whole dataset as follows:

$$\frac{dL}{dt} = K * (Linf - l) + l$$

where $dLdt$ is the length increase over time t (a year in this research) and l is the measured shell length. Figure 5 gives the growth curves for both prey species. Even though the sampling period stretched between late July and early September, for predicting growth it was assumed that the time period between the sampling was always a whole year.

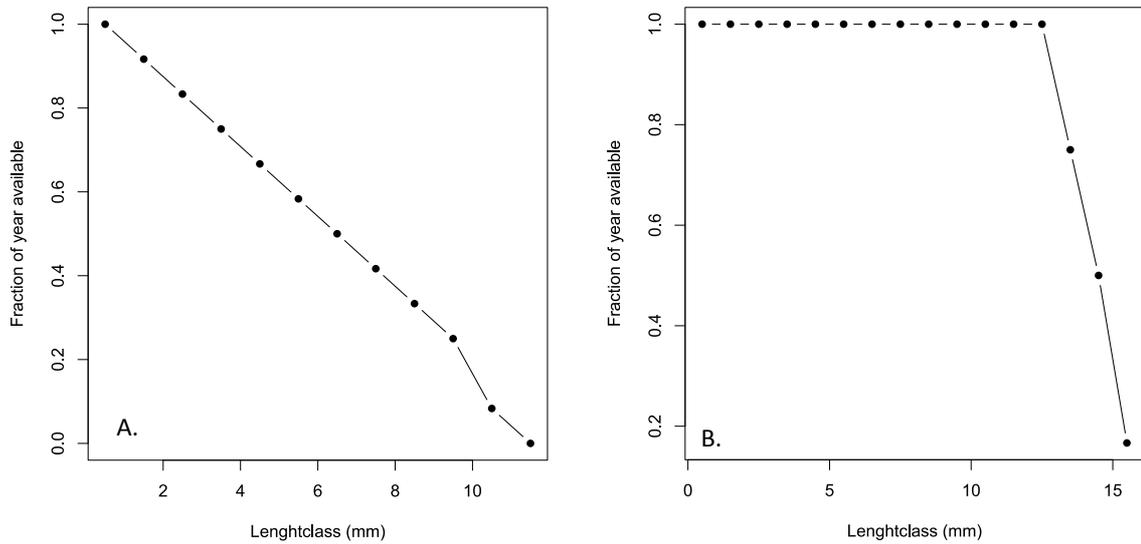


Figure 6: Fraction of the year that the prey in each edible length class is available to red knots based on the average growth per month. A) *C. edule*. B) *L. balthica*

During the year the prey also grows and can therefore become too large for red knots to ingest. This means that prey in some size classes is only available for a fraction of the year. The yearly fraction of prey availability was calculated for each length class of 1 mm using the average growth per month:

$$\frac{dL}{dt_m} = \frac{K * (Lin f - l)}{12} + l$$

Where dL/dt_m is the length increase per month, all other parameters are defined above. Using the growth per month, the fraction of the year prey in each size class of 1 mm was available for red knots to eat was calculated (see Figure 6). The predicted prey per square meter was multiplied by this fraction for each length class to compensate for this growth during the year.

For all sample years, the observed and predicted length-frequency distribution could then be compared. Prey elimination was calculated by subtracting predicted length- frequency distribution from the observed length- frequency distribution in the same year (Figure 7). Any negative difference between

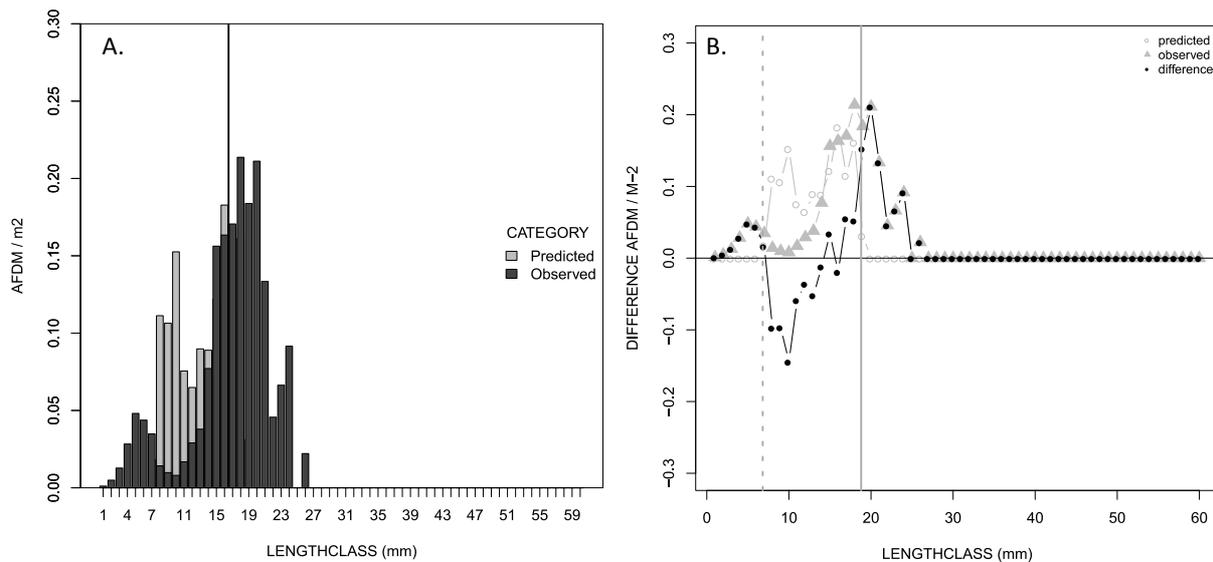


Figure 7: A) Biomass per square meter in all length classes for *L. balthica* in 2013. Dark grey indicates the observed values, light grey represents the predicted values. The vertical line indicates the upper limit taken for calculating elimination. B) Difference between the predicted and observed biomass per square meter for *L. balthica* in 2013. Open circles indicate the predicted values, triangles indicate the observed values and the black dots indicate the difference between the two. The solid vertical line indicates the maximum ingestible shell length (16 mm) plus growth during year (upper-limit), the dashed vertical line indicates the size of the smallest observed individual observed in 2012 plus growth (lower-limit). When calculating the total prey elimination these limits are taken as minimum and maximum boundary.

these length-frequency distributions in the edible size classes for red knots was taken as a measure for prey elimination (see Figure 7 and Appendix II). All prey elimination in edible size classes, between the edible limits, was summed to obtain the total prey elimination each year. The upper edible limit was taken as maximum edible shell length plus growth. The lower edible limit was minimum shell length observed in the previous year plus growth, in order to exclude prey recruits from the calculated elimination. To compensate for different sample sizes in different years, the prey in each length class was divided by the total sampling surface of the year to calculate the prey difference per square meter in each length class. The correlation between the prey elimination in prey numbers per square meter and the number of red knot bird-months was calculated.

AFDM can be seen as a measure for available energy and therefore is a more accurate way to link prey to red knot population size than the prey densities in individuals per square meter. The prey elimination is therefore also calculated in terms of prey biomass. The AFDM for the predicted shell length is calculated using the LOESS curves that were fitted to the relation between shell length and AFDM (see above). This resulted in the total predicted biomass per square meter for each length class of 1 mm for all sample years. The difference between predicted and observed edible prey biomass was calculated per length class for all sample years. The correlation between the red knots bird-months in the Vlie tidal basin and the elimination of AFDM per square meter was then calculated.

The fraction of prey elimination with respect to the original prey availability was calculated to evaluate the elimination of prey with respect to the amount of prey available each year. The fraction of prey elimination (F) is calculated for each length class using:

$$F = \frac{prey_{observed}}{prey_{predicted}}$$

This relation between this fraction of eliminated prey was then assessed.

Bird energy requirements

In order to determine if the total available biomass in the Vlie tidal basin was sufficient for all red knots visiting the area, the total available biomass was compared to the energy requirements of all red knots. To determine if the red knots might be the cause of the prey elimination in the Vlie tidal basin, the total prey elimination in the Vlie tidal basin was also compared to the energy requirements of all red knots. If the energy requirement matches the prey elimination in edible size classes, it is plausible that the red knots are responsible for the difference between observed and predicted prey densities in edible length classes.

Foraging red knots have an average energy intake requirement of 0.3 mg shellfish AFDM s⁻¹, when they forage during 10 hours each day (Piersma, 1995). The total energy requirement (E) for all red knots in the Vlie tidal basin for a whole year is therefore calculated as:

$$E = B * m * (0.3 * 10^{-3} * s)$$

Where B is the sum of the monthly number of red knots counted on Richel and Griend in a year, m is the months per year (365.25/12), $0.3*10^{-3}$ is the energy requirement for red knots in g AFDM per second and s is the amount of seconds in a day (86400 seconds). The measure E for energy requirements of all red knots each year was compared to the total edible biomass in the Vlie tidal basin and to the prey elimination over the whole Vlie tidal basin. The total available biomass and the total prey elimination per year were calculated by multiplying the average biomass in edible size classes per square meter with the total foraging area in the Vlie tidal basin. It was assumed that the foraging area in the Vlie tidal basin was constant throughout the study period (177.75 km², based on the area represented by the maximum number of benthic sampling grid points (n=711 in 2008)). We also assumed that the whole foraging area is available during the red knot foraging period (10h).

Data analysis

Data analysis was carried out in R (R Core Team, 2017). Packages used were GGPlot2 (Wickham, 2009), MGCV (Wickham, 2009), plyr (Wood, 2017), tidyr (Wickham, 2011) rgdal (Wickham & Henry, 2019) and PrettyMapR (Bivand, 2018). When fitting a regression line, a General Linear model and a Generalised Additive Model were always compared because the relation between red knot population size and prey was not necessarily expected to be linear. Based on the AIC the best fitting model was chosen.

RESULTS

For simplicity, in this result section the focus is on prey biomass per square meter. The biomass directly relates to the energy intake for red knots and is therefore an intuitive measure for how prey availability translates to red knot numbers. The analyses for red knot numbers and prey densities in individuals per square meter can be found in Appendix III.

Red knot population size

Red knot populations in the Vlie tidal basin as counted on Richel and Griend, varied over time. Within years, the number of red knots showed a seasonal pattern (Figure 8). Red knots leave the Wadden Sea and migrate to their breeding grounds in the North early May, which is reflected in the observed bird counts. From May onwards the least red knots were counted in the Vlie tidal basin (ranging between 4 and 25000 red knots counted). From July (the start of the year as defined for this research) the knots return to the Wadden Sea and the number of observations increased. The highest number of red knots counted in a single month in Vlie (91012 individuals) was observed in October 2013. In the winter the spread of the red knot numbers was largest, these counts mainly represent *islandica* subspecies wintering in the Vlie tidal basin.

All monthly counts of red knots are added up to arrive at the red knots bird-months in the Vlie tidal basin each year (Figure 8). The number of bird-months varied widely throughout years. A strong decrease in red knot bird-months was observed from 1998 onwards, with the lowest number of 65215 red knot bird-months in the Vlie tidal basin observed in 2002. From 2006 the population size started to increase again. The number of red knot bird-months at the start of the study period was comparable to those at the end of the study period. The highest number of red knots bird-months in the Vlie tidal basin (423658) was observed in 2013.

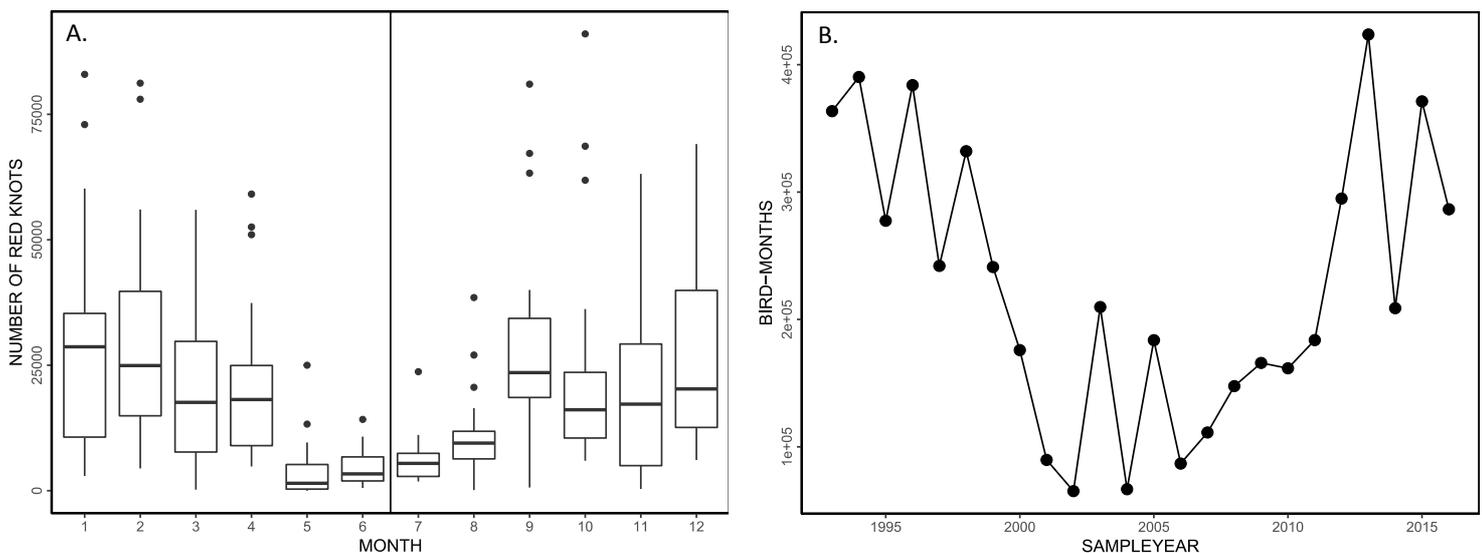


Figure 8: A) numbers of red knots counted per month. Boxes represent the median, quartiles and interquartile outliers in the sum of red knots counted or imputed on Richel and Griend each month. The vertical line indicates the separation of a year as used in this research (July-June). B) Sum of numbers of red knots counted or imputed (bird-months) each month per sample year.

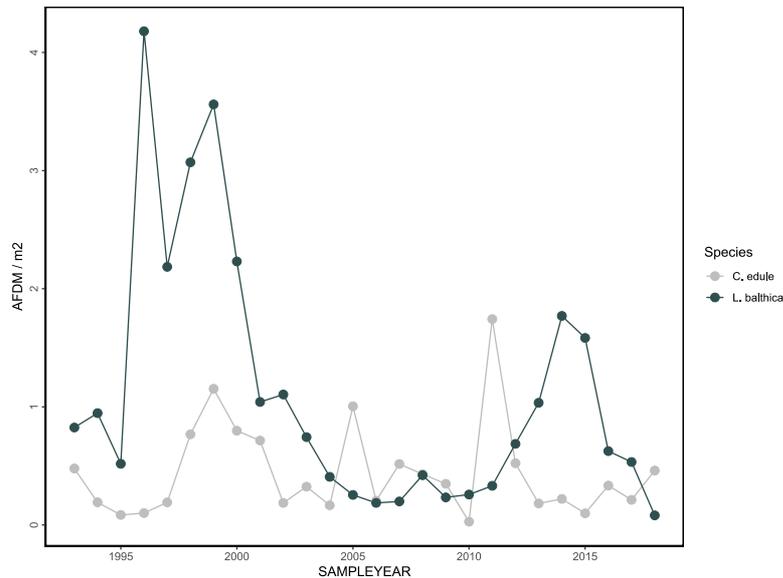


Figure 9: Mean edible prey biomass (AFDM) per square meter each year for both prey species. Light grey represents *C. edule* and dark grey represents *L. balthica*.

Availability of prey

The total *L. balthica* biomass ranged between 0.05g AFDM m⁻² and 157.8g AFDM m⁻². For *C. edule*, the biomass ranged between 0.002g AFDM m⁻² and 355.1g AFDM m⁻². The average *L. balthica* biomass per year varied between 0.13g AFDM m⁻² in 2018 and 8.3g AFDM m⁻² in 1999. The biomass of *C. edule* varied between 0.36g AFDM m⁻² in 1996 and 10.2g AFDM m⁻² in 1998. Of this biomass a minimum of 3% (in 2010) and a maximum of 35% (in 2011) of *C. edule* was ingestible for red knots. Of *L. balthica* the minimum percentage ingestible biomass was 11% (in 2018) and the maximum was 49% (in 2014). On average, 10% of all *C. edule* and 31% of all *L. balthica* biomass was available to red knots. Figure 9 shows the average edible biomass per square meter for both prey species each year. There was a decline in available prey biomass from 1999 onwards, and the prey biomass increased again from 2010 onwards. The fluctuations in edible biomass for *L. balthica* were larger than those of *C. edule*. The years when maximum numbers, biomass and availability of prey was found, were years where an extremely large spat fall was observed in the Wadden Sea and the prey densities were unusually high (especially in 2011 for *C. edule*).

The spatial distribution of prey was not homogenous, Figure 10 gives an overview of the distribution of the mean prey biomass in edible size classes over all sample years for both prey species. Edible *L. balthica* was more widely distributed and sample points with a higher biomass were more common for *L. balthica* than for *C. edule*. In general, the area around Griend, the mudflats just south of Richel and the area just off the Frisian coast contained the most edible biomass. In 74% of all sample points *L.*

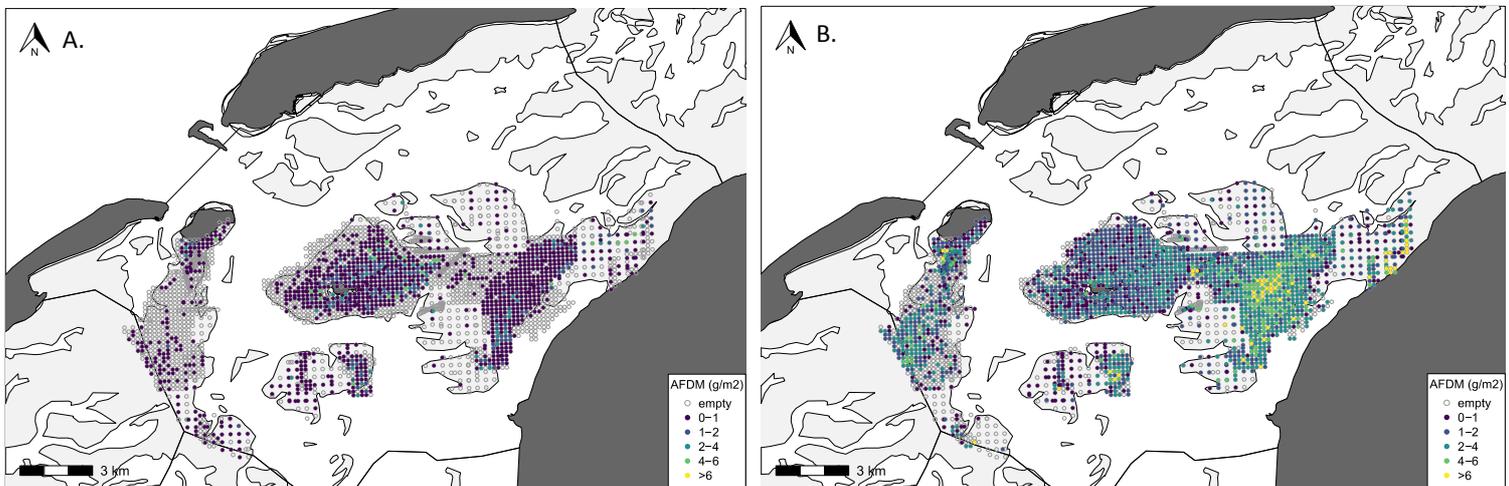


Figure 10: Spatial distribution of mean prey biomass in edible size classes over the whole sampling period. Open circles represent sample points where no prey biomass was found. Lighter colours represent higher average biomass per square meter. A) *C. edule* B) *L. balthica*.

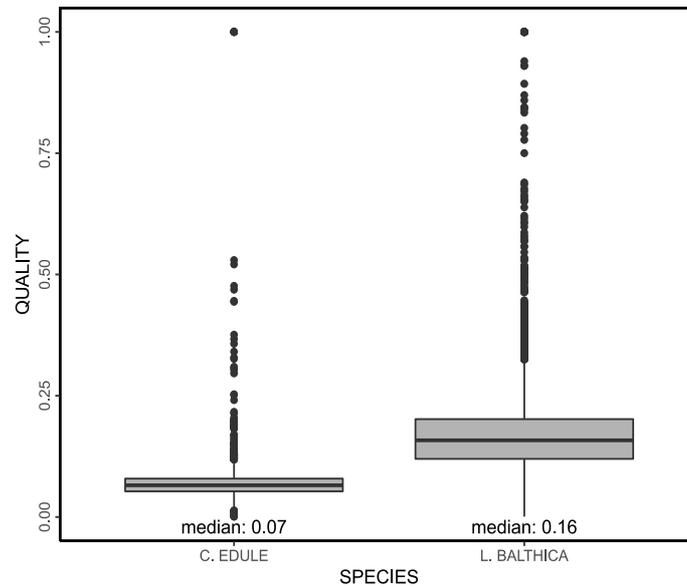


Figure 11: Boxplot for the prey quality for both prey species. Boxes represent the median, quartiles and interquartile outliers in prey quality per sample for *C. edule* (n=3305) and *L. balthica* (n=7599).

balthica in edible size classes was found in at least one sample year. For *C. edule* this was in 44% of all sample points. For the distribution of the densities of edible prey in individuals per square meter for both prey species, please refer to appendix III.

Quality of prey

The two prey species had a different prey quality. As shown in Figure 11, the general flesh to shell ratio is lower for *C. edule* than for *L. balthica*. The median quality per sample for *C. edule* is 0.07, and for *L. balthica* this is 0.16. The range of prey quality per sample was similar for both prey species, but the interquartile range of the quality per sample was smaller for *C. edule* than for *L. balthica*.

Red knots and prey throughout years

The number of red knot bird-months counted on Richel and Griend did not correlate with the available biomass per square meter of *C. edule* per year (Figure 12A). For *L. balthica* on the other hand, a linear correlation was found between the amount of edible biomass per square meter and the red knot bird-months in the Vlie tidal basin (n=23, $R^2=0.17$, $p=0.04$) (Figure 12B). Therefore, any decrease in *L. balthica* resulted in a decrease in the red knot population in the Vlie tidal basin.

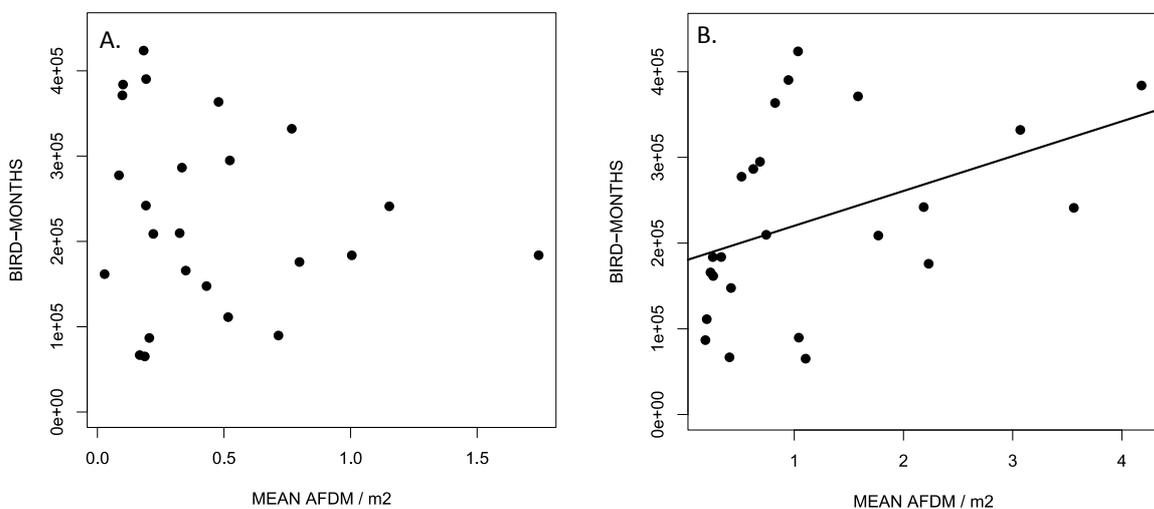


Figure 12: Yearly red knot bird-months plotted against the AFDM per square meter for both prey species. Each data point represents one sample year and the solid line indicates the fit is significant. A) *C. edule*. B) *L. balthica*.

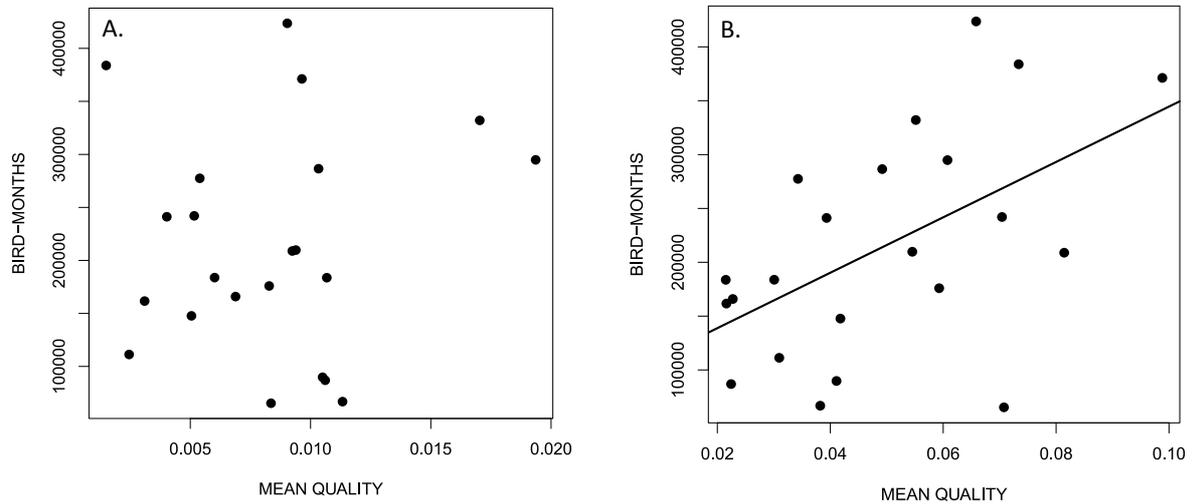


Figure 13: Red knot bird-months plotted against the mean quality of prey for both prey species. Each data point represents one sample year and the solid line indicates the fit is significant. A) *C. edule* B) *L. balthica*.

The prey quality was variable over time (Appendix V). The variations in prey quality of *C. edule* did not correlate with the red knot population size in the Vlie tidal basin (Figure 13A). The number of red knot bird-months did however correlate positively with the quality of *L. balthica* ($n=22$, $R^2=0.25$, $p=0.01$) (Figure 13B). This means that any decrease in quality of *L. balthica* led to a decreasing red knot population in the Vlie tidal basin.

Prey elimination

At first it appeared that there was no correlation between the elimination of biomass and the red knot bird-months for either prey species (Appendix IV). However, for both prey species there was an extreme outlier in years with an extreme spat fall (2011 for *C. edule* and 2014 for *L. balthica*). The value of the outlier was 27.9 times the interquartile range for *C. edule* and 3.2 times the interquartile range for *L. balthica*. In order to further investigate the relation between the elimination and the red knot numbers, these outliers were excluded (the analysis with outlier can be found in Appendix IV). Still, no relation was found between the difference in predicted and observed *C. edule* biomass per square meter and red knot bird-months (Figure 14A). In contrast, it did result in a significant correlation between the elimination of *L. balthica* biomass per square meter and the number of red knot bird-months in the Vlie tidal basin ($n=23$, $R^2=0.46$, $p=0.003$) (Figure 14B). The best fit was found using a General Additive Model, taking into account the non-linear nature of the relationship. The elimination of *C. edule* increased slightly with larger *C. edule* biomass per square meter (see Appendix VII). It increased strongly with an increasing prey density in individuals per square meter (see Appendix VII).

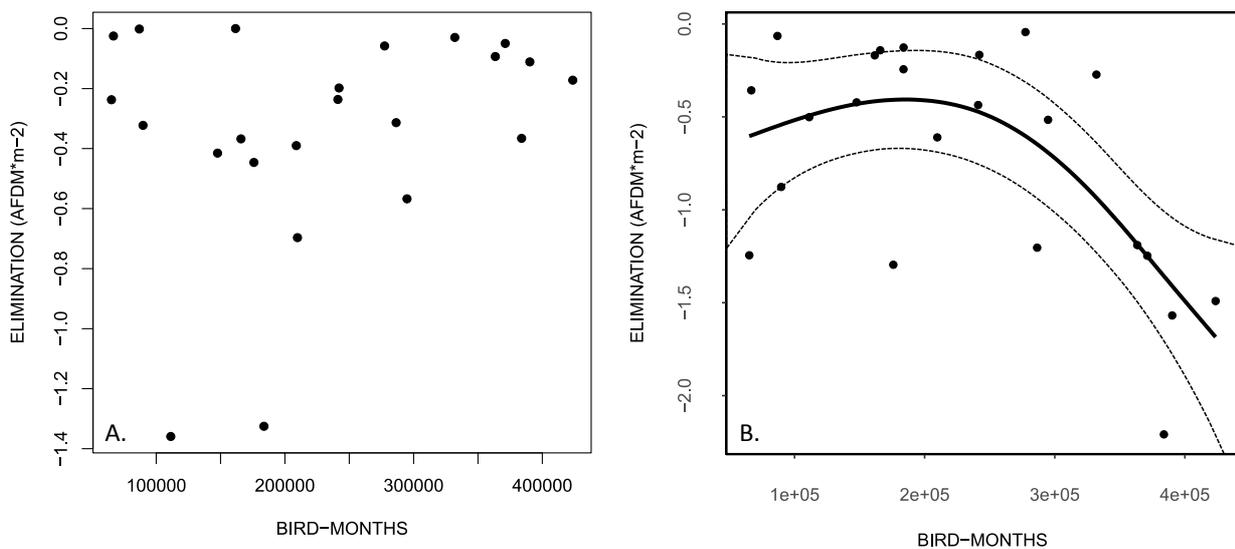


Figure 14: The difference in predicted versus observed prey AFDM per square meter (as a measure for prey elimination) for both prey species plotted against the red knot bird-months. Each data point represents one sample year and the solid line indicates the significant GAM fit, the dashed line gives the 95% confidence interval. A) *C. edule*. B) *L. balthica*

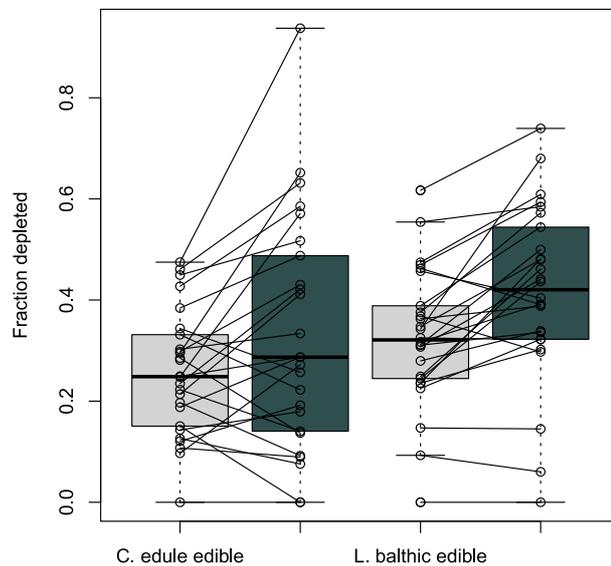


Figure 15: Fraction of prey depletion in edible size classes (dark grey) versus all size classes (light grey). Boxes represent the median, quartiles and interquartile outliers in fractions of prey eliminated. Line segments between the boxes link the two fractions for each year. The two boxes on the left are for *C. edule*, whereas the boxes on the right represent *L. balthica*.

For *L. balthica* the prey elimination increased with both the available biomass as well as the prey density (Appendix VII). This could imply that mainly small individuals (with a low biomass) were eliminated. The fraction of prey that was eliminated was constant, and did not correlate to the number of red knot bird-months counted yearly on Griend and Richel for both prey species (see Appendix VI). The fraction of elimination of prey biomass with respect to the available biomass was higher for *L. balthica* than for *C. edule*. For *C. edule* the fraction of prey that was eliminated centred around 0.36, for *L. balthica* the fraction eliminated centred around 0.48 (see Appendix VI). The fraction of prey eliminated was higher in edible size classes than the fraction of depletion over all shell lengths for both prey species (Figure 15). This difference was larger for *L. balthica* than for *C. edule*.

Red knot energy requirements

In order to understand if the available biomass would be sufficient for the number of red knots staging in the Vlie tidal basin, the biomass in the whole foraging area was compared to the biomass required by all the red knots staging in the Vlie tidal basin during a year. For *C. edule* the general energy requirements were higher than the available biomass (see Appendix VIII). For *L. balthica* the available biomass corresponded better with the energy requirements of the red knots (see Appendix VIII). The energy requirements of the red knots were also compared to the eliminated prey biomass, in order to understand if the missing prey biomass could be eaten by red knots. For *C. edule*, the eliminated biomass was much lower than the requirements of red knots (Figure 16 & Appendix VIII). There was one extreme

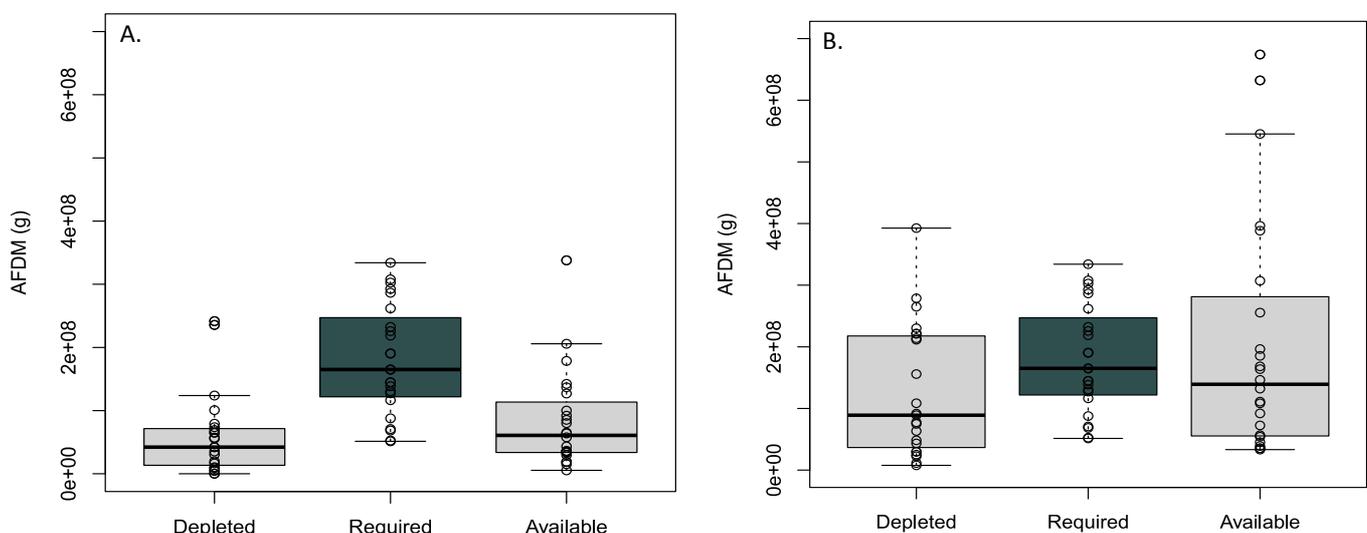


Figure 16: The biomass required by all red knots in Vlie each year (middle box in both panels) versus the prey depletion (left boxes) and prey biomass available (right boxes) in the Vlie tidal basin. Boxes represent the median, quartiles and interquartile outliers in biomass. The open circles indicate the different years. A) *C. edule* B) *L. balthica*

outlier in the total prey elimination in the Vlie tidal basin for both species in years with an extreme spat fall. In order to be able to visually compare between the prey species, this outlier was excluded. The same figure with outlier can be found in Appendix IV. For *L. balthica* the biomass that was eliminated was more in accordance with the red knot energy requirements (Figure 16 & Appendix VIII). There is more overlap in the total biomass required by red knots and the biomass available or eliminated for *L. balthica* than for *C. edule*, as would be expected because *L. balthica* is the preferred prey.

DISCUSSION

In this study, the relation between long-term variation in availability of prey and prey elimination through foraging during the year and the number of red knots in the Western Wadden Sea was examined over 24 years. We showed a relation between the preferred prey (*L. balthica*) and the number of red knots in the Vlie tidal basin, but no such relation was found for the alternative prey (*C. edule*). Population size of red knot also increased with increasing quality of *L. balthica*. There was a non-linear relationship between the red knot population and elimination of *L. balthica*. Prey elimination was highest in edible size classes and was roughly in accordance with the biomass required by the red knot population. This now allows us to evaluate how variations in red knot numbers are linked to food availability in the Wadden Sea.

Red knots and available prey biomass

Our analyses showed variation in the numbers of birds counted on Griend and Richel both within and between years. Within years, the red knot counts showed a clear seasonal pattern that was closely related to the migration itinerary. Between years, a strong drop in the red knot population size was observed between 2000 and 2010, before and after that period the population size was larger. In roughly the same study period, Kraan *et al.* (2009) also observed a decreasing number of red knots in the Western Wadden Sea and the trend they observed was similar to the observations in this research. However, using the counted number of red knots, it is impossible to indicate whether a decrease in red knot numbers is due to increasing mortality or due to emigration (Kraan *et al.*, 2009). In order to estimate (local) survival, individuals have to be marked and recaptured (as reviewed by Brochard *et al.*, 2002; Bearhop *et al.*, 2003; Sandercock, 2003; Piersma, 2007). Early on it was suggested that local survival of red knots has decreased in the Western Wadden Sea during the study period (van Gils *et al.*, 2006), but this was not confirmed later (although the local seasonal survival did vary, see Rakhimberdiev *et al.*, 2015). Alternatively, decreased reproductive success could have played a role in the decreasing red knot numbers. However, Boyd and Piersma (2001) showed a negative relation between juvenile percentages and total red knot population size. They suggested that negative density dependent recruitment leads to increased recruitment of red knots when the population size is smaller, which might contribute to stabilisation of the red knot population (Boyd & Piersma, 2001). The total *islandica* red knot population along the flyway over the period of our study has been relatively stable, therefore the declines in red knots may mostly be caused by relocation during wintering period (van Roomen *et al.*, 2018). The results found in our study suggest that food availability and depletion of food resources during the year might play an important role.

Previous research already showed the (spatial) relation between red knots and their food on shorter time scales (e.g. Piersma *et al.*, 1993; van Gils *et al.*, 2005; Kraan *et al.*, 2009; Folmer *et al.*, 2012; Bijleveld *et al.*, 2016). In this research, the relation between availability of the preferred prey and red knot population size is also shown on the scale of the whole Vlie tidal basin using the average prey per year as data points, a remarkable possibility in itself. Based on the notion that less knots are present when there is less suitable foraging area, Kraan *et al.*, (2009) conclude that the Western Wadden Sea is used to capacity. The results found in our research are consistent with this conclusion, as there are fewer red knots in the Wadden Sea when there is less *L. balthica* biomass available. This means that any change in *L. balthica* availability will be reflected in red knot numbers. Our results suggest that for investigating red knots and their prey, *L. balthica* or preferably a combination of prey species should be used. From a conservation perspective our results imply that it might be possible to use the availability of *L. balthica* as a measure for the red knot population that can be sustained by the Western Wadden Sea.

Previous research bases their conclusions on availability of *C. edule* as prey species whereas no relation between *C. edule* and the red knot population in the Vlie tidal basin was found in this research (van Gils *et al.*, 2004; Bijleveld *et al.*, 2015). However, our results are in line with the expectations, as *L. balthica* is the preferred prey (Zwarts & Blomert, 1992). We confirm that *C. edule* is a less profitable prey for knots, because it has a lower quality. The stock of *C. edule* biomass edible for red knots in the Vlie tidal basin proved to be insufficient for red knots to survive on in most years. However, our maximum size limit of 12 mm for ingestible *C. edule* is relatively conservative. Different research has taken different lengths as maximum ingestible size for *C. edule*; ranging from 8 to 16 mm, based on field observations (e.g. Zwarts & Blomert, 1992; Piersma *et al.*, 1993; Dekinga *et al.*, 1993; Piersma *et al.*, 1995; van Gils *et al.*, 2004). The maximum ingestible size of prey has a large impact on the amount of biomass that is edible for red knots; a larger ingestible size limit increases the amount of edible biomass. This could lead to a better correspondence between the total edible biomass and the red knot population, but in the field red knots are rarely observed eating larger *C. edule* (Piersma, personal communication). However, it is important to note that red knots have a flexible choice of prey (e.g. Zwarts & Blomert, 1992; Dekinga *et al.*, 1993; Piersma *et al.*, 1993; van Gils *et al.*, 2005), that varies within and between years based on the availability of prey. Therefore, evaluating just one prey species at a time does not fully capture the foraging of red knots.

The measure used to link prey to the red knot population was the average prey densities per square meter each year. The simplicity of this method comes with a trade-off, as using this basic measure for prey availability means that any extreme densities (high or low biomass) in could not be taken into account. The variation of the biomass per square meter within years within the Vlie tidal basin is considerable. Additionally, there were sample points that always had a higher or lower prey density than average (as is shown on the maps in the result section). Previous research suggests that it might be this variation in prey density that proves critical when an area is used to capacity (van Gils *et al.*, 2004; Kraan *et al.*, 2009). Red knots have been shown to choose foraging sites where the (predicted) rate of foraging is profitable (van Gils *et al.*, 2004). Therefore, these areas with an overall lower biomass might be avoided. On the other hand, patches with high prey density can compensate for food shortage when the mean prey densities are too low in an area (Zwarts, Blomert, *et al.*, 1992; van Gils *et al.*, 2005; van Gils, Piersma, *et al.*, 2006). By taking average prey biomass over a larger area (Vlie tidal basin) and over a longer timescale (24 years) these effects were taken into account implicitly in our study.

Red knots and prey elimination

The elimination of *L. balthica* in edible length classes increased as a function of the number of red knots counted in the Vlie tidal basin. Additionally, the energy requirement of all red knots in the Vlie tidal basin was in the same order of magnitude as the amount of prey biomass eliminated in the Vlie tidal basin. This is in contrast with the findings of van der Meer and colleagues (2001), who expected to find this result, but found that prey production was almost always much (up to a threefold) higher than the bird energy requirement they calculated. Our results showed that the amount of prey elimination for *L. balthica* was slightly less than the requirements of the total amount of red knots in the Vlie tidal basin. This is not unexpected, as red knots do not exclusively forage on *L. balthica*. Van Gils and colleagues found that red knots were able to deplete up to 25% of the prey within one low-tide (van Gils *et al.*, 2003). The fraction of prey eliminated over a year found here (0.36 for *C. edule*, 0.48 for *L. balthica*) is therefore not an unlikely number. The fraction of prey eliminated for *L. balthica* that we found, is similar to the mortality found in previous research (van der Meer *et al.*, 2001). The observed fraction of prey eliminated for *C. edule* was lower in this study than found by van der Meer who found a mean mortality of 73% in winter and 45% in summer (van der Meer *et al.*, 2001). However, they took all size classes into account whereas we only considered size classes edible for knots in our study.

We showed that the amount of prey elimination increased with prey densities; in years with higher densities, more prey disappeared. The prey species used in this research show density-dependent mortality (Philippart *et al.*, 2003; Parada & Molares, 2008). This could indicate that density-dependent mortality from other causes than red knot predation, as found in previous studies, might explain the elimination we observed. Despite the relation between prey densities and prey elimination, we found no strong relation between increasing prey biomass and increasing prey elimination. This could mean that mainly small individuals (with a low biomass) were eliminated. This would lead to increasing prey

elimination with prey density but no effect with an increased biomass. We also showed that the fraction of prey eliminated was higher in edible length classes, than the overall mortality in all length classes and that the elimination was strongest for the preferred prey species. This supports the premise that the observed prey elimination is indeed caused by red knots. Which could mean that the red knots play an important role in the Wadden Sea ecosystem, as they are able to significantly alter the abundances of their prey. In order to determine whether the elimination of prey is actually caused by red knots, and to rule out a common driver for both prey species and red knots, large scale experiments would have to be carried out. Exclosure experiments are a common way to study prey depletion. However, it can be argued that these experiments are not ideal because they alter the natural environment and the scale of the exclosure is often a lot smaller than the foraging area of the predator (Raffaelli & Moller, 1999; Thrush, 2009).

Leaving the Wadden Sea?

We showed that red knot population size in the Vlie tidal basin correlates to the prey availability and that red knots deplete their food resources through foraging during the year. When prey availability is too low, red knots die, skip the Wadden Sea (*canutus* subspecies) or leave during the winter (*islandica* subspecies). Rakhimberdiev *et al.* (2015) showed a decreased winter survival of red knots in the Wadden Sea during a period when food was limiting, which was counterbalanced by an increased summer survival. This was not the case when food was more abundant, indicating that red knots are indeed not residing in the Wadden Sea when the food availability is low (Rakhimberdiev *et al.*, 2015). Instead, red knots move away to other wintering areas in Northern Europe when food is limiting (Rakhimberdiev *et al.*, 2015). In light of this previous research and the close relation between the red knot population and food availability in the Western Wadden Sea, we suggest that during years when less knots were found in the our study area (2001-2011) a large share of the *islandica* population must have been wintering in other locations in Northern Europe.

Red knots are able to alter the average prey quality, as after a period of predation by red knots the prey with a thicker shell was left in a plot (Bijleveld *et al.*, 2015). This might mean that the higher quality prey might be depleted first, which is not unlikely because prey with a higher quality has a lower digestive cost and is therefore more profitable for red knots (Zwarts & Blomert, 1992; van Gils *et al.*, 2005; Bijleveld *et al.*, 2015). We found a positive relation between the red knots and quality of *L. balthica*, where more red knots were present in years when the prey quality was higher. This could be caused by one of two things; either red knots die or they move to a different area if there is too little high quality prey available. Certain individual red knots (explorative red knots) are specialised in finding this high-quality prey which means they have a lower intake of shell mass, and therefore need a smaller digestive organ (gizzard) (Bijleveld *et al.*, 2014; Bijleveld *et al.*, 2015). When prey quality decreases, fewer red knots with a small gizzard mass are observed in the Western Wadden Sea (van Gils *et al.*, 2006). van Gils *et al.* (2006) linked this to a decreased survival of individuals with a smaller gizzard size. However, it was shown later that survival was not affected by gizzard size (Bijleveld *et al.*, 2014; Oudman *et al.*, 2016). Bijleveld *et al.* (2014) showed that the explorative individuals are more likely to permanently leave the Wadden Sea for different tidal flats in Europe (e.g. Germany, England).

The amount of prey available to red knots changes with the preference for quality (Bijleveld *et al.*, 2014). The explorative red knots, who are picky eaters and prefer high quality prey, have a smaller range of prey to choose from. The giving-up density for the explorative individuals might be at a higher absolute prey density as the high-quality prey is depleted first (van Gils *et al.*, 2006). The searching cost of looking for high quality food might become higher during the year, as the prey is depleted and high-quality prey becomes even more scarce. In winter the exploration scores of red knots are lower than in summer (Haanen, unpublished data). This indicates that as the year progresses and the high-quality prey is depleted, there are less explorative birds. In years when the availability of sufficient high quality food is low, the explorative red knots might be the first to leave the Wadden Sea in search for food. One might imagine the different European areas of the East Atlantic Flyway to function in unity, where the availability of high quality food determines the local number of red knots, but the overall population is relatively stable.

CONCLUSIONS

While this research took two different prey species into account, no relations were found between *C. edule* and the red knot population in the Vlie tidal basin. The size of the red knot population in the Western Wadden Sea was directly related to the amount of edible *L. balthica* in the area. Therefore, any change in availability of *L. balthica* could influence the number of red knots in the Dutch Wadden Sea. The energy requirements of the red knot population roughly related to the amount of edible *L. balthica* biomass. This means that the availability of *L. balthica* could potentially be used as an indicator for the foraging conditions for red knots in the Wadden Sea. We showed that there is a positive correlation between the quality *L. balthica* and red knot numbers. Therefore, the quality of the prey is vital for maintaining the red knot population in the Vlie tidal basin. The amount of *L. balthica* eliminated in the Western Wadden Sea related to the number of red knots staging in the study area. This elimination was roughly in accordance with the amount of biomass required by all red knots each year and elimination in edible size classes was higher than overall elimination. This means that the prey elimination is likely to be caused by red knots, rather than other causes such as density dependent mortality. We therefore suggest that red knots could in fact play an important role in the Wadden Sea ecosystem. However, experimental studies would have to confirm the correlation we found to exclude a common driver. Prey depletion by red knot would decrease the amount of (high quality) prey available during the winter, which might force red knots to leave the Western Wadden Sea. Future research would have to confirm if explorative red knots are the first to escape to other areas in North-West Europe insufficient high-quality food is available.

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BIBLIOGRAPHY

- Ahmedou Salem, M. V., van der Geest, M., Piersma, T., Saoud, Y., & van Gils, J. A. (2014). Seasonal changes in mollusc abundance in a tropical intertidal ecosystem, Banc d'Arguin (Mauritania): Testing the “depletion by shorebirds” hypothesis. *Estuarine, Coastal and Shelf Science*. <https://doi.org/10.1016/j.ecss.2013.11.009>
- Andrewartha, H. G., & Birch, L. C. (1954). *The distribution and abundance of animals*. University of Chicago press.
- Bearhop, S., Ward, R. M., & Evans, P. R. (2003). Long-term survival rates in colour-ringed shorebirds – practical considerations in the application of mark–recapture models: Capsule serious violations of the model assumptions were seen. *Bird Study*, *50*(3), 271–279. <https://doi.org/10.1080/00063650309461319>
- Bell, M. C. (1995). UINDEX 4. A computer programme for estimating population index numbers by the Underhill-method. The Wildfowl & Wetlands Trust, Slimbridge.
- Beukema, J. J. (1974). Seasonal changes in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, *8*(1), 94–107. [https://doi.org/10.1016/0077-7579\(74\)90028-3](https://doi.org/10.1016/0077-7579(74)90028-3)
- Bijleveld, A. I., MacCurdy, R. B., Chan, Y.-C., Penning, E., Gabrielson, R. M., Cluderay, J., ... Piersma, T. (2016). Understanding spatial distributions: negative density-dependence in prey causes predators to trade-off prey quantity with quality. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1828), 20151557. <https://doi.org/10.1098/rspb.2015.1557>
- Bijleveld, A. I., Massourakis, G., van der Marel, A., Dekinga, A., Spaans, B., van Gils, J. A., & Piersma, T. (2014). Personality drives physiological adjustments and is not related to survival. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1783), 20133135–20133135. <https://doi.org/10.1098/rspb.2013.3135>
- Bijleveld, A. I., Twietmeyer, S., Piechocki, J., van Gils, J. A., & Piersma, T. (2015). *Natural selection by pulsed predation: survival of the thickest*. *Ecology* (Vol. 96).
- Bivand, R., Keitt, T., & Rowlingson, B. (2018). rgdal: Bindings for the “Geospatial” Data Abstraction Library. R package version 1.3-6. Retrieved from <https://cran.r-project.org/package=rgdal>
- Boyd, H., & Piersma, T. (2001). Changing balance between survival and recruitment explains population trends in Red Knots *Calidris canutus islandica* wintering in Britain, 1969-1995. *Ardea*, *89*(2), 301–317.
- Brochard, C., Spaans, B., Prop, J., & Piersma, T. (2002). Use of individual colour-ringing to estimate annual survival in male and female red knot *Calidris canutus islandica*: a progress report for 1998–2001. *Wader Study Group Bull.*, *99*, 54–56.
- Dekinga, A., & Piersma, T. (1993). Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *calidris canutus*. *Bird Study*, *40*(2), 144–156. <https://doi.org/10.1080/00063659309477140>
- Dhondt, A. A. (1988). Carrying capacity: A confusing concept. *Acta Oecologica*, *9*(4), 337–346. <https://doi.org/10.1108/17506200710779521>
- Engelmoer, M., Boere, G. C., & Nieboer, E. (2006). Thirty years of Arctic wader monitoring in the Dutch part of the Wadden Sea. In *Waterbirds around the world* (pp. 140–146).
- Folmer, E. O., Olff, H., & Piersma, T. (2012). The spatial distribution of flocking foragers: Disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modeling. *Oikos*, *121*(4), 551–561. <https://doi.org/10.1111/j.1600-0706.2011.19739.x>
- Folmer, E. O., & Piersma, T. (2012). The contributions of resource availability and social forces to foraging distributions: A spatial lag modelling approach. *Animal Behaviour*, *84*(6), 1371–1380. <https://doi.org/10.1016/j.anbehav.2012.08.031>
- Goss-Custard, J. D., & West, A. D. (1997). *The concept of carrying capacity and shorebirds*. Retrieved from <http://nora.nerc.ac.uk/policies.html#access>
- Kraan, C., van Gils, J. A., Spaans, B., Dekinga, A., Bijleveld, A. I., van Roomen, M., ... Piersma, T. (2009). Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *Journal of Animal Ecology*, *78*(6), 1259–1268. <https://doi.org/10.1111/j.1365-2656.2009.01564.x>
- Leopold, A. (1993). The conservation ethic. *Journal of Forestry*, *31*(6), 634–643.
- Lotka, A. J. (1925). *Elements of Physical Biology*. Baltimore: Williams.
- Malthus, T. (1798). An essay on the principle of population. *Printed for J. Johnson. St. Paul's Church-Yard, London*, 1–126.
- McNamara, J. M., & Houston, A. I. (1987). Starvation and Predation as Factors Limiting Population Size. *Ecology*, *68*(5), 1515–1519.
- Nolet, B. A., Gyimesi, A., & Klaassen, R. H. G. (2006). Prediction of bird-day carrying capacity on a staging site : A test of Depletion Models. *Journal of Animal Ecology*, *75*(6), 1285–1292. <https://doi.org/10.1111/j.1365-2656.2006.01150.x>
- O'Connor, R. J., & Brown, R. A. (1977). Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. *Oecologia*, *27*(1), 75–92. <https://doi.org/10.1007/BF00345686>
- Oudman, T., Bijleveld, A. I., Kavelaars, M. M., Dekinga, A., Cluderay, J., Piersma, T., & van Gils, J. A. (2016). Diet preferences as the cause of individual differences rather than the consequence. *The Journal of Animal Ecology*, *85*(5), 1378–1388. <https://doi.org/10.1111/1365-2656.12549>
- Oudman, T., Piersma, T., Ahmedou Salem, M. V., Feis, M. E., Dekinga, A., Holthuijsen, S., ... Bijleveld, A. I. (2018). Resource landscapes explain contrasting patterns of aggregation and site fidelity by red knots at two wintering sites. *Movement Ecology*, *6*(1). <https://doi.org/10.1186/s40462-018-0142-4>
- Parada, J. M., & Molares, J. (2008). Natural mortality of the cockle *Cerastoderma edule* (L.) from the Ria of Arousa (NW Spain) intertidal zone. *Revista de Biología Marina y Oceanografía*, *43*(3), 501–511. <https://doi.org/10.4067/s0718-19572008000300009>
- Philippart, C. J. M., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadée, G. C., Dekker, R., ... Cadée, G. C. (2003). of the bivalve *Macoma balthica* in recruitment changes. *Limnology and Oceanography*, *48*(6), 2171–2185.
- Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. In *Journal of Ornithology* (Vol. 148). <https://doi.org/10.1007/s10336-007-0240-3>
- Piersma, T. (2012). What is habitat quality? Dissecting a research portfolio on shorebirds. *Birds and Habitat*, (2004), 383–407. <https://doi.org/10.1017/cbo9781139021654.019>

- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P., & Wiersma, P. (1993). Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the Western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research*, *31*(4), 331–357. [https://doi.org/10.1016/0077-7579\(93\)90052-t](https://doi.org/10.1016/0077-7579(93)90052-t)
- Piersma, T., van Gils, J., de Goeij, P., & van der Meer, J. (1995). Holling's Functional Response Model as a Tool to Link the Food-Finding Mechanism of a Probing Shorebird with its Spatial Distribution. *The Journal of Animal Ecology*, *64*(4), 493–504. <https://doi.org/10.2307/5652>
- Raffaelli, D., & Moller, H. (1999). Manipulative field experiments in animal ecology: do they promise more than they can deliver? In *Advances in Ecological Research Vol.30* (pp. 299–338). Academic Press.
- Rakhimberdiev, E., van den Hout, P. J., Brugge, M., Spaans, B., & Piersma, T. (2015). Seasonal mortality and sequential density dependence in a migratory bird. *Journal of Avian Biology*, *46*(4), 332–341. <https://doi.org/10.1111/jav.00701>
- Sandercock, B. K. (2003). Estimation of survival rates for wader populations: a review of mark-recapture methods. *Wader Study Group Bulletin*, *100*(April), 163–174. Retrieved from <http://k-state.co/bsanderc/2003wsqb.pdf>
- Schneider, C., & Harrington, B. A. (1981). TIMING OF SHOREBIRD TO PREY MIGRATION DEPLETION IN MANY arctic migrants leave their breeding grounds well before the collapse of local food supplies (Thomson 1926 : 260 ; Pitelka 1959). Migratory departure before this collapse of local food supplies wou. *The Auk*, *98*(October), 801–811.
- Sinclair, A. R. E., & Krebs, C. J. (2002). Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1425), 1221–1231. <https://doi.org/10.1098/rstb.2002.1123>
- Soldaat, L., van Winden, E., van Tournhout, C., Berrevoets, C., van Roomen, M., & van Strien, A. (2004). *De berekening van indexen en trends bij het watervogelmeetnet*.
- Soldaat, L., Visser, H., van Roomen, M., & Strien, A. (2007). Smoothing and trend detection in waterbird monitoring data using structural time-series analysis and the Kalman filter. *Journal of Ornithology*, *148*(SUPPL. 2), 351–357. <https://doi.org/10.1007/s10336-007-0176-7>
- SOVON. (2015). *watervogels uitgebreide werkwijze*.
- Team, R. C. (2017). R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Thrush, S. F. (2009). Complex role of predators in structuring soft-sediment macrobenthic communities: *Austral Ecology*, (February 1998), 344–354. Retrieved from <http://www3.interscience.wiley.com/journal/122544933/abstract>
- Underhill, L. G., & Prys-Jones, R. P. (1994). Index Numbers for Waterbird Populations. I. Review and Methodology. *Journal of Applied Ecology*, *31*(3), 463–480.
- van der Meer, J., Piersma, T., & Beukema, J. J. (2001). Population dynamics of benthic species on tidal flats: the possible roles of shorebird predation.
- van Gils, J. A., de Rooi, S. R., Dekinga, A., Piersma, T., Drent, R., van der Meer, J., & van Belle, J. (2005). Digestive bottleneck affects foraging decisions in red knots *Calidris canutus* . I. Prey choice. *Journal of Animal Ecology*, *74*(1), 105–119. <https://doi.org/10.1111/j.1365-2656.2004.00903.x>
- van Gils, J. A., Dekinga, A., Spaans, B., Vahl, W. K., & Piersma, T. (2005). Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. II. Patch choice and length of working day. *Journal of Animal Ecology*, *74*(1), 120–130. <https://doi.org/10.1111/j.1365-2656.2004.00904.x>
- van Gils, J. A., Edelaar, P., Escudero, G., & Piersma, T. (2004). Carrying capacity models should not use fixed prey density thresholds : a plea for using more tools of behavioural ecology. *Oikos*, *104*(1), 197–204.
- van Gils, J. A., Piersma, T., Dekinga, A., Spaans, B., & Kraan, C. (2006). Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biology*, *4*(12), 2399–2404. <https://doi.org/10.1371/journal.pbio.0040376>
- van Gils, J. A., Schenk, I. W., Bos, O., & Piersma, T. (2003). Incompletely Informed Shorebirds That Face a Digestive Constraint Maximize Net Energy Gain When Exploiting Patches. *The American Naturalist*, *161*(5), 777–793. <https://doi.org/10.1086/374205>
- van Gils, J. A., Spaans, B., Dekinga, A., & Piersma, T. (2006). Foraging in a tidally structured environment by red knots (*Calidris canutus*): Ideal, but not free. *Ecology*, *87*(5), 1189–1202. [https://doi.org/10.1890/0012-9658\(2006\)87\[1189:FIATSE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1189:FIATSE]2.0.CO;2)
- van Roomen, M., Koffijberg, K., Noordhuis, R., & Soldaat, L. (2006). Long-term waterbird monitoring in The Netherlands: a tool for policy and management. In *Waterbirds around the world* (pp. 463–470).
- van Roomen, M., Nagy, S., Citegetse, G., & Schekkerman, H. (2018). East Atlantic Flyway assessment 2017 The status of coastal waterbird populations and their sites.
- van Roomen, M., van Tournhout, C., Nienhuis, J., Willems, F., & van Winden, E. (2002). *Monitoring van watervogels als niet-broedvogel in de Nederlandse Waddenzee: evaluatie huidige opzet en voorstellen voor de toekomst*. Beek-Ubbergen.
- Verhulst, P. . (1847). Deuxième mémoire sur la loi d'accroissement de la population. *Mem. Acad. R. Bruxelles*, *20*, 3–22.
- Verhulst, P. F. (1838). Notice sur la loi que la population suit dans son accroissement. *Correspondance Mathématique et Physique*, *10*, 113–125.
- Verhulst, P. F. (1844). Recherches mathématiques sur la loi d'accroissement de la population. *Mem. Acad. R. Bruxelles*, *18*, 3–39.
- Volterra, V. (1926). Variazioni e uttuazioni del numero d'individui in specie animali conviventi. *Memorie R. Accad. Lincei*, *6*(2), 31–113.
- von Bertalanffy, L. (1938). A Quantitative Theory of Organic Growth (Inquiries on Growth Laws. II). *Human Biology*, *10*(2), 181–213.
- Wickham, H. (2009). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
- Wickham, H. (2011). The Split-Apply-Combine Strategy for Data Analysis. 1-29. *Journal of Statistical Software*, *40*(4), 1–29.
- Wickham, H., & Henry, L. (2019). tidy: Easily Tidy Data with “spread()” and “gather()” Functions. R package version 0.8.3. Retrieved from <https://cran.r-project.org/package=tidy>

- Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R (wvd edition)*. (C. and Hall/CRC, Ed.).
- Zharikov, Y., & Skiller, G. S. (2003). Depletion of benthic invertebrates by bar-tailed godwits *Limosa lapponica* in a subtropical estuary. *Marine Ecology Progress Series*, 254, 151–162.
- Zwarts, L., & Wanink, J. . (1993). How the food supply harvestable by waders in the wadden sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research*, 31(4), 441–476.
- Zwarts, Leo. (1991). Seasonal variation in body weight of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden sea. *Netherlands Journal of Sea Research*, 28(3), 231–245. [https://doi.org/10.1016/0077-7579\(91\)90021-R](https://doi.org/10.1016/0077-7579(91)90021-R)
- Zwarts, Leo, & Blomert, A. M. (1992). Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Marine Ecology Progress Series*, 83(2–3), 113–128. <https://doi.org/10.3354/meps083113>
- Zwarts, Leo, Blomert, A. M., & Wanink, J. H. (1992). Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. *Marine Ecology Progress Series*, 83(2–3), 129–139. <https://doi.org/10.3354/meps083129>
- Zwarts, Leo, & Wanink, J. . (1989). Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. *Marine Biology*, 100, 227–240.

APPENDICES

APPENDIX I – Red knot counts in all areas and months

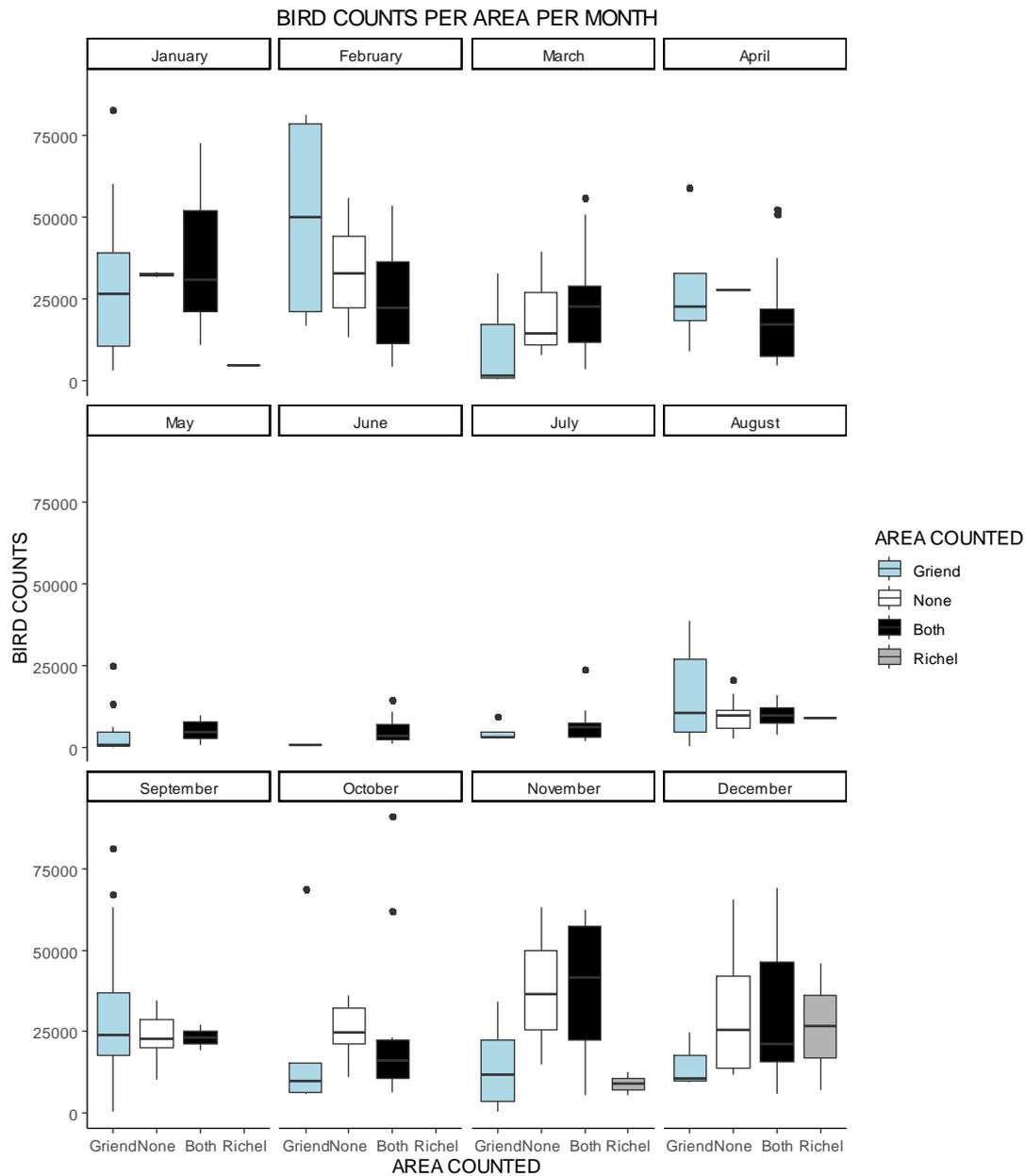


Figure I-1: Overview of the number of red knots numbers on the roosts each month of the year. The boxes represent the spread of the combined counted data and imputed data. Blue and grey boxes are the red knot numbers when either Griend or Richel were counted respectively. White boxes indicate months when neither of the roosts was counted and the black boxes represent months when both Griend and Richel were counted.

Figure I-1 shows the spread of the red knot counts each month split by area that was counted. The difference between the boxes for each area indicate that not one roost could be used to substitute for the counts on both roosts. The spread of the bird counts was lowest in the months September until November, and large in all other months.

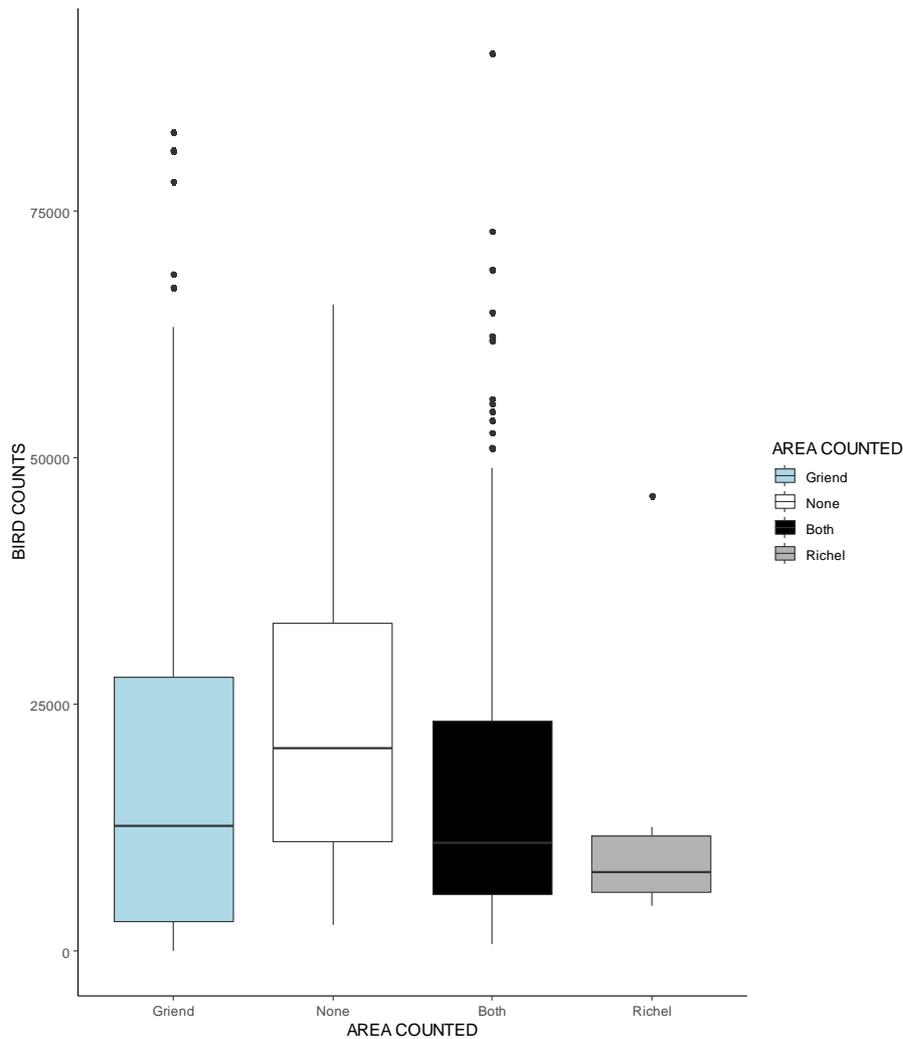


Figure I-2: Overview of the number of red knots counted in the different areas. The boxes represent the spread of the combined counted data and imputed data. Blue and grey boxes are the red knot numbers when either Griend or Richel are counted respectively and the counts for the other roost is imputed using U-index. Black boxes indicate both roosts are counted. The white boxplots contain only values imputed by U-index.

Figure I-2 shows the spread of the red knot counts in the different areas. The other areas were imputed by the program U-index. When counts for both roosts were imputed by U-index, there seems to be an overestimation of the number of red knots. The red knot numbers on Richel show a much smaller spread than in the other areas, however Richel was counted less frequently (main text figure 2) which could also cause this result. The red knot numbers when only Griend was counted seem to be relatively similar to the red knot numbers when both areas were counted. However, Griend was also not always counted and could therefore not be used as substitute for the counts on both roosts.

Figure I-3 shows the correlation between the red knots counted each month. These correlations vary, and there is not a similar trend for all months. Therefore, not one single month could be used to represent all red knots counted within a year.

CORRELATIONS BETWEEN MONTHS COUNTED

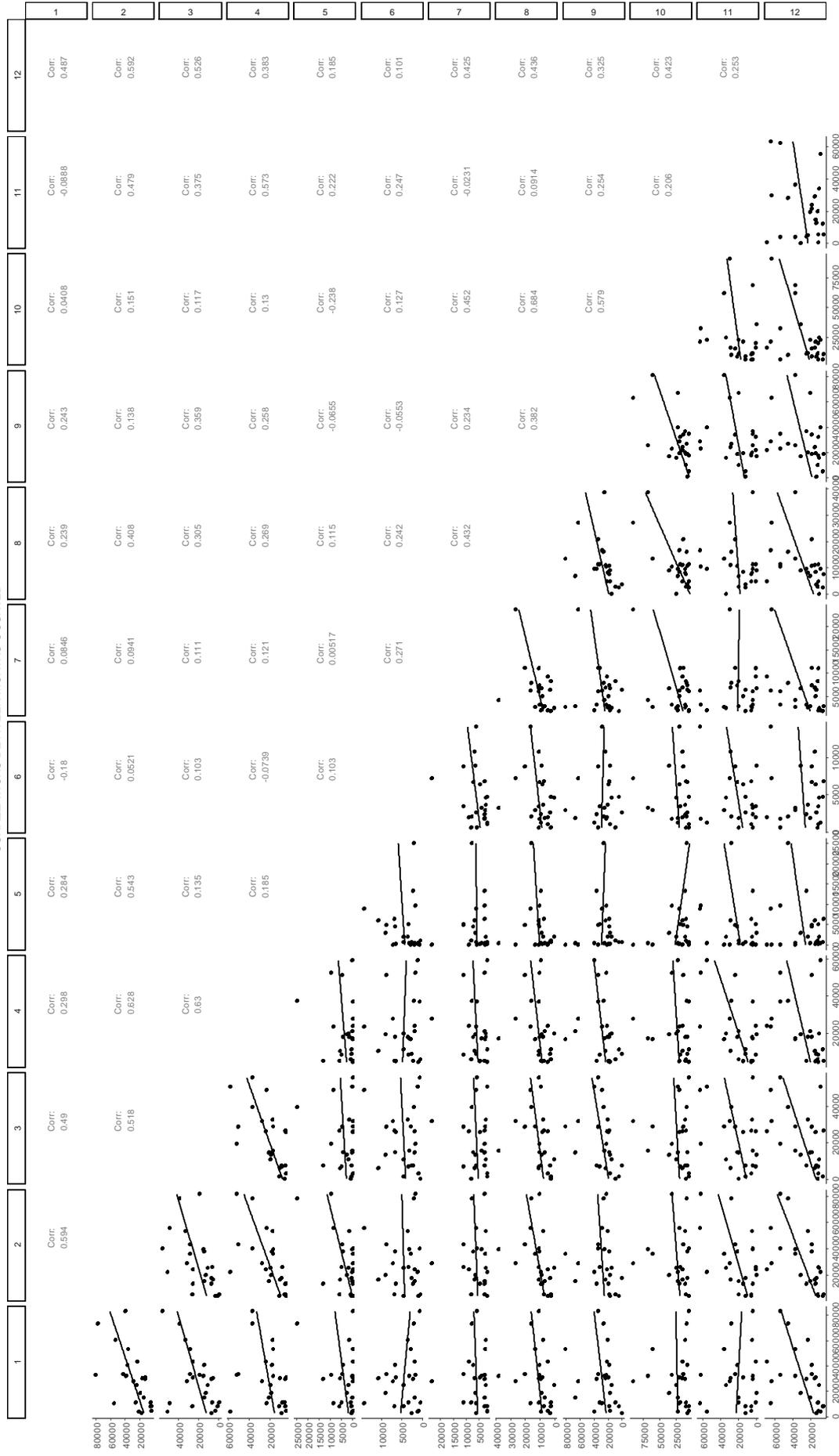


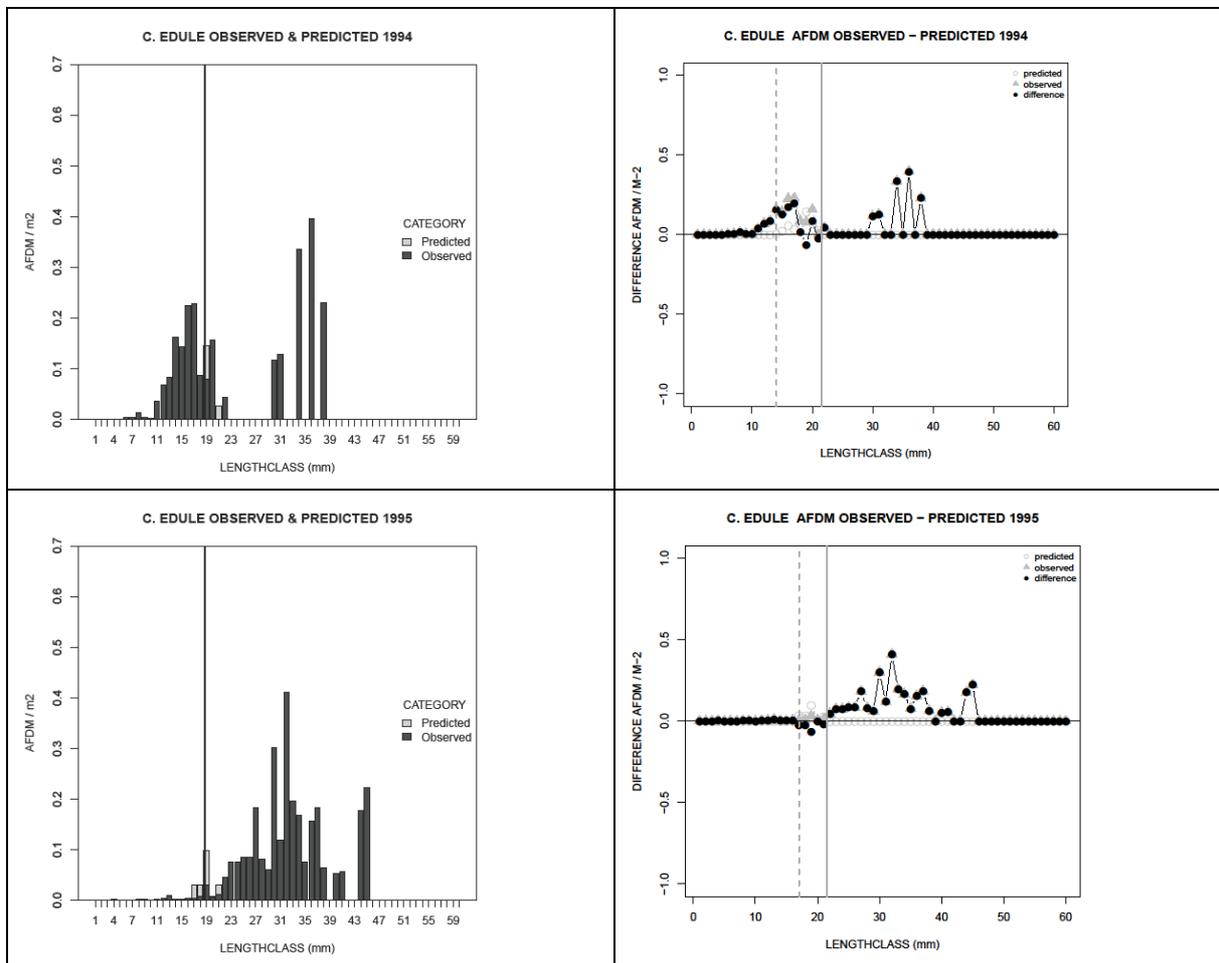
Figure 1-3: Correlations between the red knot counts each month (from left to right and top to bottom January until December). The lines indicate the correlation and the data points are the number of red knots counted each year.

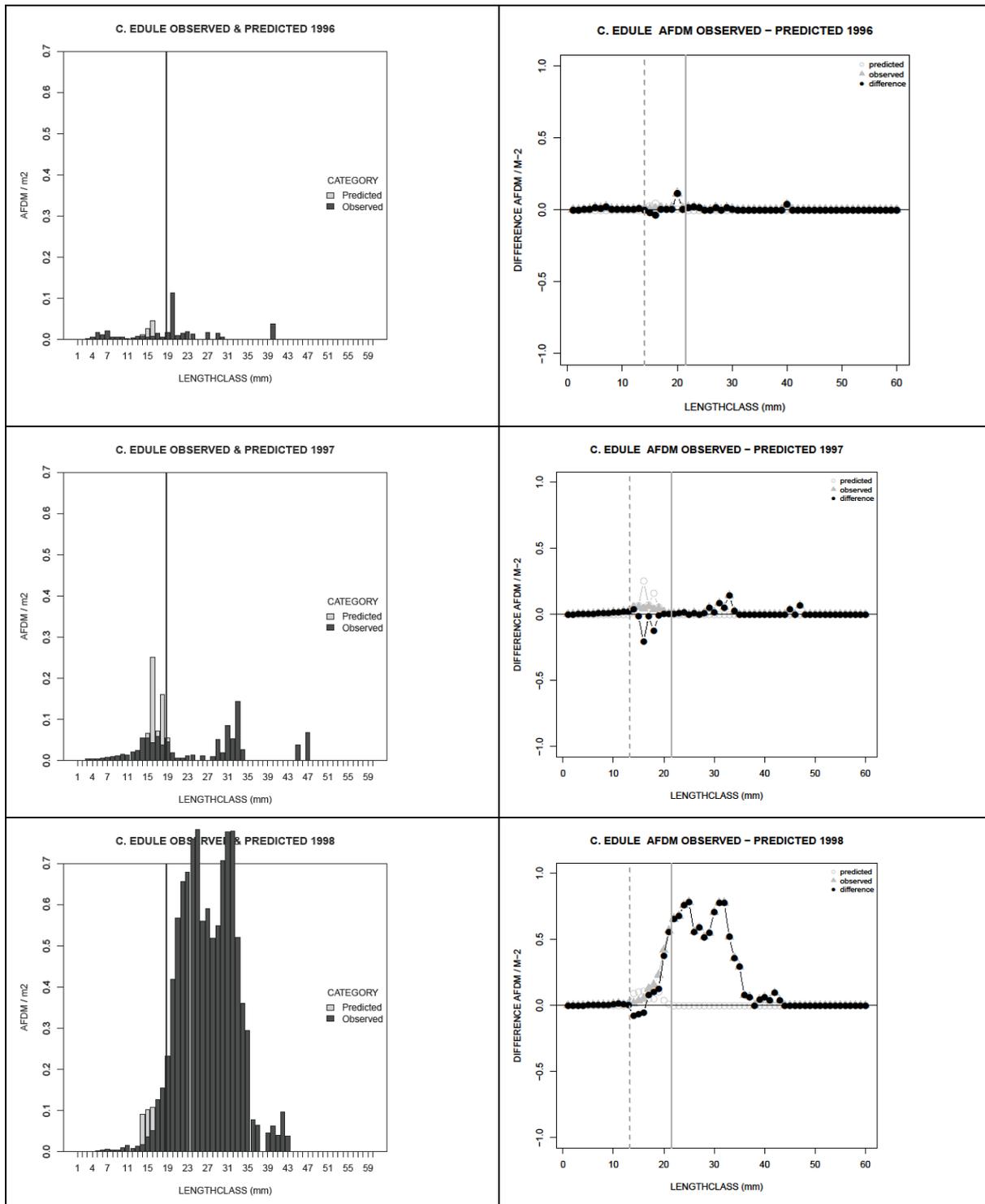
APPENDIX II – Prey elimination all sample years

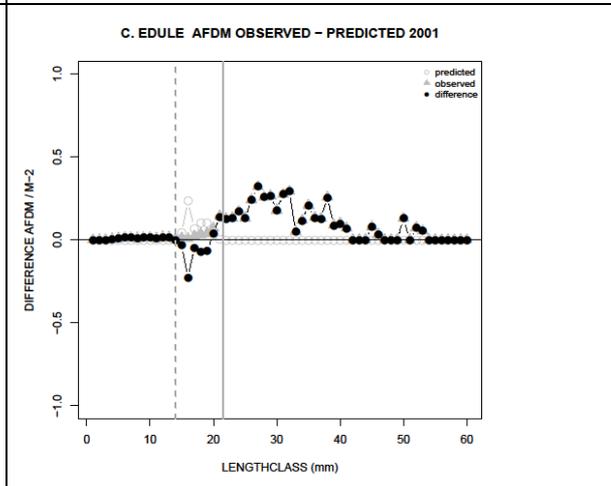
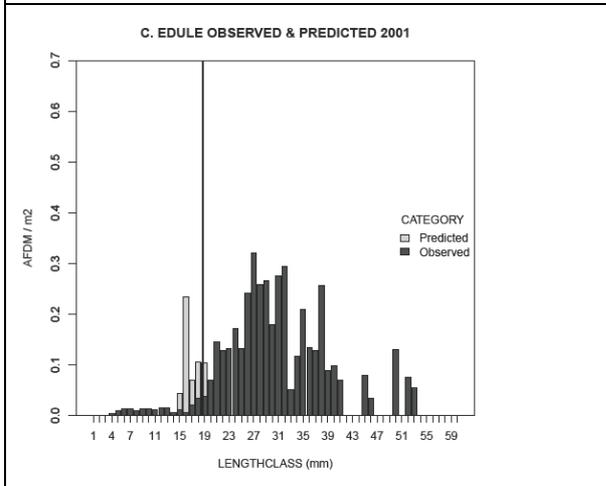
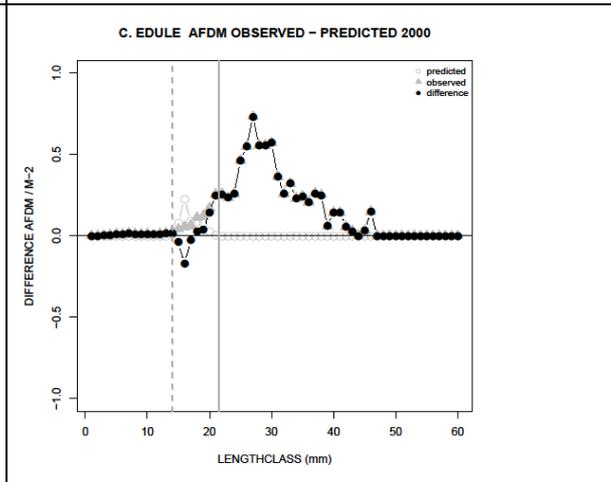
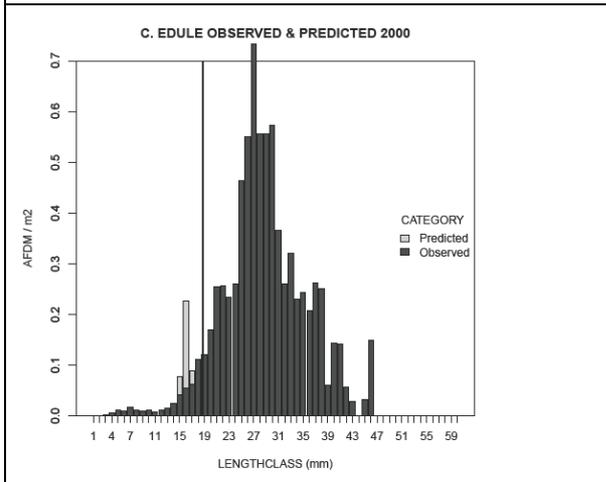
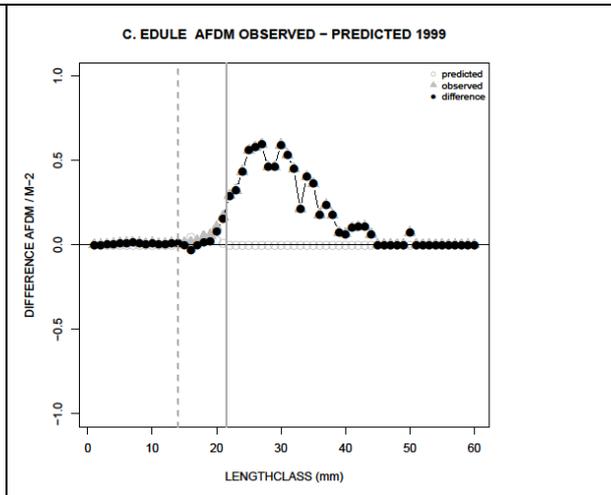
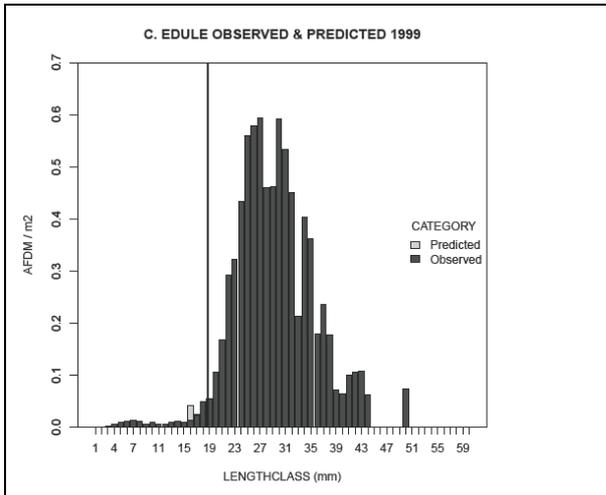
This appendix gives an overview of the different length-frequency distributions used to calculate the prey elimination per year. On the left side the observed and predicted length-frequency distributions are displayed for each year for both biomass per square meter and prey individuals per square meter. Dark grey indicates the observed values, light grey represents the predicted values. The vertical line indicates the upper limit for calculating the eliminated prey. On the right side, the difference between the predicted and observed biomass and individuals per square meter in all length classes for both prey species is displayed for each year. Open circles indicate the predicted values, triangles indicate the observed values and the black dots indicate the difference between the two. The solid vertical line indicates the maximum ingestible shell length plus growth during year (upper-limit), the dashed vertical line indicates the size of the smallest observed individual observed in 2012 plus growth (lower-limit). When calculating the total prey elimination these limits are taken as minimum and maximum boundary.

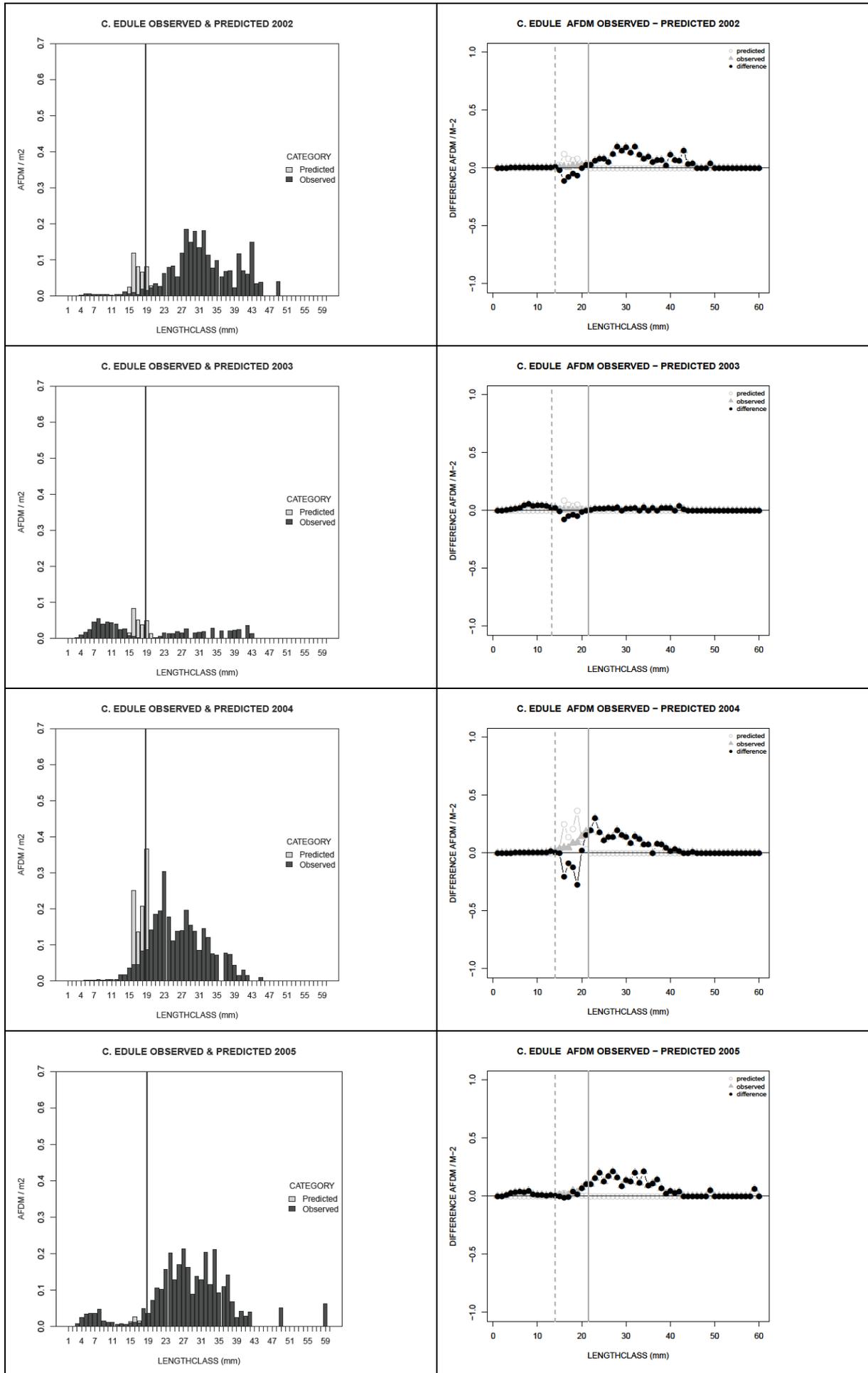
Prey biomass per square meter

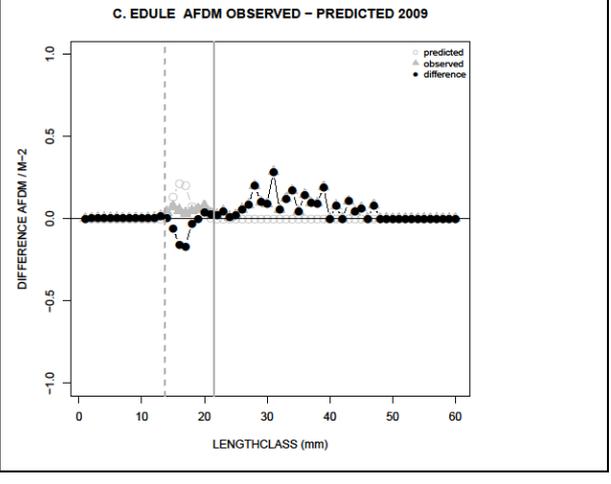
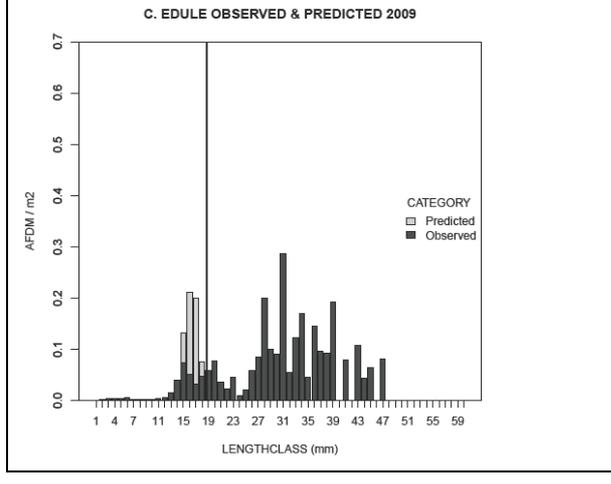
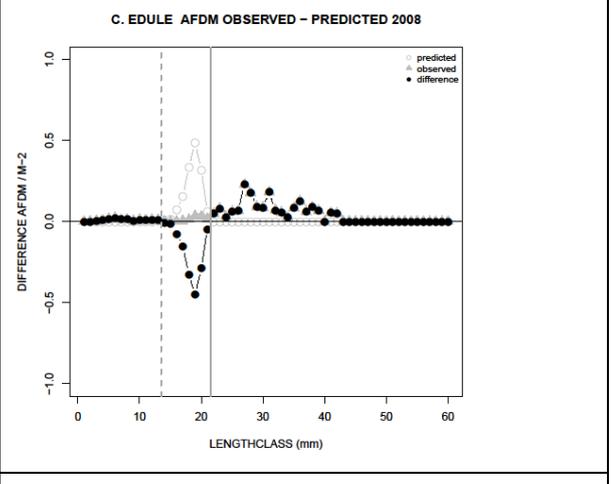
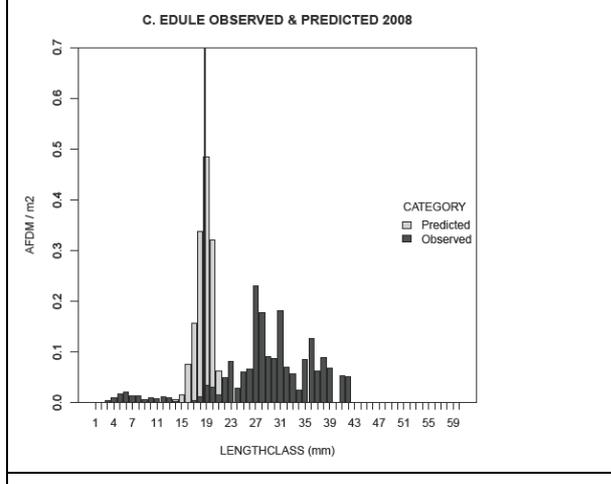
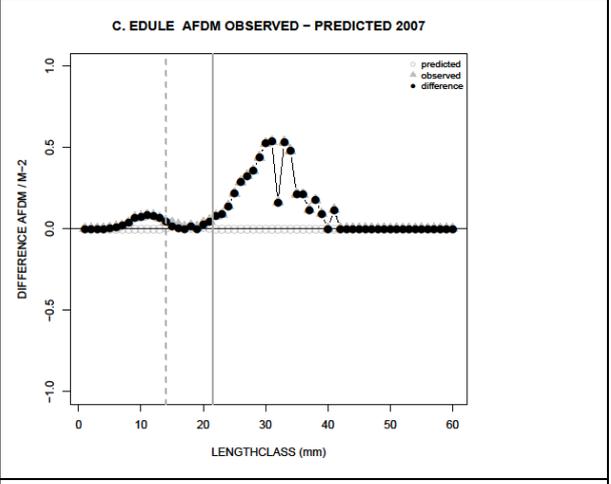
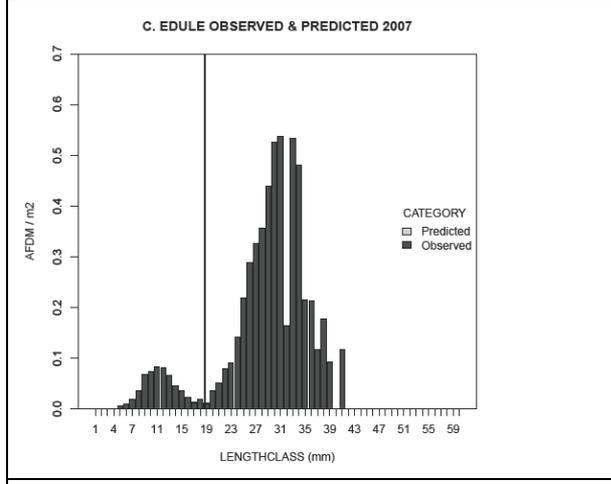
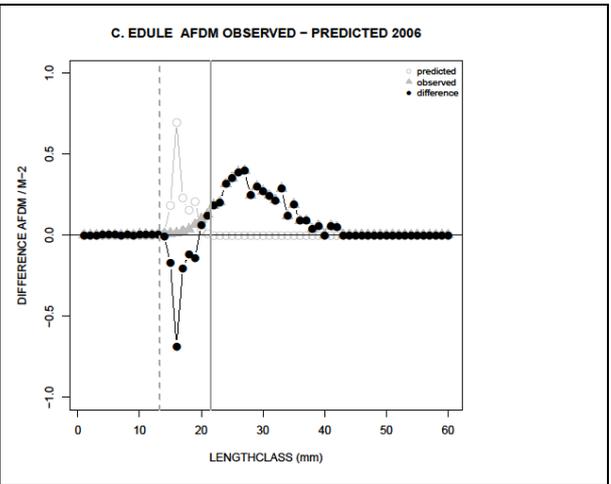
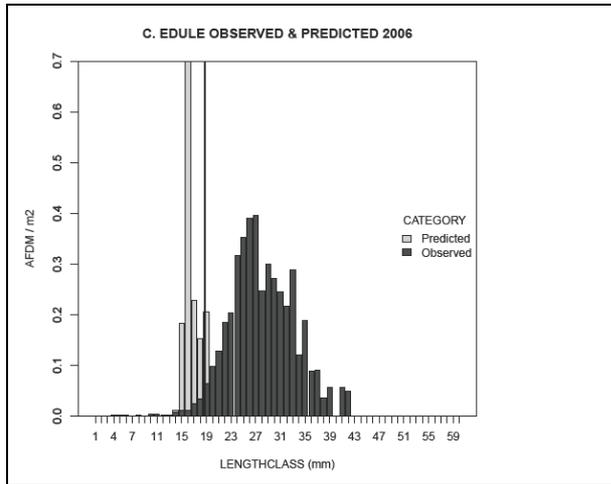
C. edule

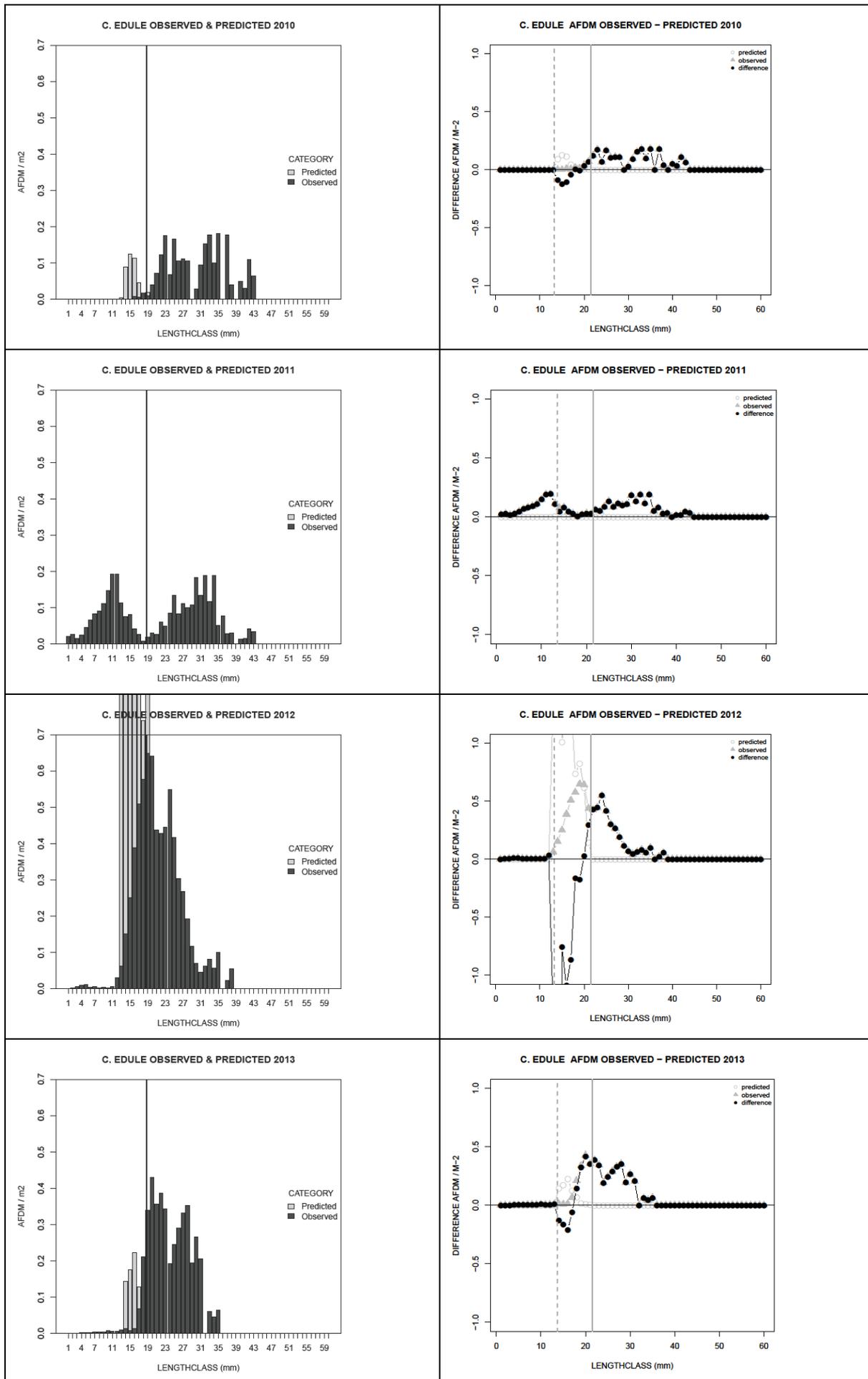


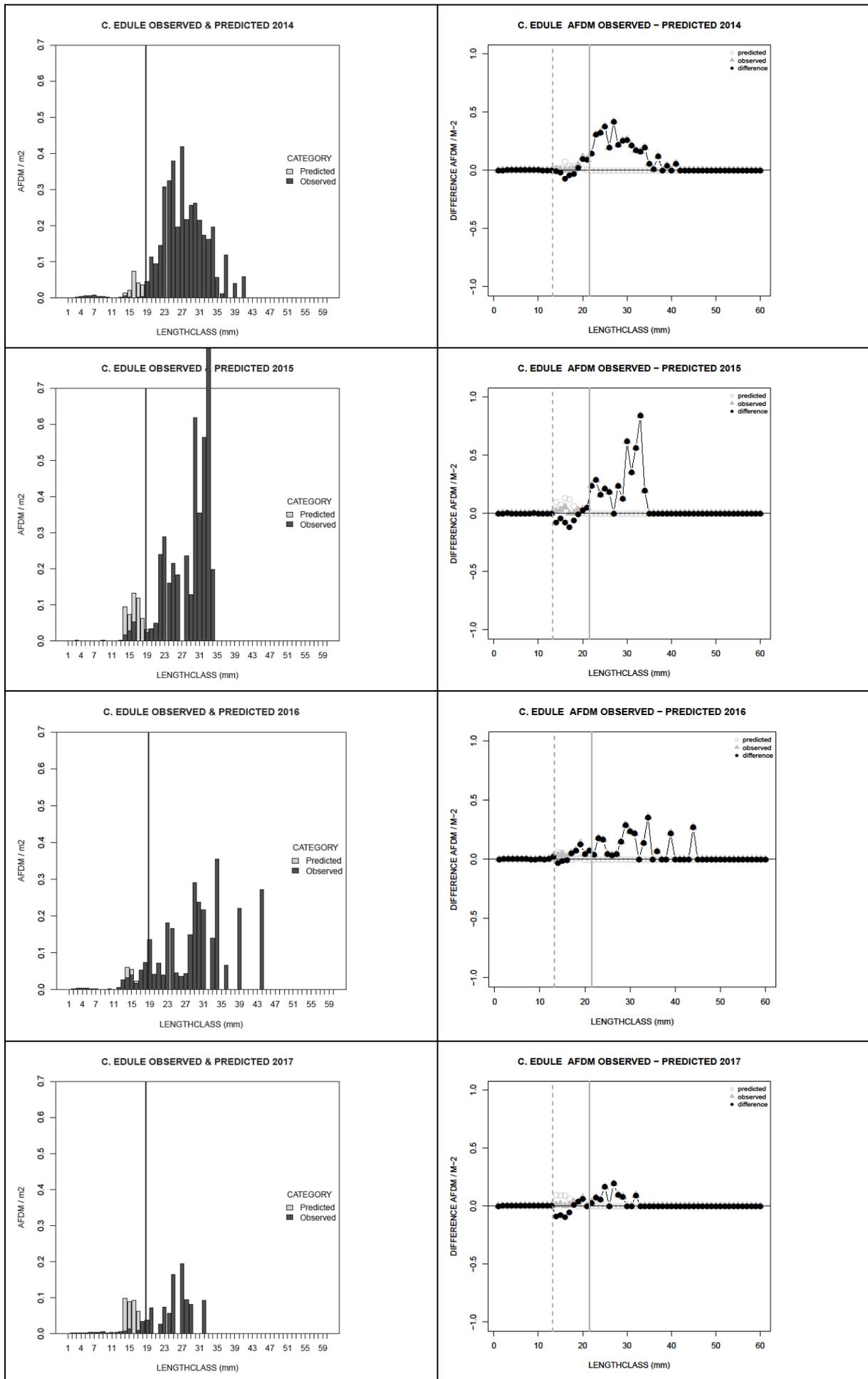


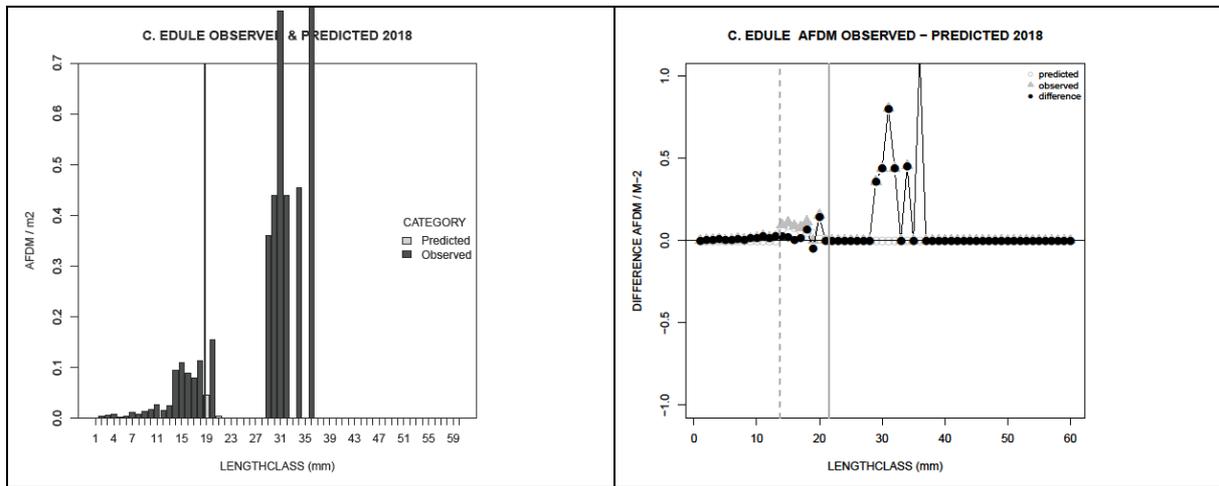




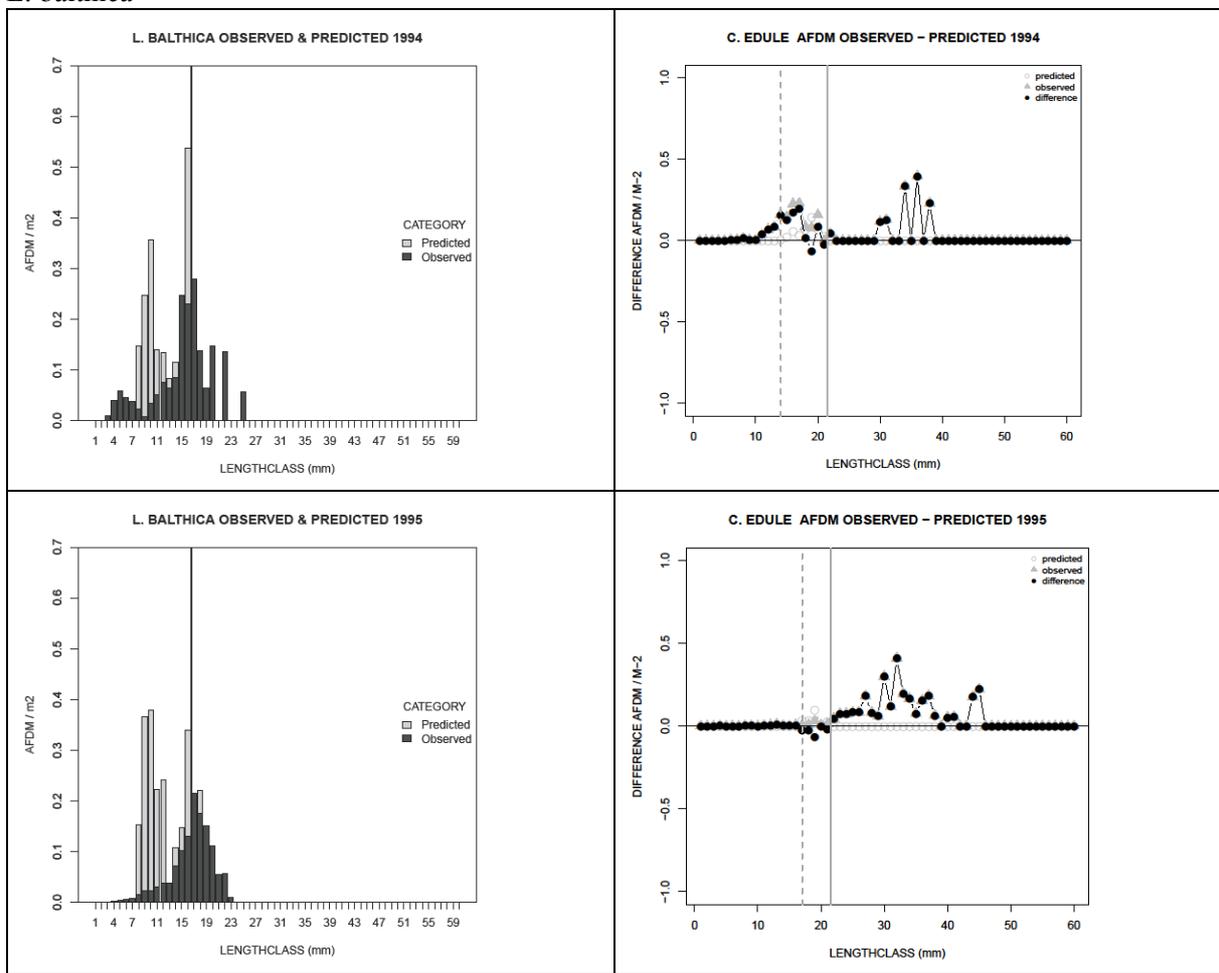


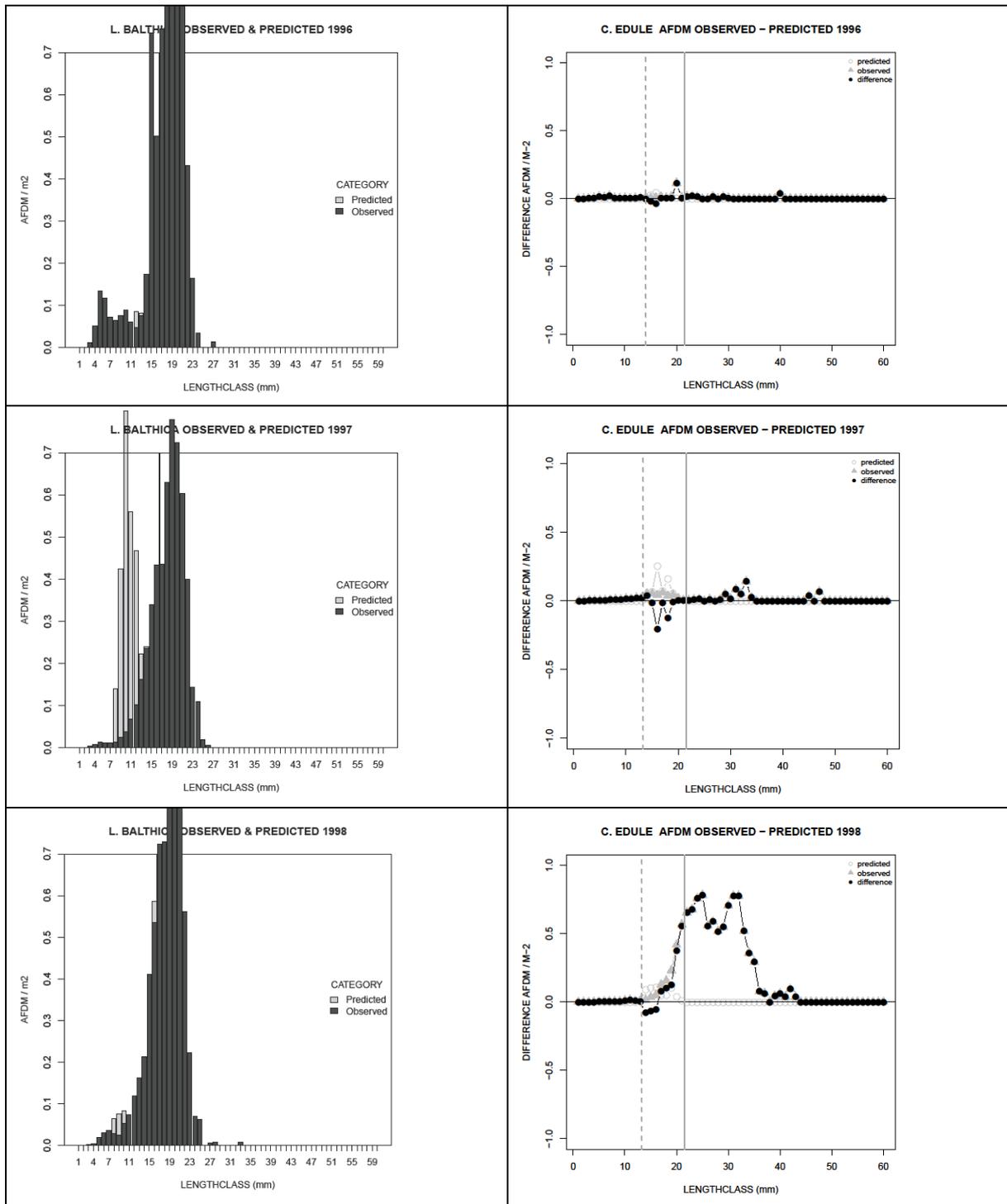


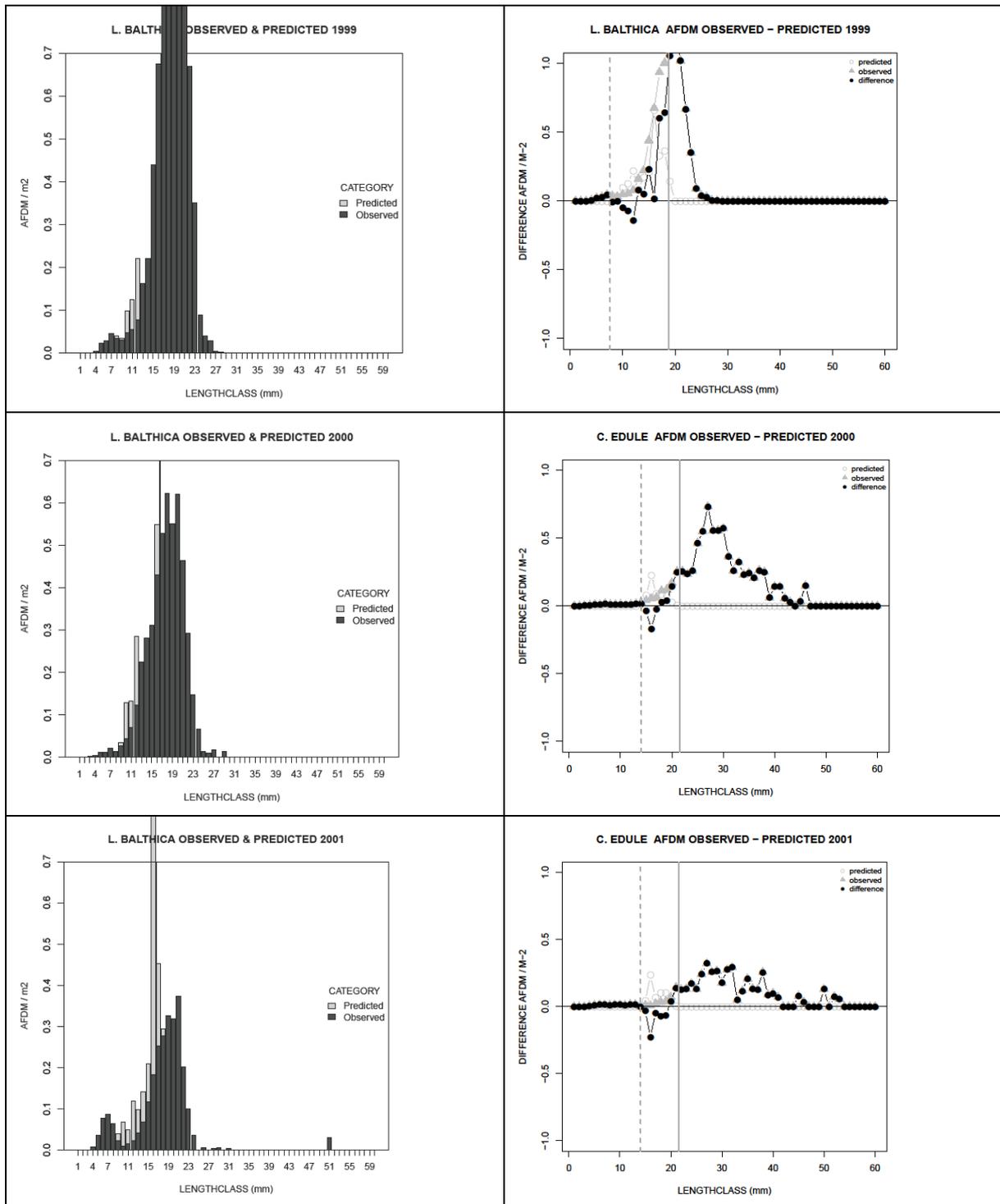


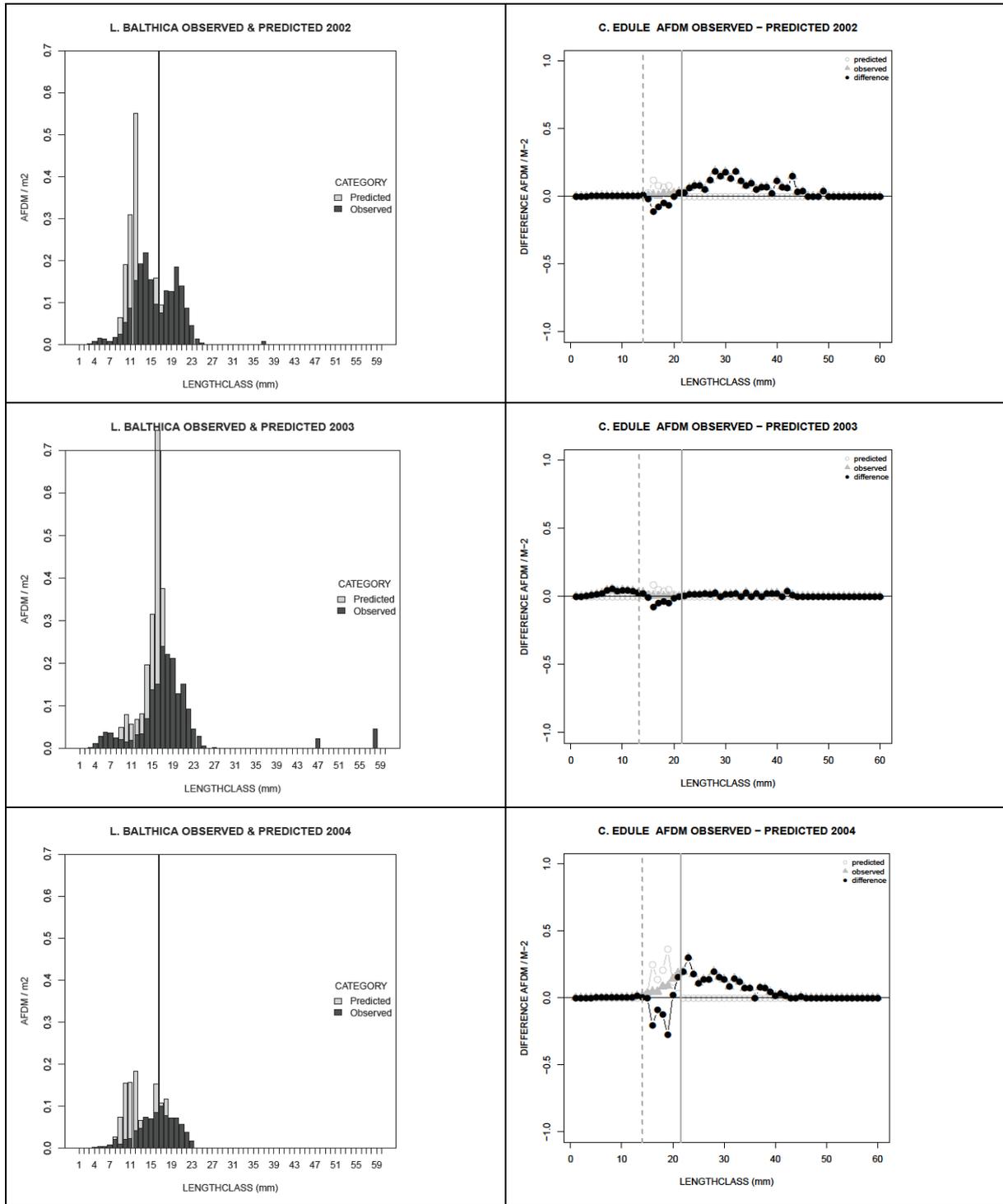


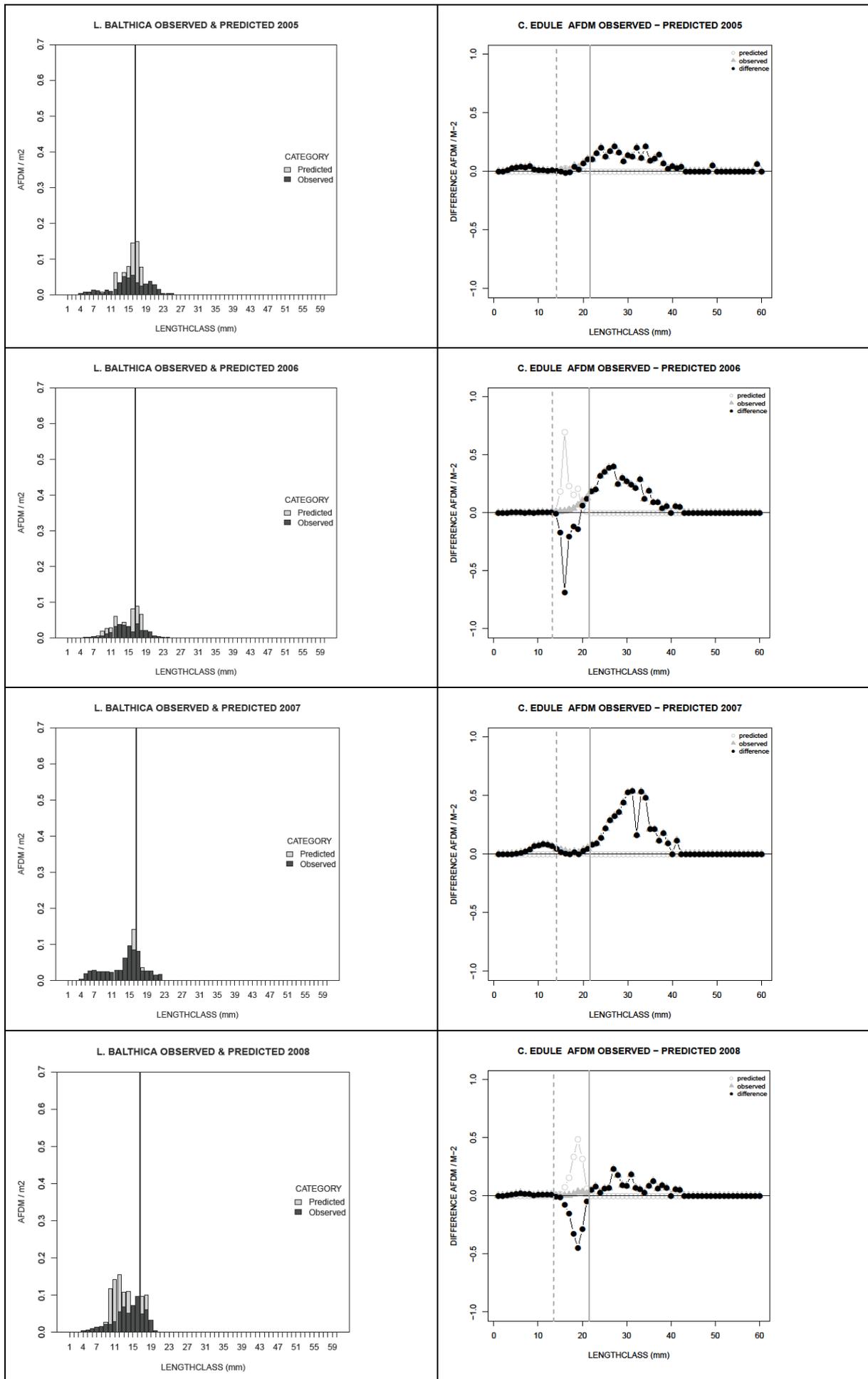
L. balthica

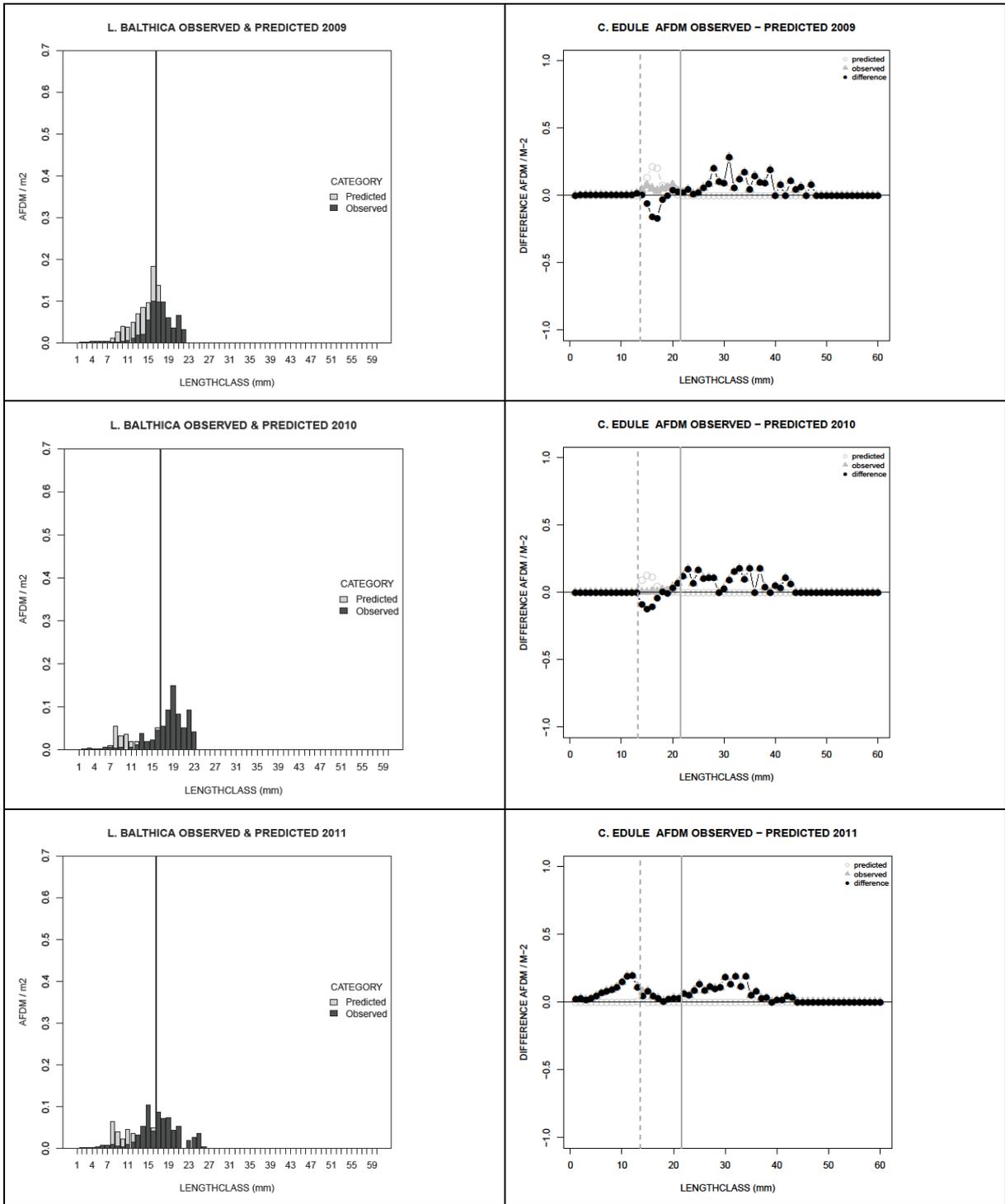


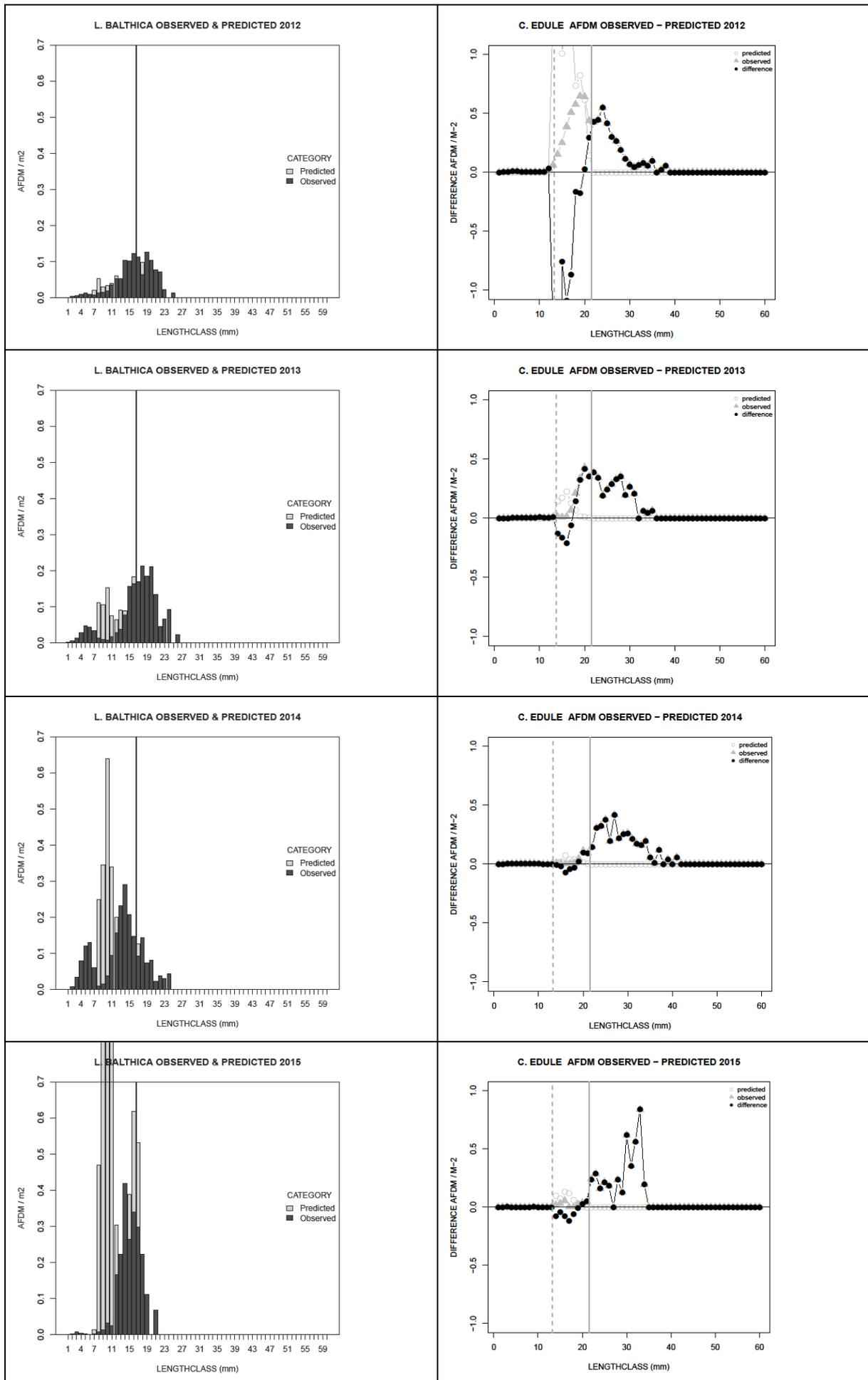


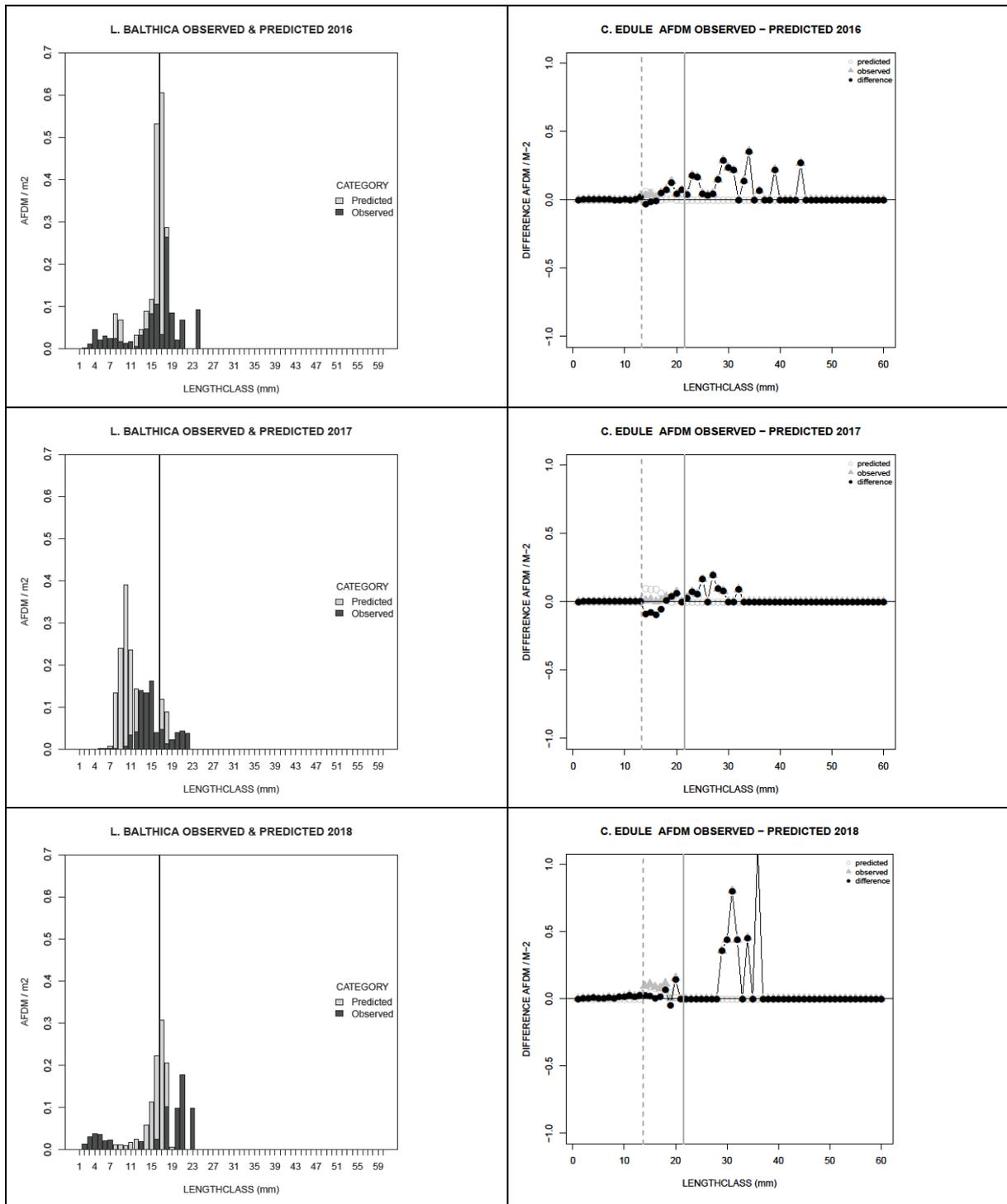






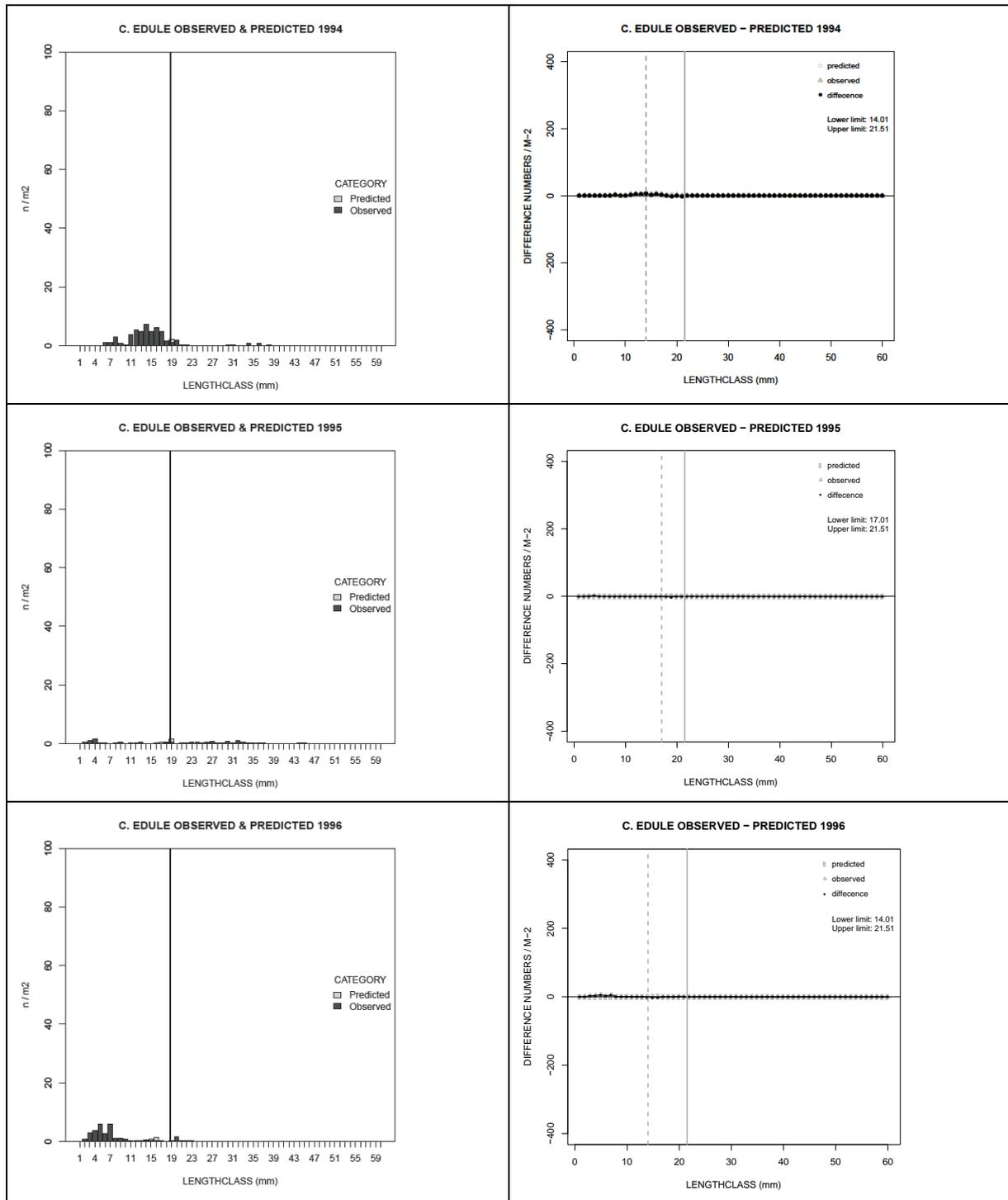


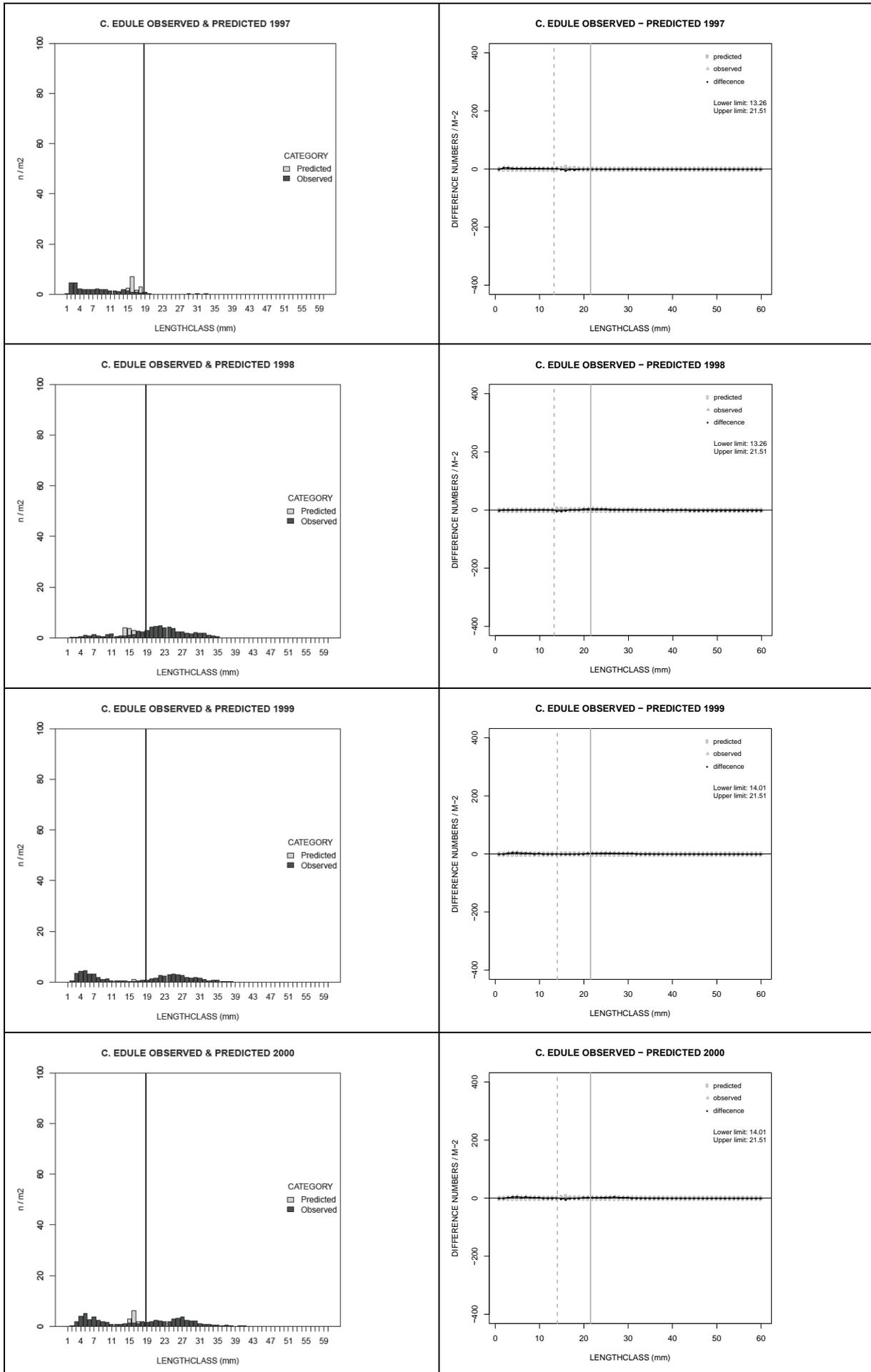


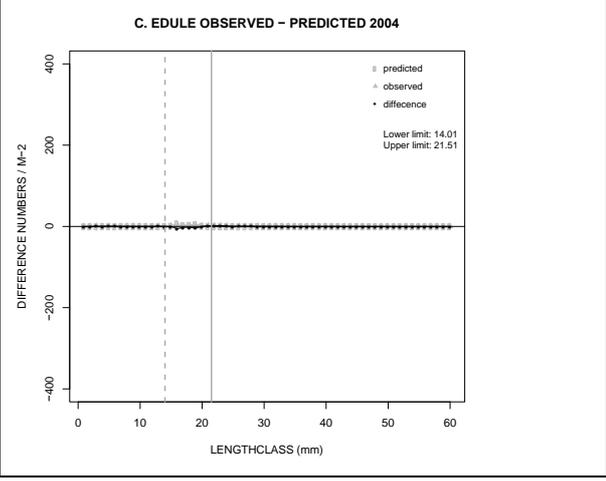
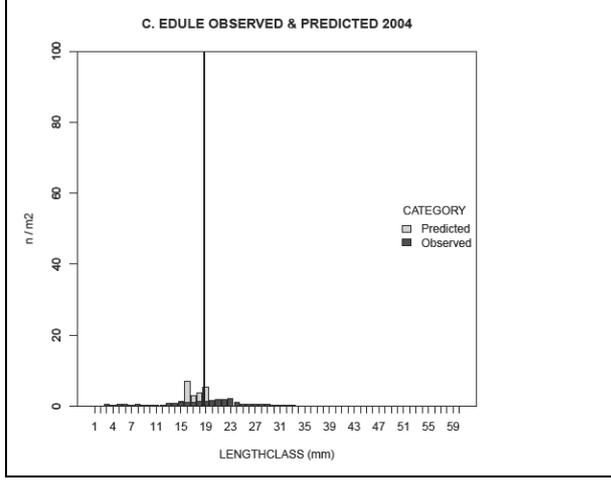
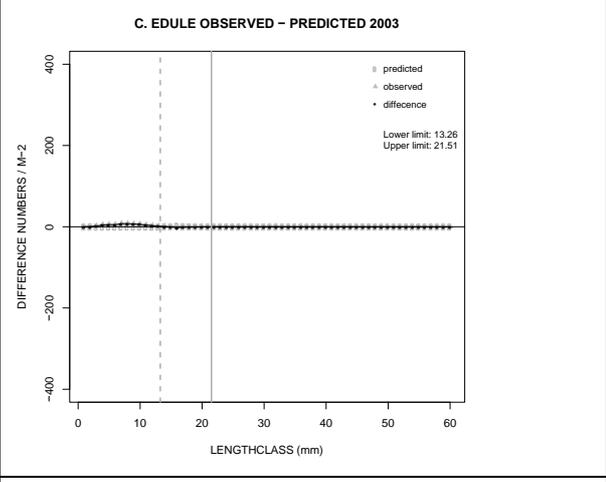
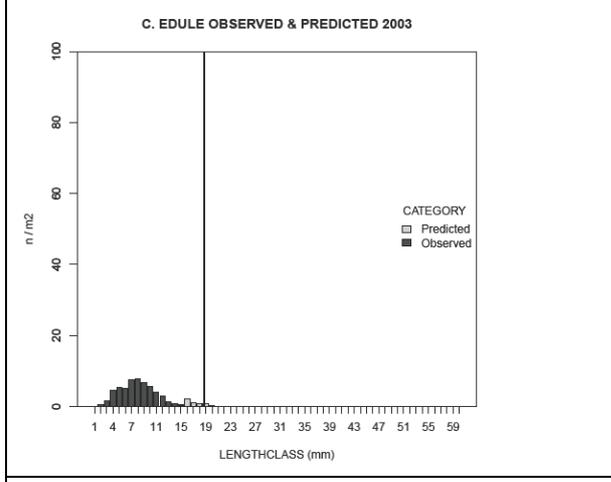
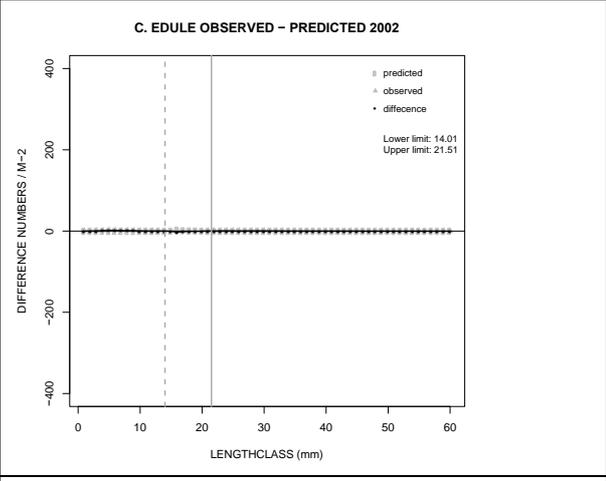
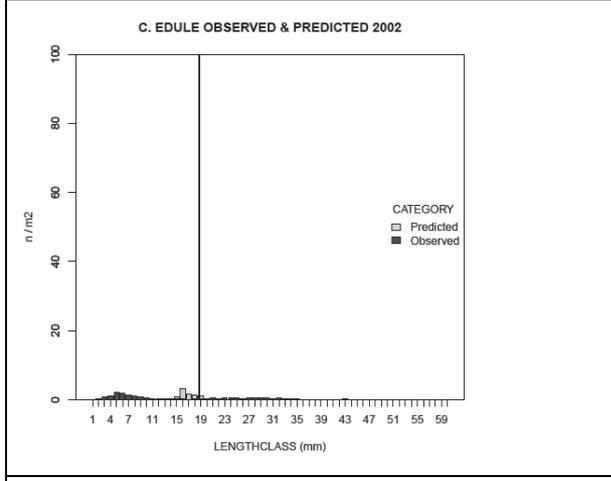
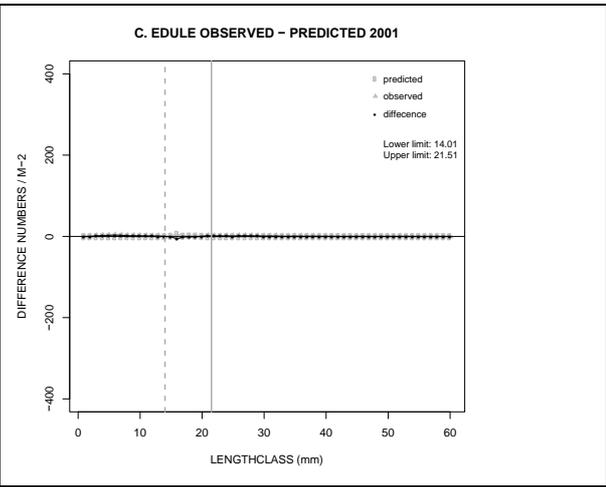
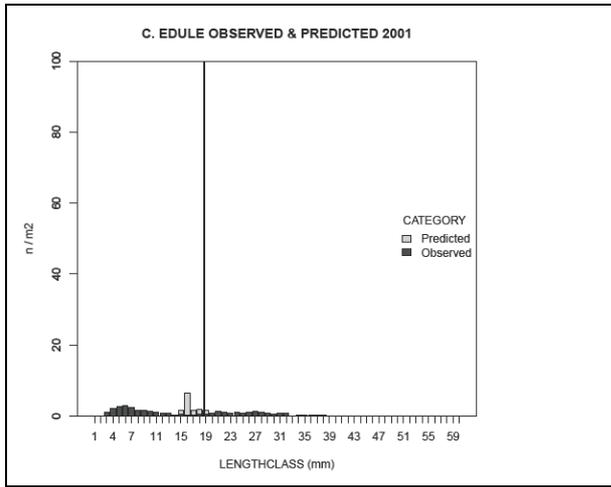


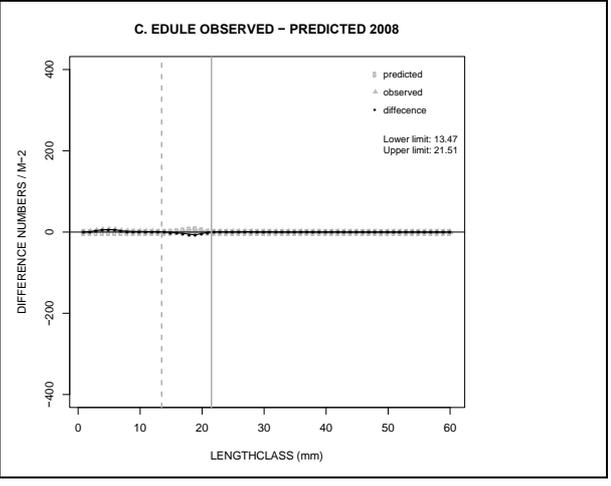
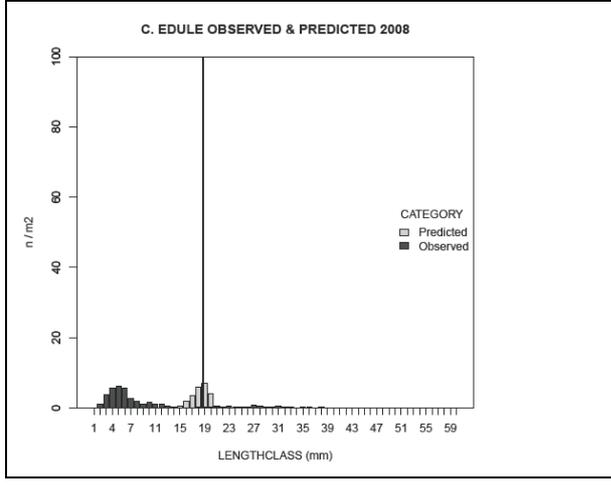
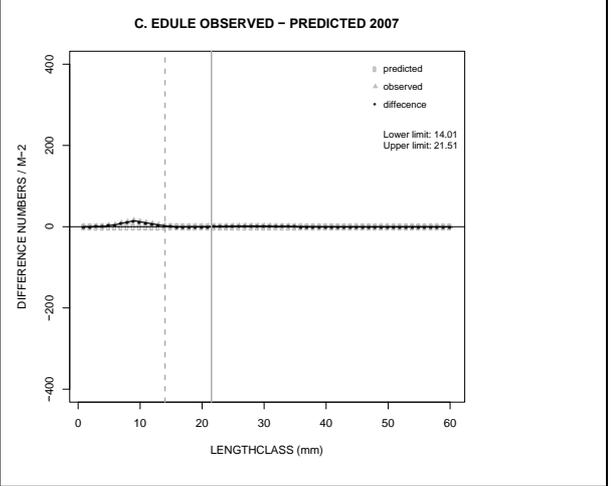
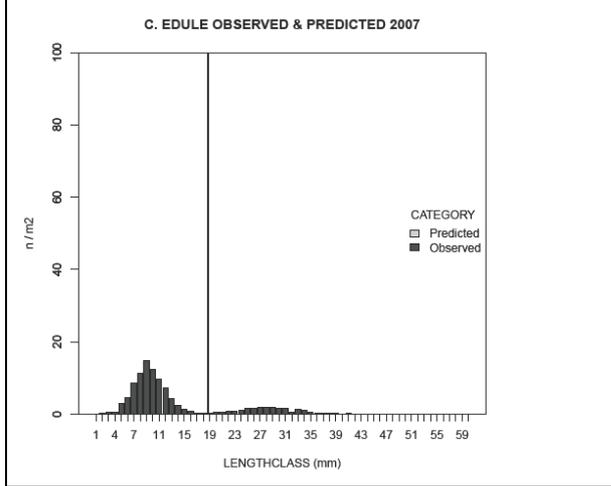
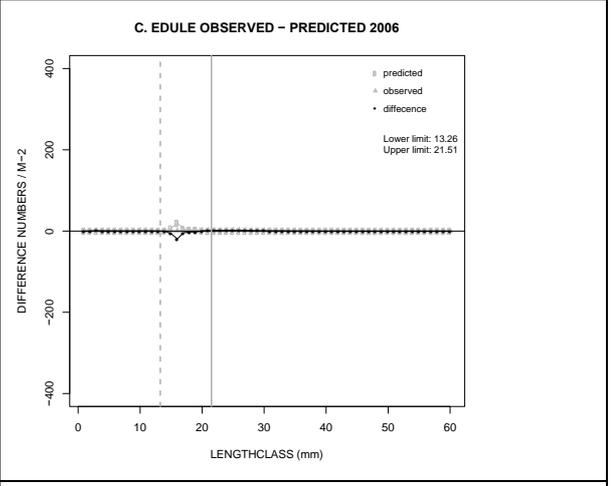
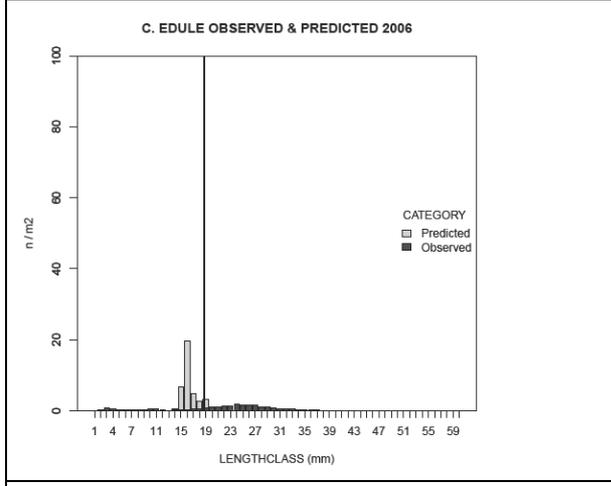
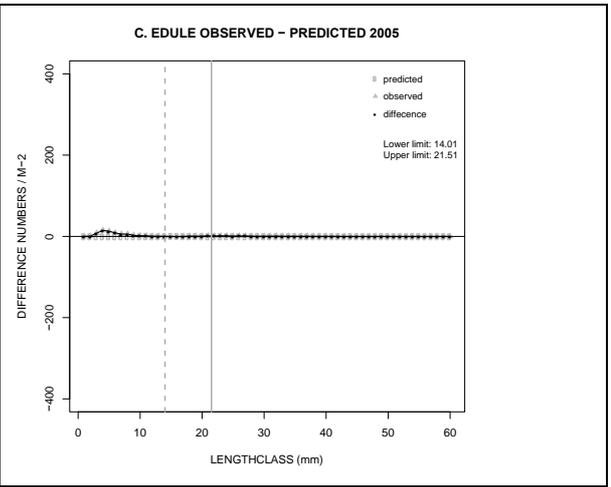
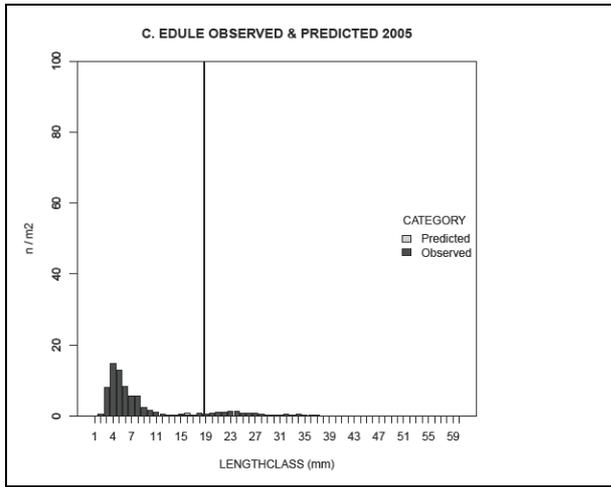
Prey abundances per square meter

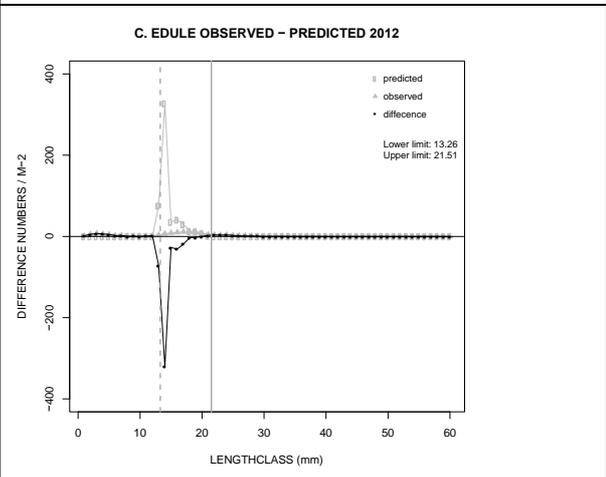
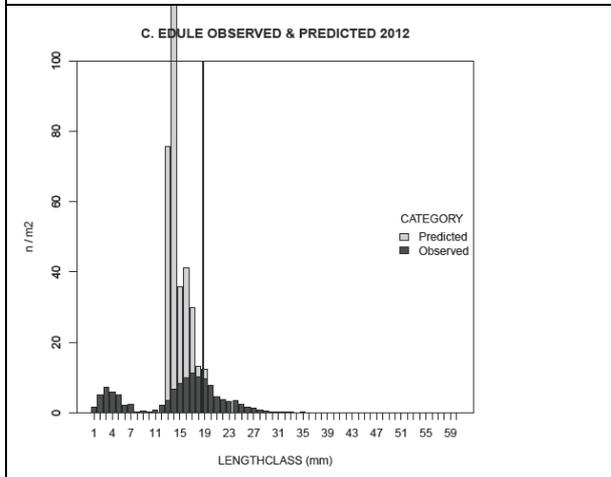
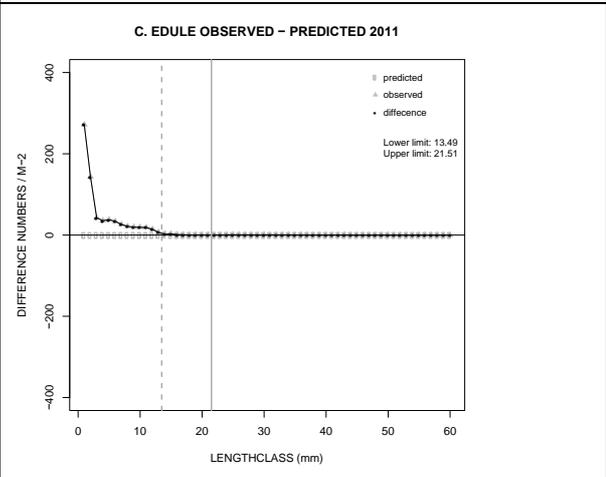
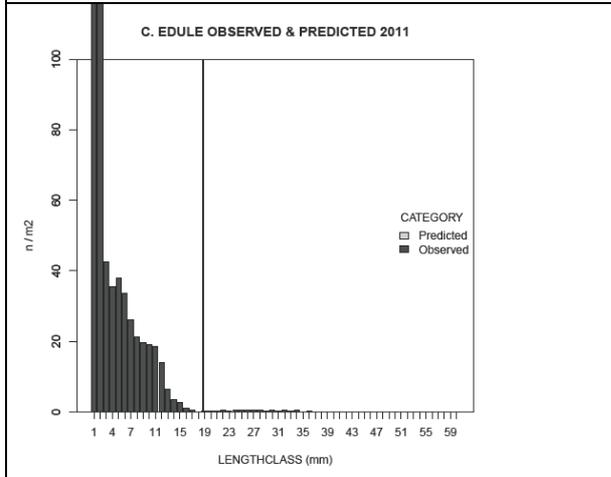
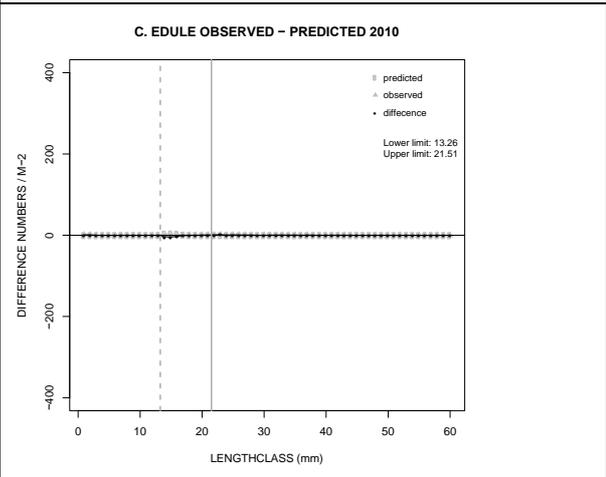
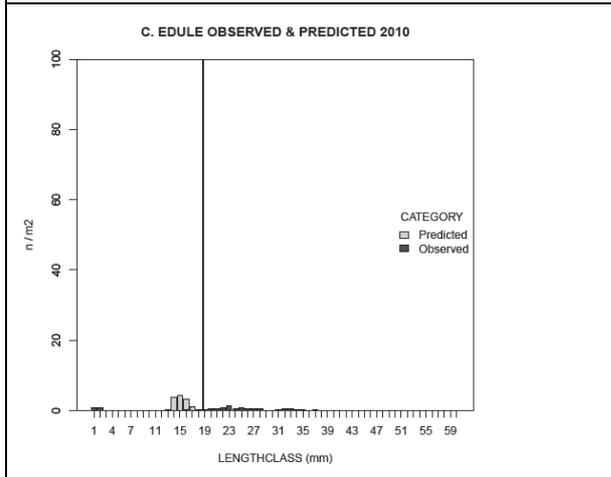
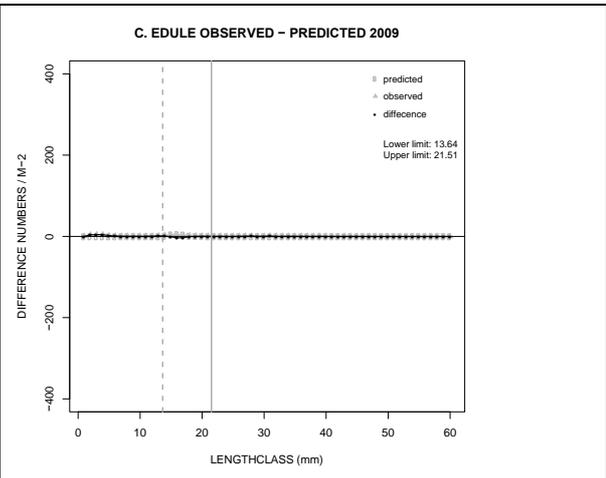
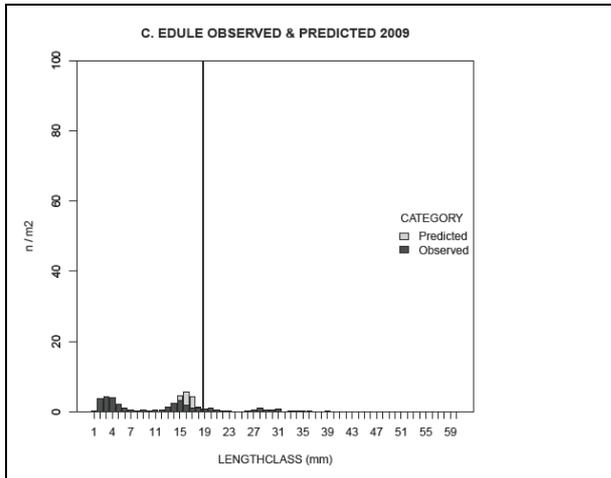
C. edule

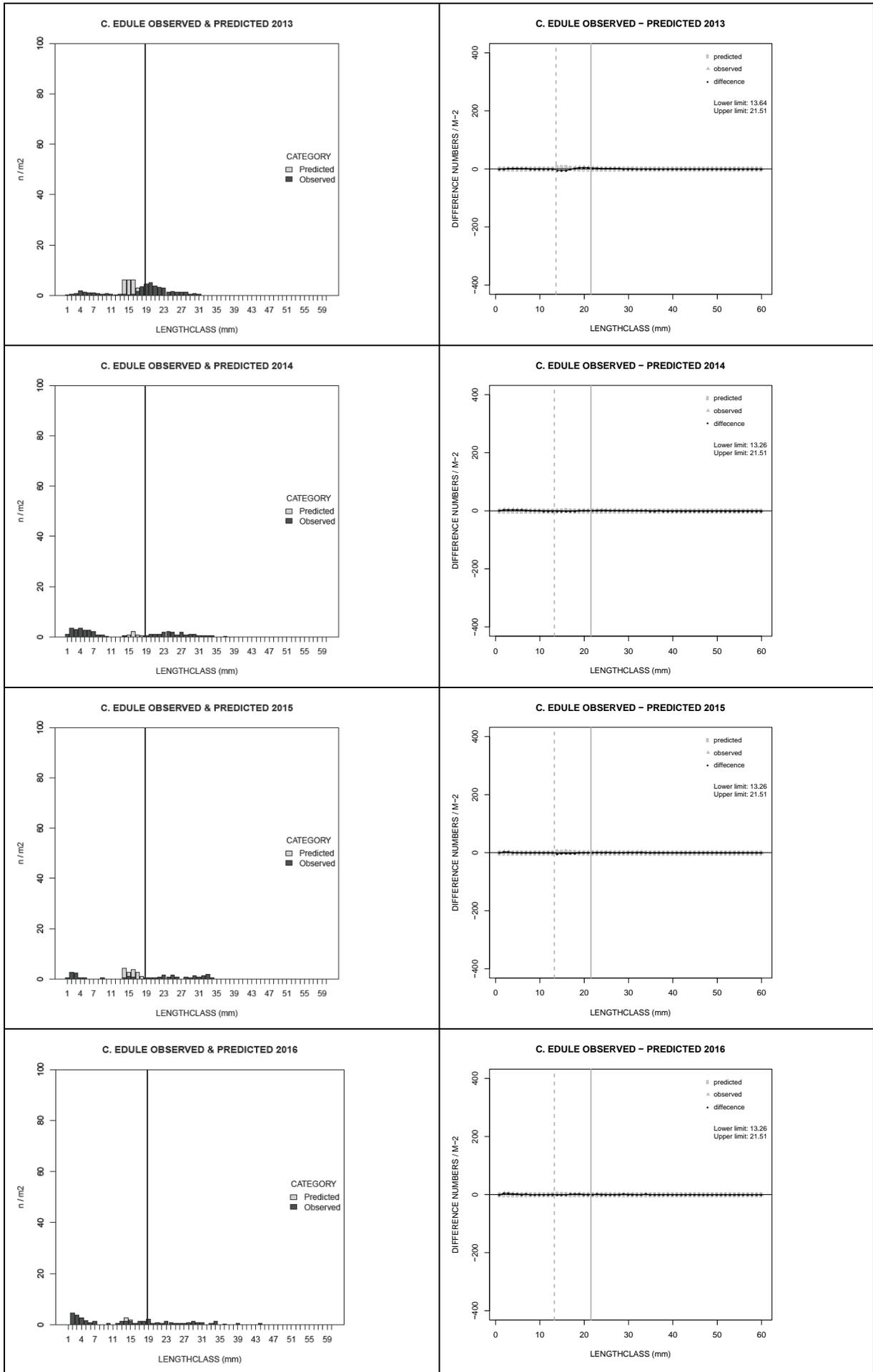


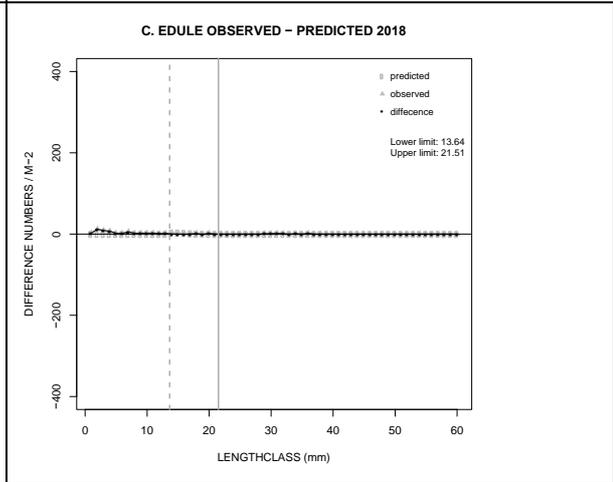
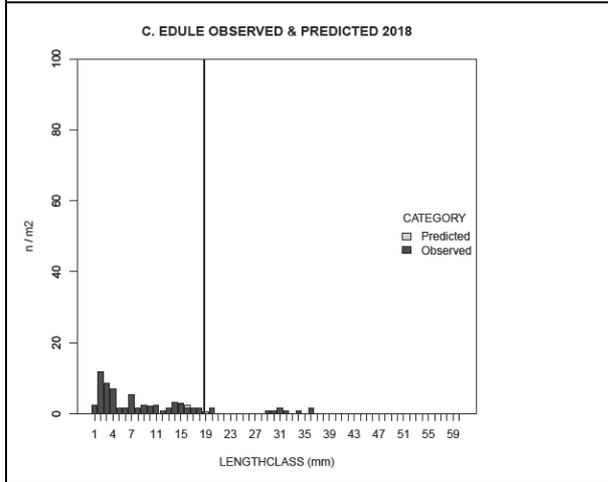
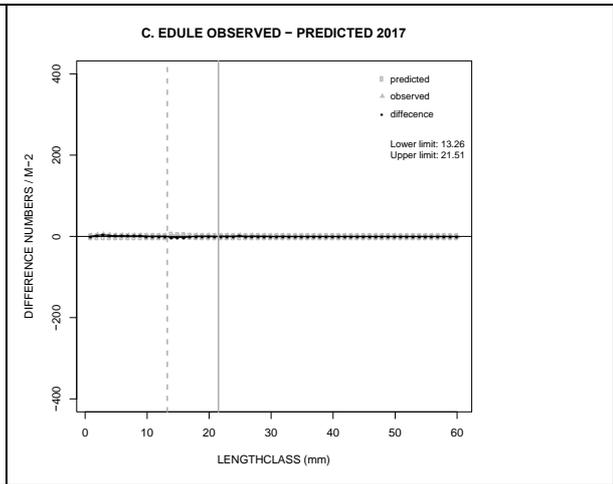
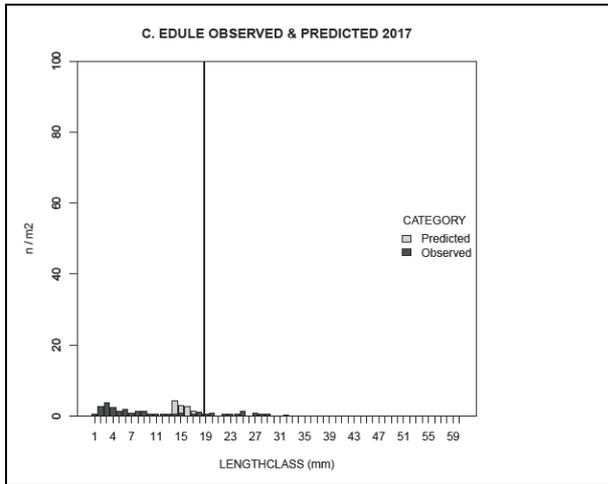




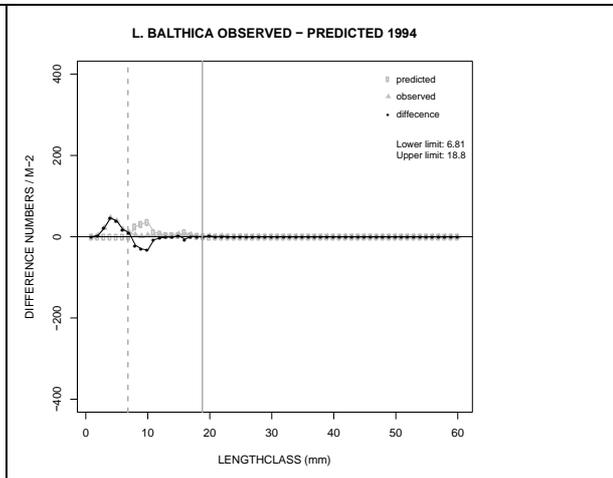
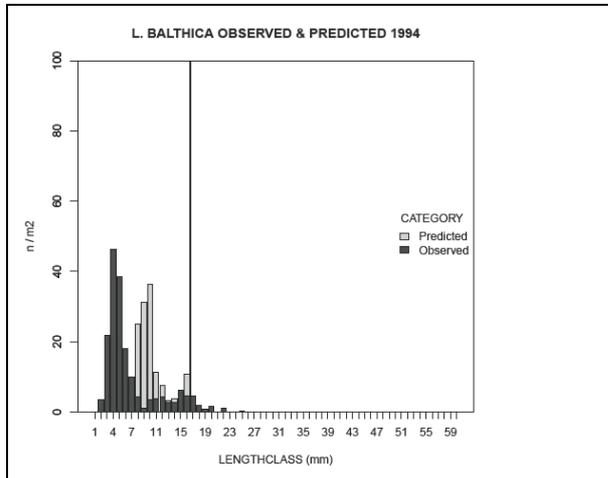


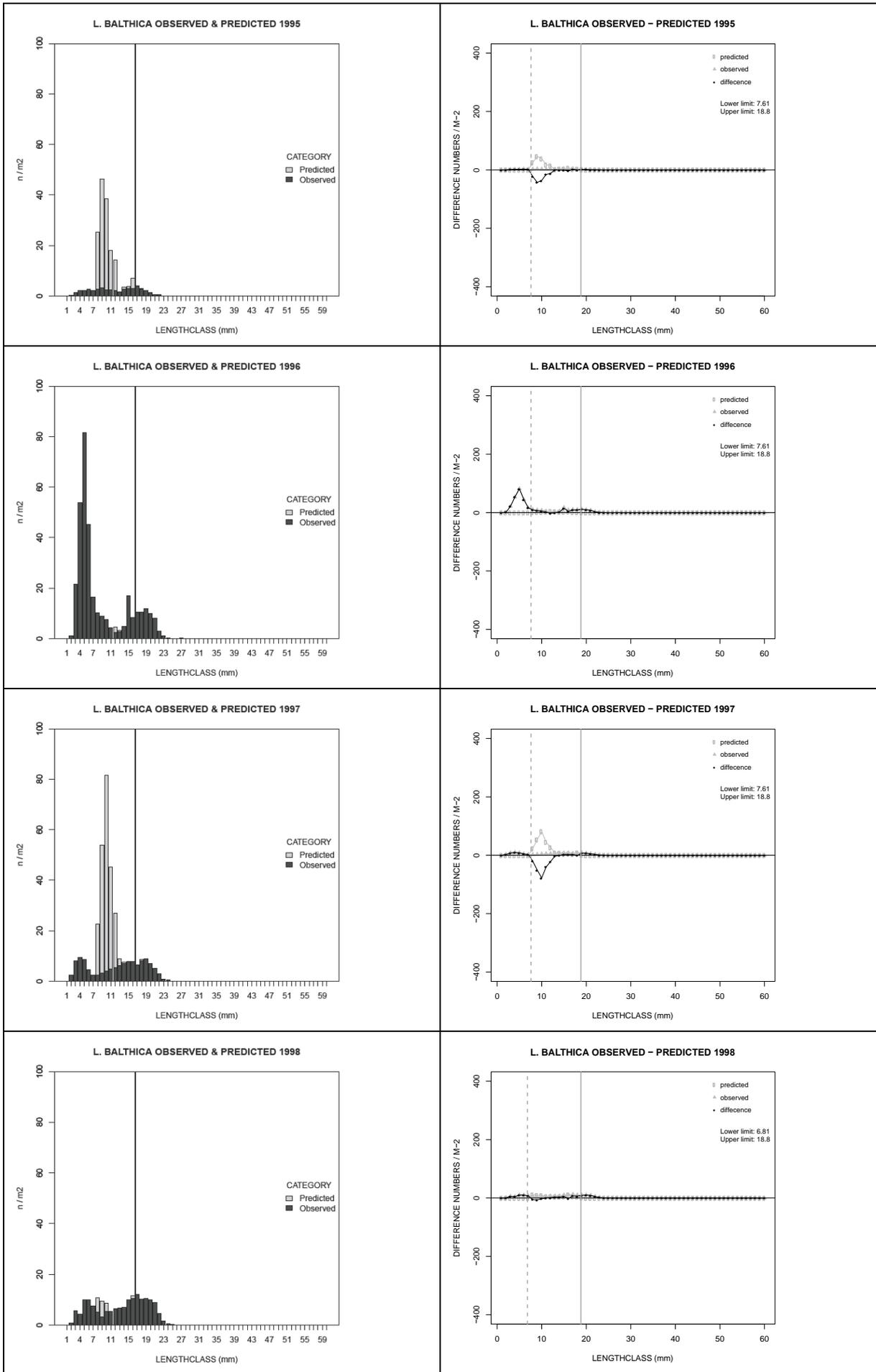


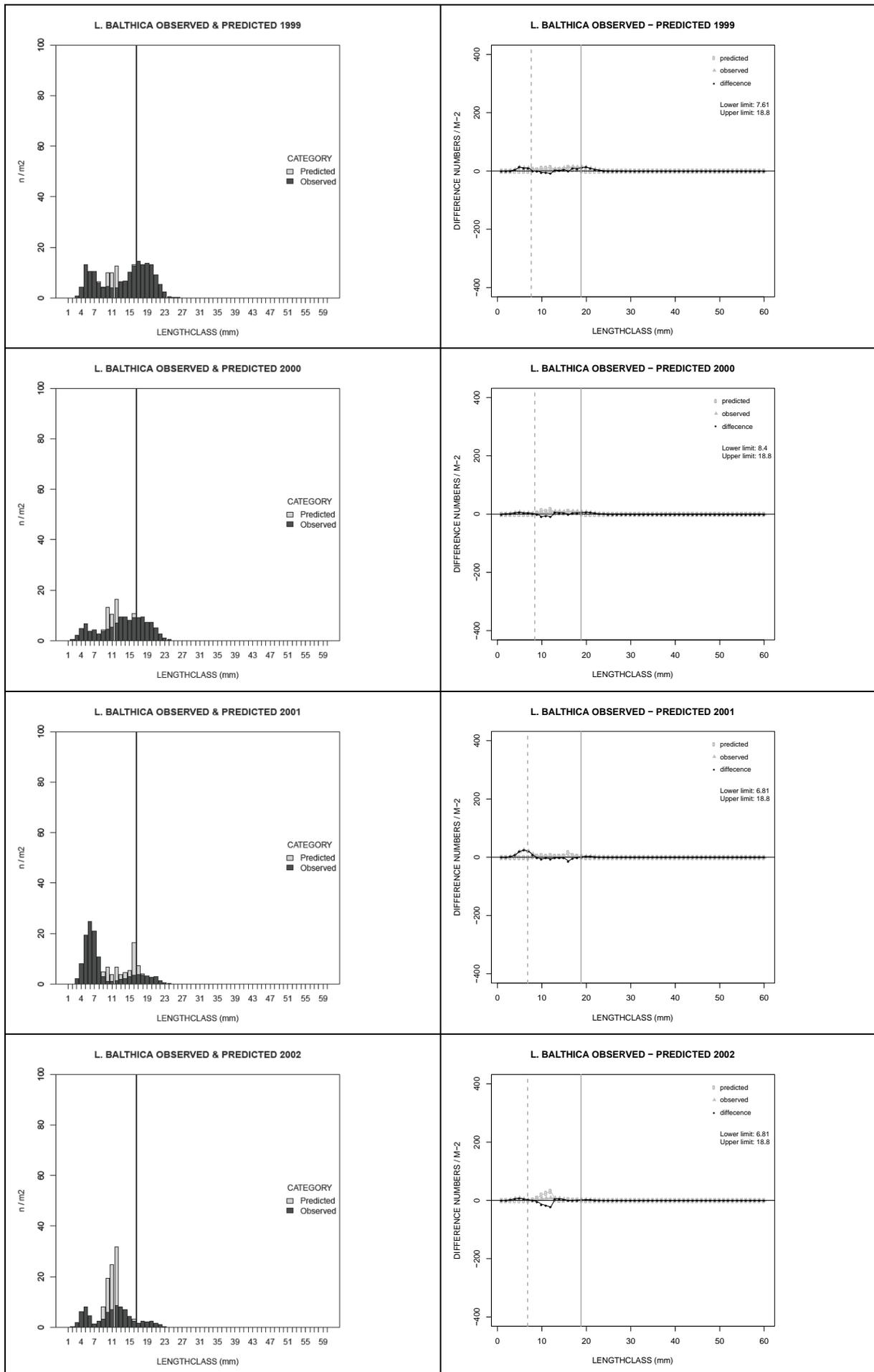


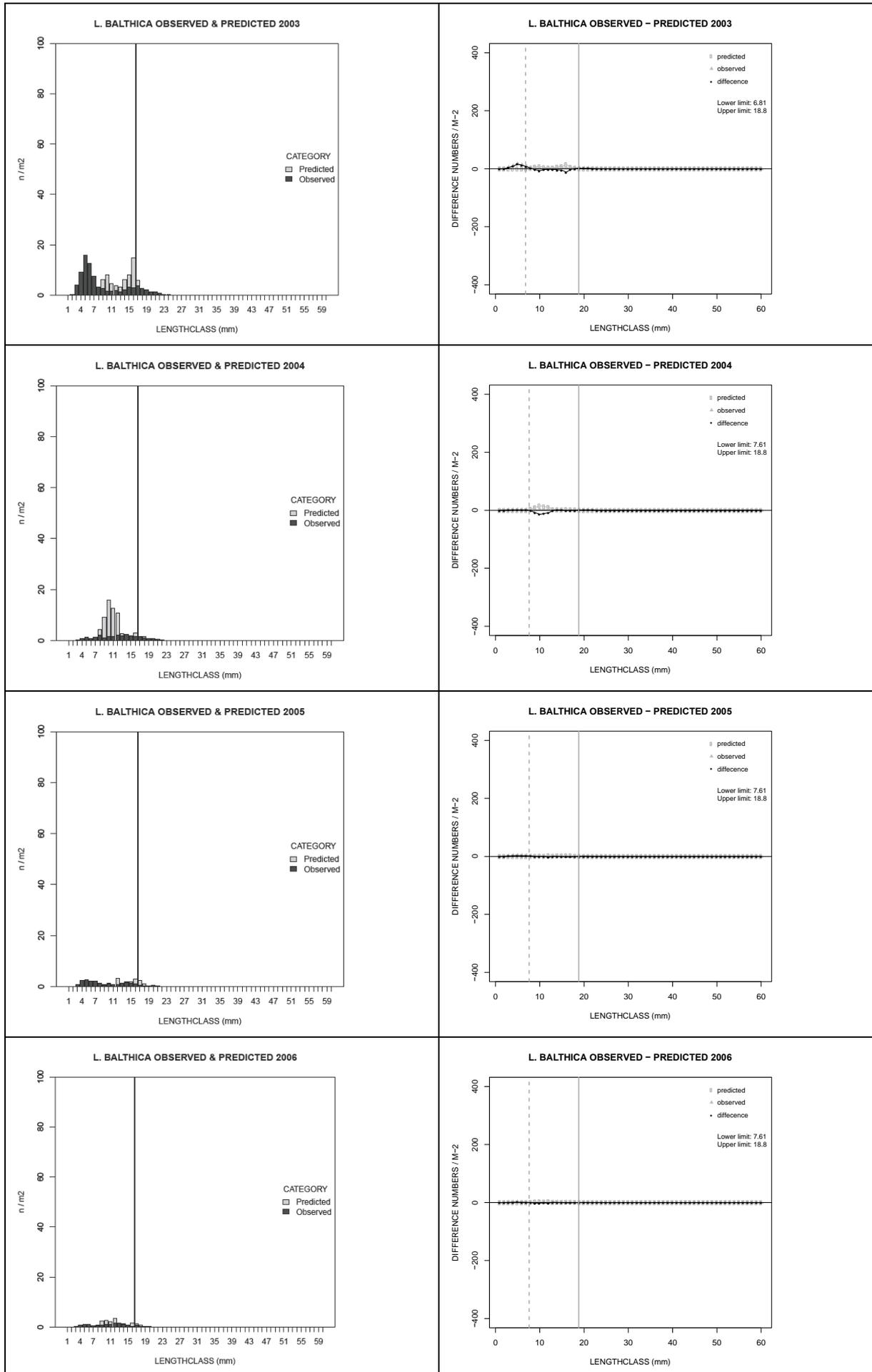


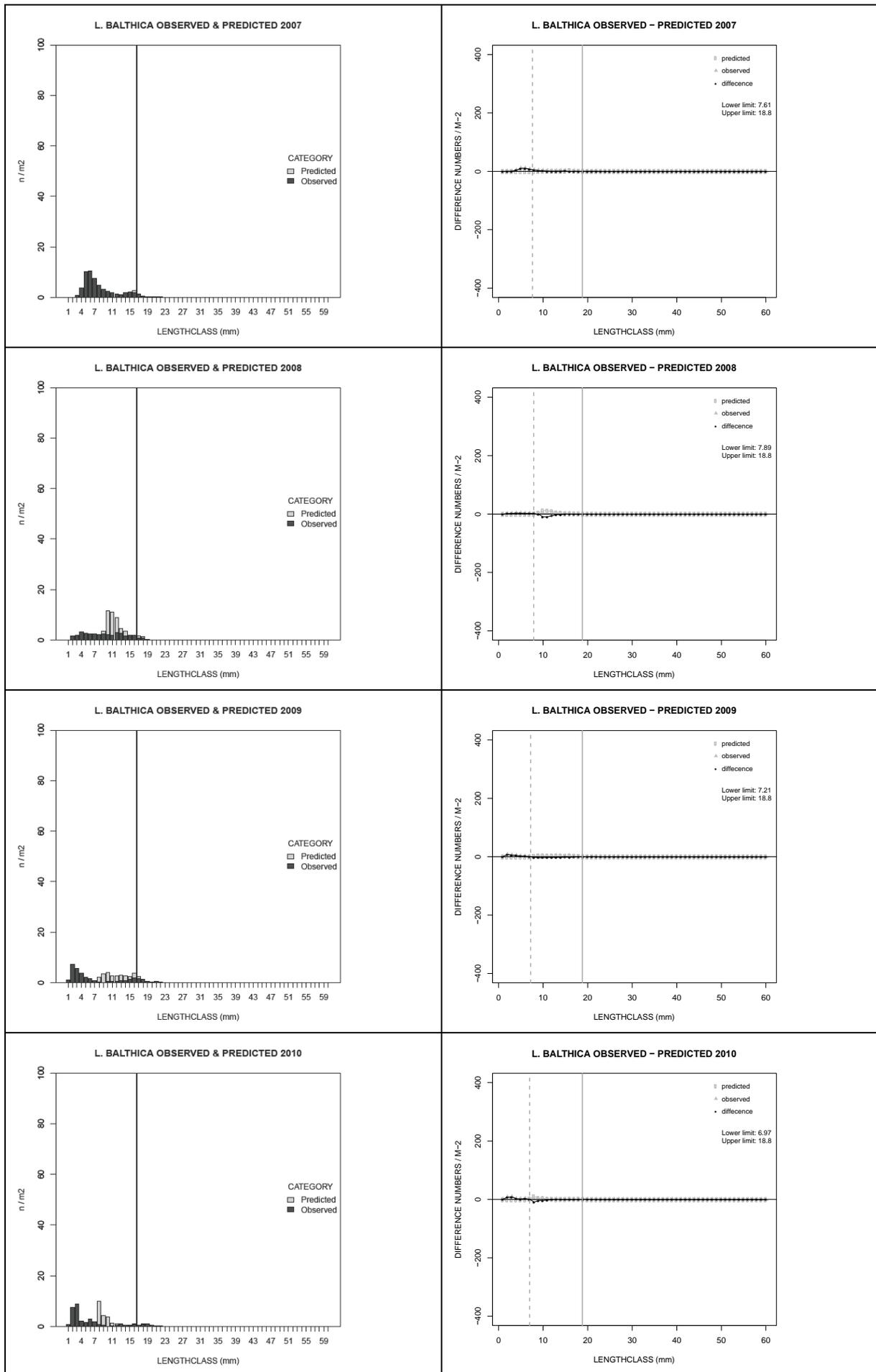
L. balthica

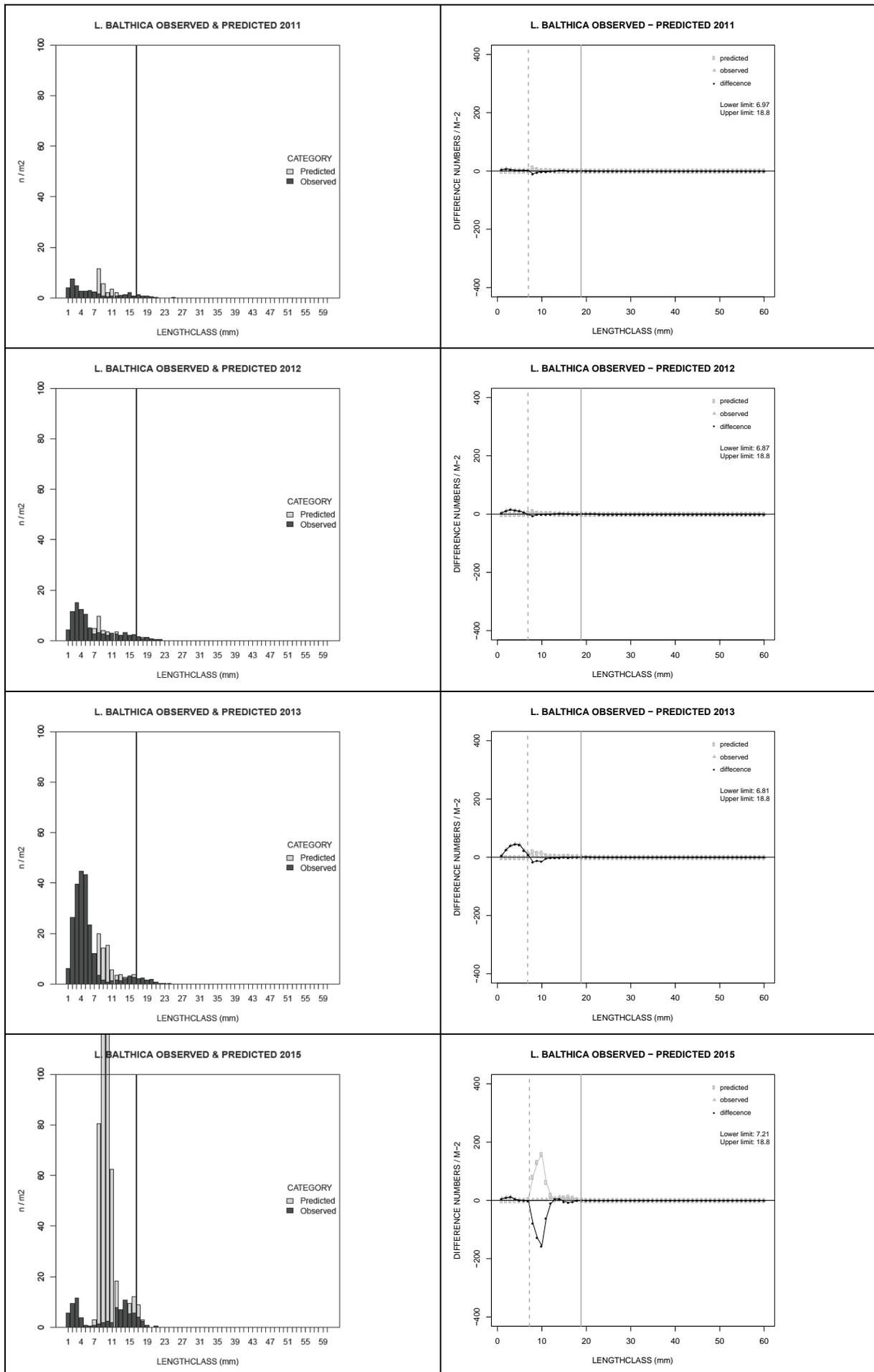


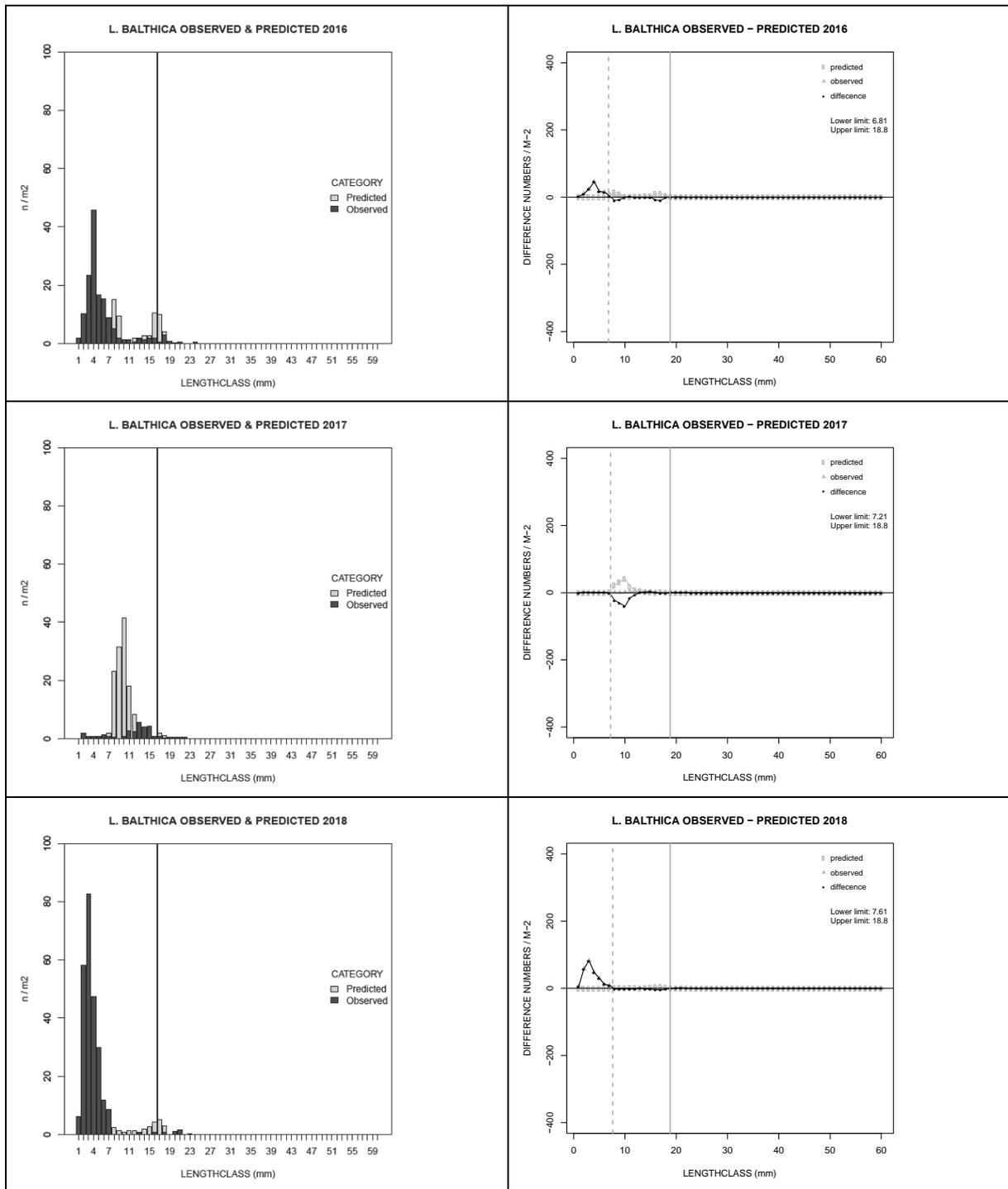












APPENDIX III – Red knots and prey in numbers per square meter

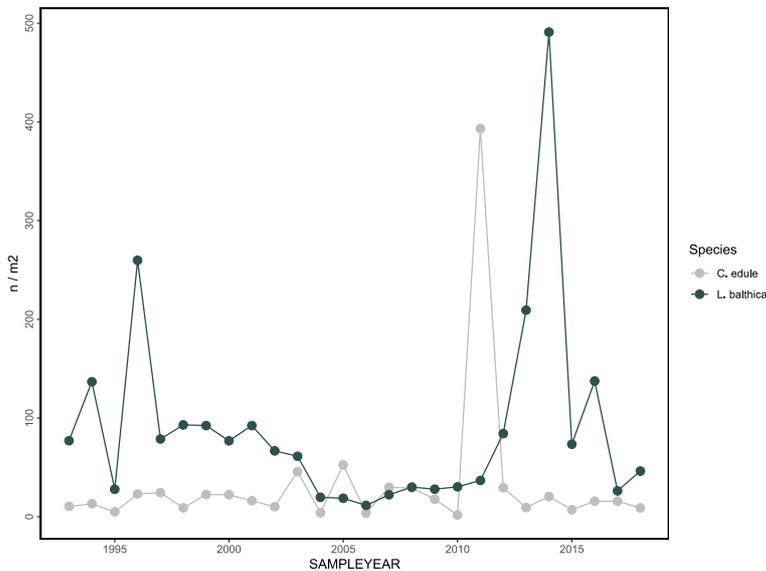


Figure III-1: Densities of edible prey in number of individuals per square meter throughout years. Grey indicates *C. edule*, and black shows the available *L. balthica* each year.

The maximum number of *L. balthica* individuals found per sample was 18108.3. The maximum number of *C. edule* individuals found per sample was 13015. The average prey densities of *L. balthica* per year ranged between 13.2 individuals per m² in 2006 and 618.8 individuals per m² in 2014. The average prey densities of *C. edule* per sample year ranged between 11.8 individuals per m² in 2010 and 740 individuals per m² in 2011. The available prey abundances per square meter per year for the sample period are shown in Figure III-1. In general, the availability of *L. balthica* was higher than the availability of *C. edule*. There were two sample years where the prey numbers are extremely high; 2011 for *C. edule* and 2014 for *L. balthica*. These years were years with an extreme spat fall for the respective prey species. Figure III-2 shows the distribution of the prey numbers per square meter, averaged over the whole sampling period. Edible *L. balthica* was more widely distributed.

There were also more areas with a higher density of *L. balthica* than was the case for *C. edule*. In general the areas east of Griend and just off the Frisian coast had the highest prey densities.

In first instance, there was no correlation between the prey abundances and the number of red knot months in the Vlie tidal basin. However, there was one extreme outlier in years with an extreme spat fall (22.6 times the interquartile range for *C. edule* in 2011 and 4.8 times the interquartile range for *L. balthica* in 2014). These outliers were therefore excluded from the analyses, the results with outlier can be found in Appendix IV. Without outlier, there was no relation between the abundances of *C. edule* and the red knot months (Figure III-3). In contrast, there was a significant linear correlation between red knot numbers and the abundances of edible *L. balthica* ($n=23$, $R^2=0.48$, $p>0.01$) (Figure III-3).

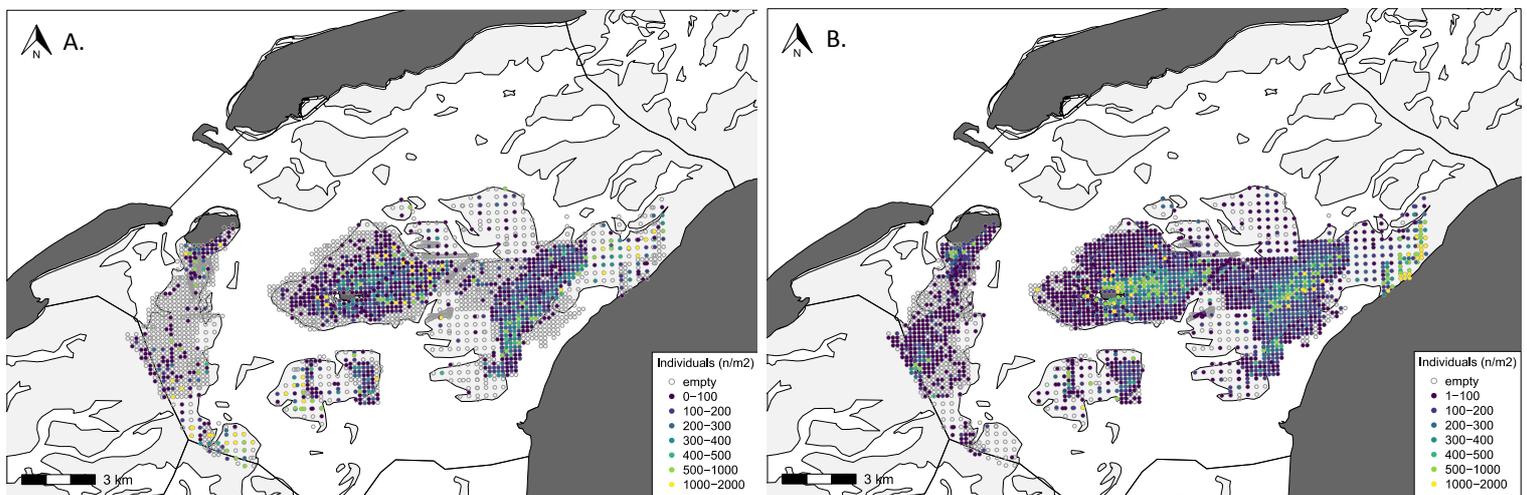


Figure III-2: Distribution of the average prey in number of individuals per square meter during the whole sample period. Lighter colours indicate higher prey abundances. Open circles represent empty sample points. A) *C. edule*. B) *L. balthica*.

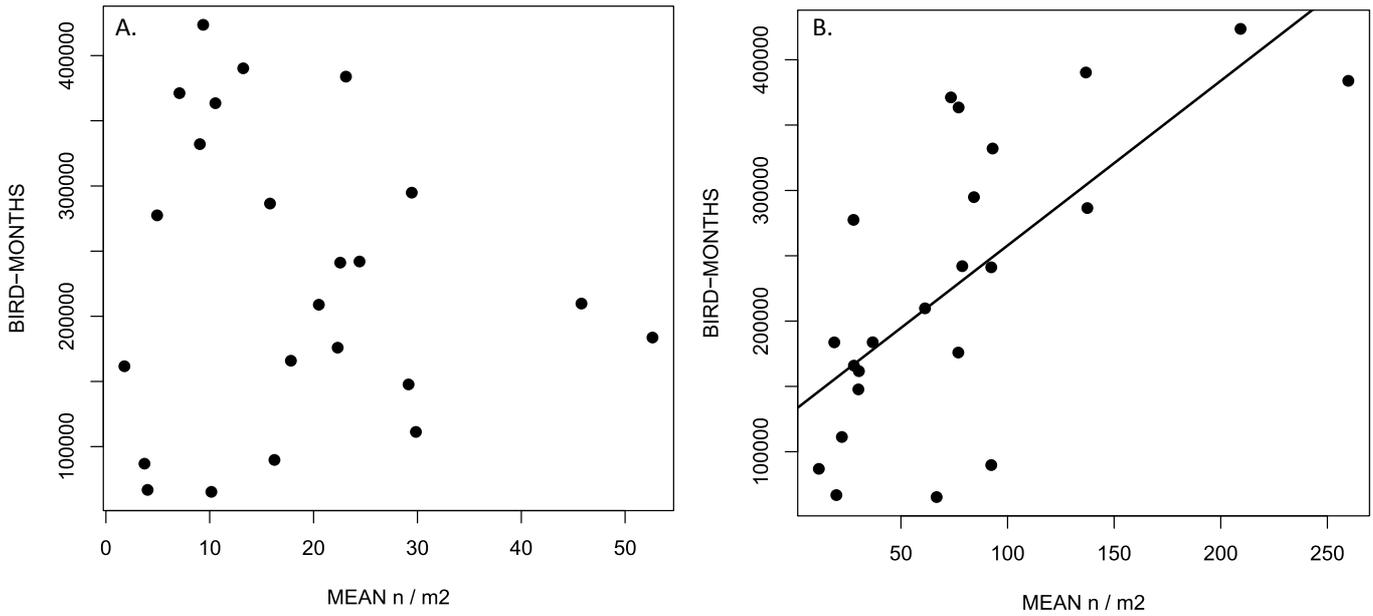


Figure III-3: Relation between the average prey abundance in individuals per square meter and the red knot months in the Vlie tidal basin. The solid line indicates a significant correlation. Each sample point represents one year. A) *C. edule*. B) *L. balthica*.

In first instance, there was no correlation between the prey elimination and the number of red knots in the Vlie tidal basin and the size of the red knot population. However, there were two extreme outliers (38.96 times the interquartile range for *C. edule* in 2011 and 7.22 times the interquartile range for *L. balthica* in 2014). The outliers were excluded, but still no significant correlation was found for *C. edule*. However for *L. balthica* the prey elimination correlated significantly with the number of bird-months in the Vlie tidal basin (n=23, R²=0.44, p>0.01).

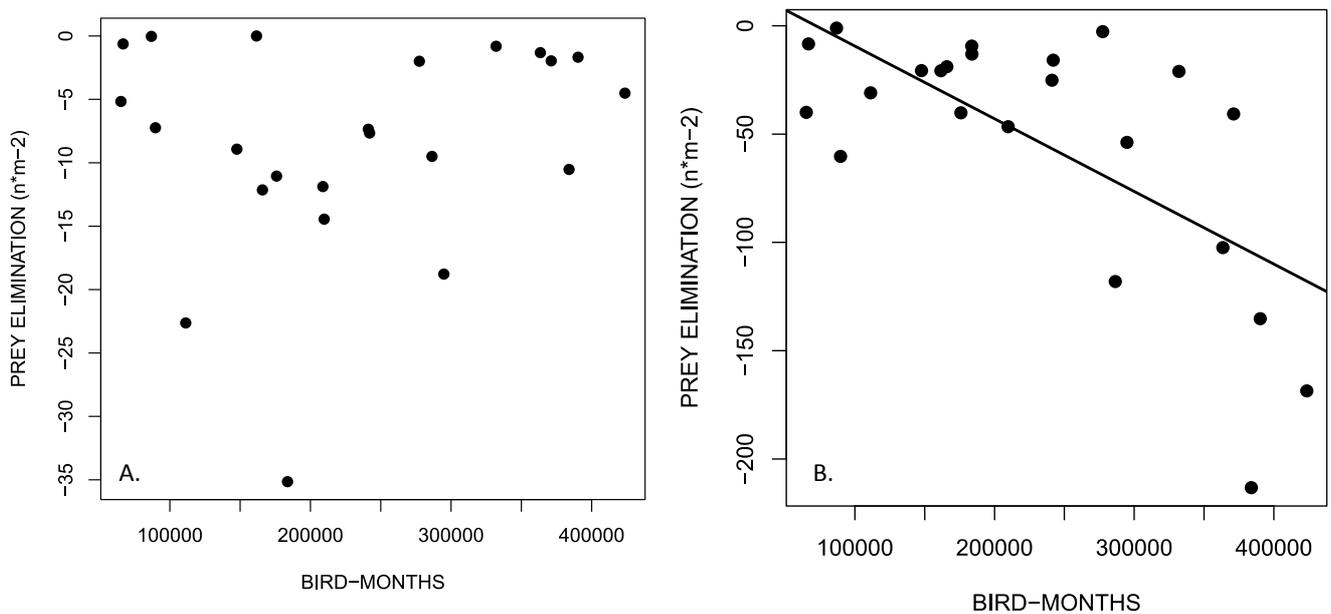


Figure III-4: Relation between the red knot months and the prey elimination per sample year. Each sample point represents one year, the solid line indicates a significant correlation. A) *C. edule*. B) *L. balthica*.

APPENDIX IV – Analyses with outliers

For none of the analyses with outlier included a relation was found between red knot population size and prey. Therefore, the outlier was removed and the analyses were rerun. Figure 1 gives an overview of all the results with outlier.

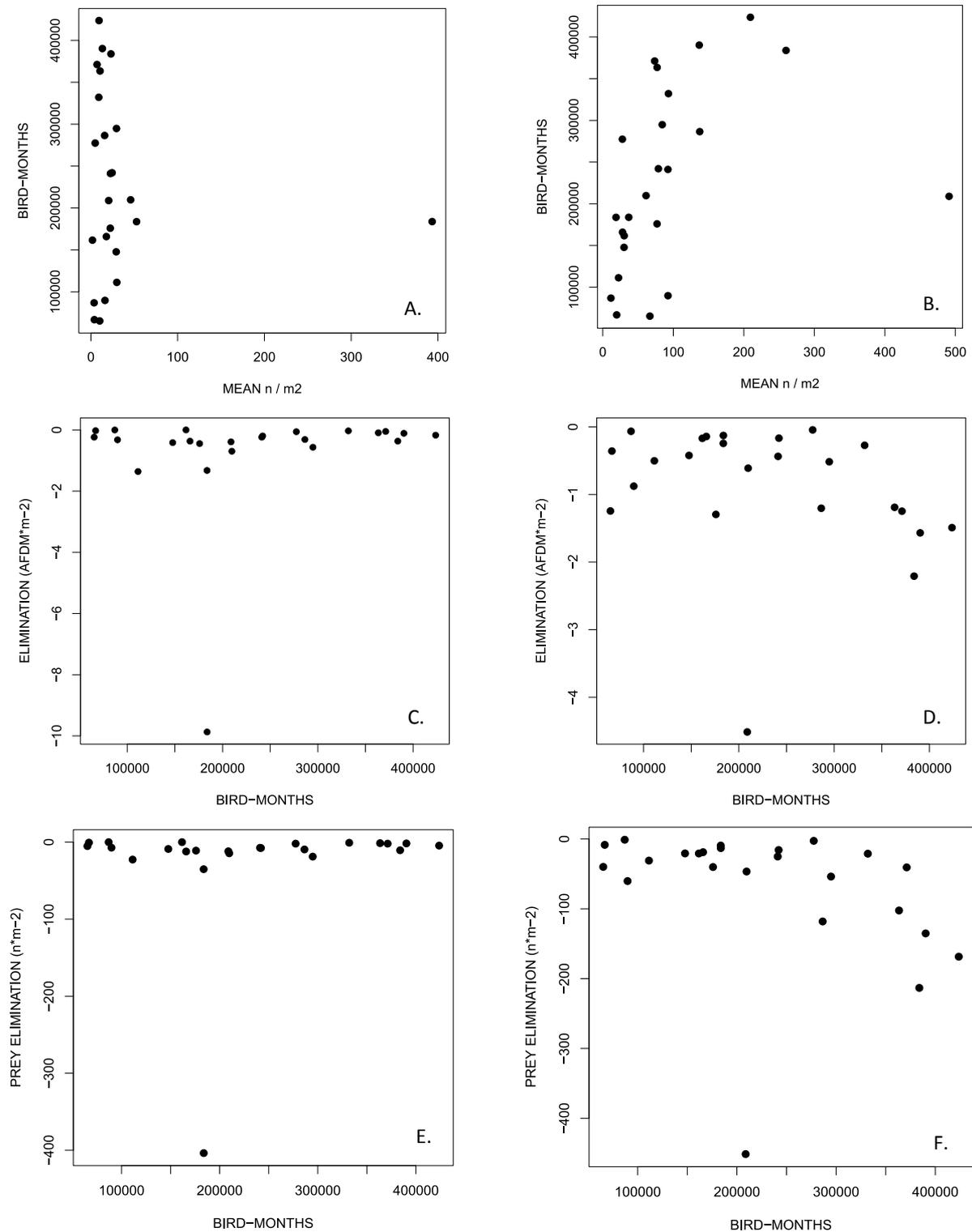


Figure IV-1: Analyses of red knots and prey with outliers. A) The relation between red knots and *C. edule* abundance in individuals per square meter. B) The relation between red knots and *L. balthica* abundance in individuals per square meter. C) The relation between the red knot population size and the biomass elimination of *C. edule* per square meter. D) The relation between the red knot population size and the biomass elimination of *L. balthica* per square meter. E) The relation between the red knot population size and the elimination of *C. edule* in individuals per square meter. F) The relation between the red knot population size and the elimination of *L. balthica* in individuals per square meter.

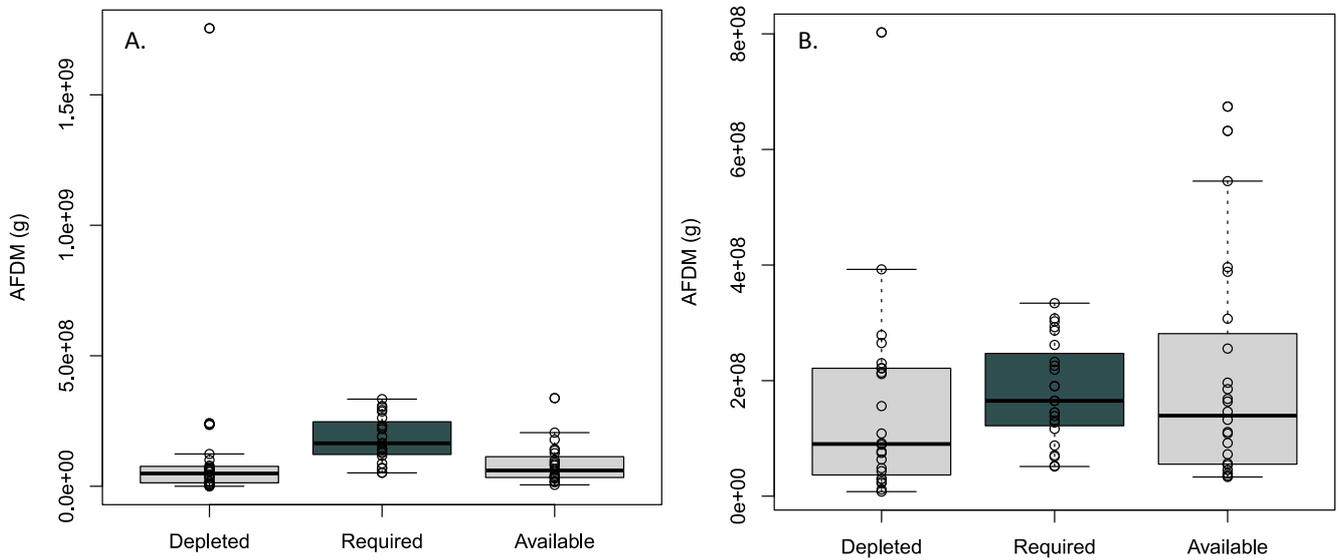


Figure IV-2: The biomass required by all red knots in Vlie each year (middle box in both panels) versus the prey depletion (left boxes) and prey biomass available (right boxes) in the Vlie tidal basin. The open circles indicate the different years. A) *C. edule* B) *L. balthica*

Also for the boxplot showing the depleted, required and available biomass there was one extreme outlier for prey elimination for both species in years with an extreme spat fall. This outlier was excluded in the main results in order to be able to better compare the two figures.

APPENDIX V – Prey quality over time

The prey quality varied throughout years (Figure 0-3). In the early 2000s the spread of the quality was largest. The mean prey quality centres between 0.15 and 0.25. The spread of the prey quality is lowest in 2016, 2017 and 2018, but these are years when relatively few samples were available (only the 20% random sample points had been sorted in the lab) and there were only a few measures for both shell and flesh available, which likely influenced these results.

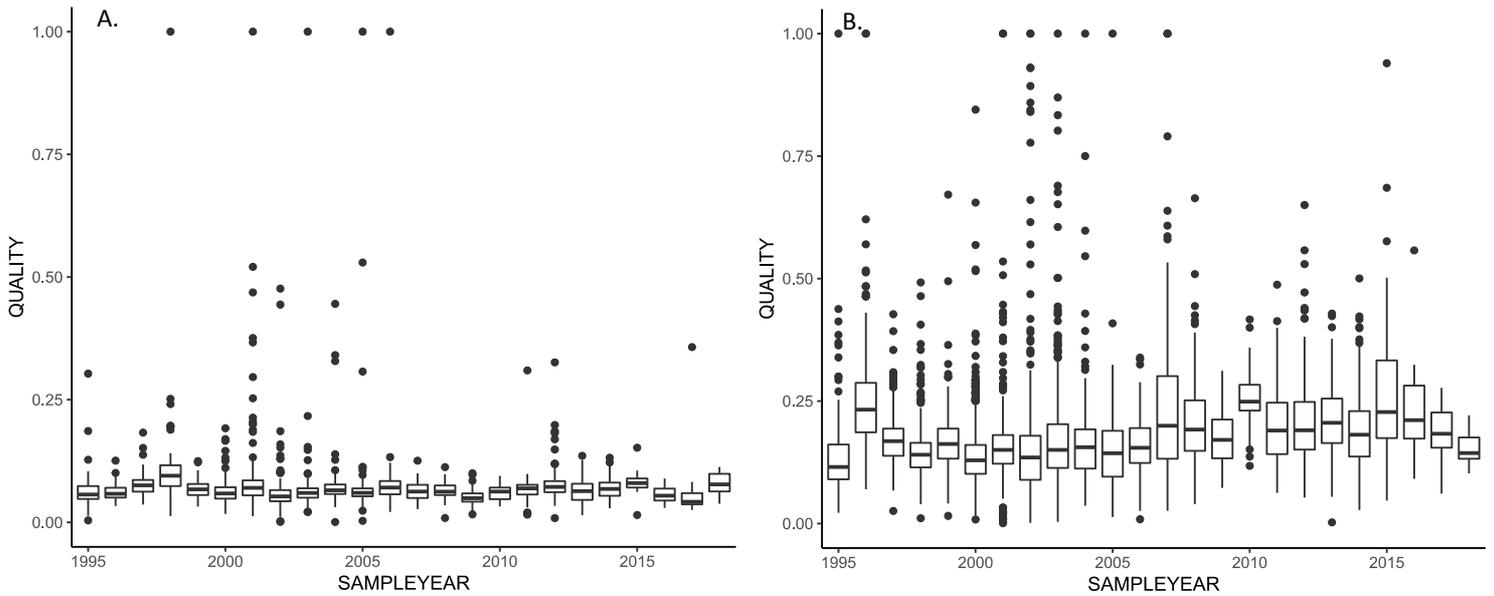


Figure 0-3: the variation in prey quality over time. Boxes represent the median, quartiles and interquartile and outliers for the prey quality per sample. A) *C. edule*, B) *L. balthica*

APPENDIX VI – Prey elimination as fraction of available prey at the start of the year

The fraction of prey eliminated over the year with respect to the prey available at the start of the year was calculated and the relation to the red knot months in the Vlie tidal basin for both prey species is shown in Figure 0-4. For both prey species there was no correlation between the fraction of prey eliminated and the amount of red knot months in the Vlie tidal basin for either prey biomass or prey abundance in number of individuals per square meter. The fraction of prey eliminated centred around 0.36 for *C. edule* and around 0.48 for *L. balthica*.

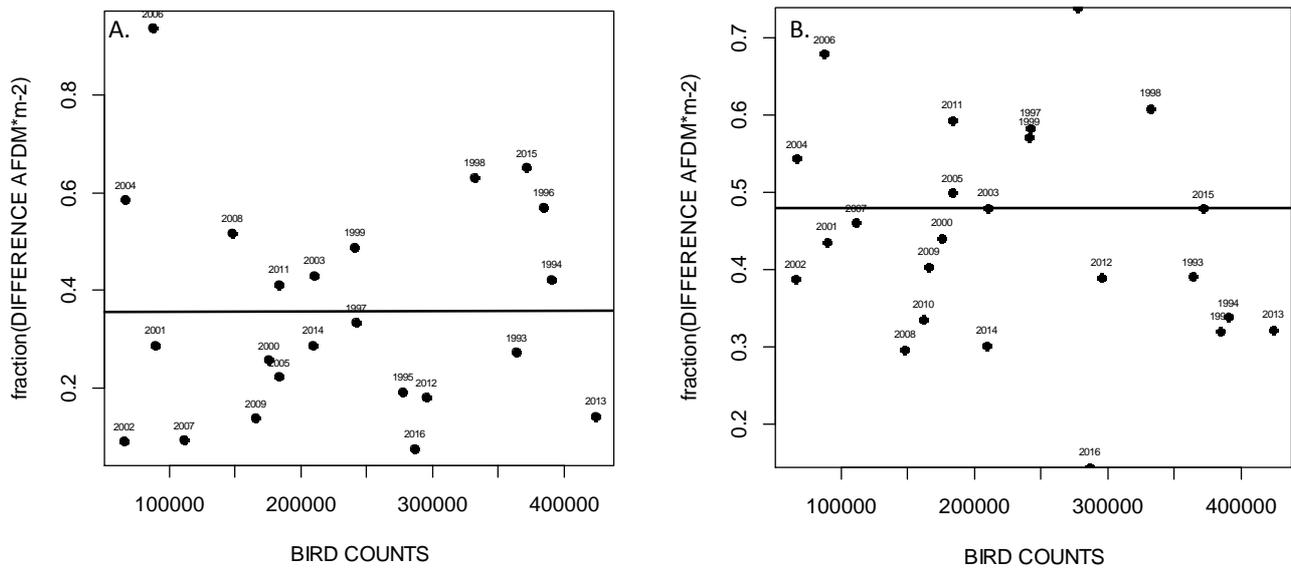


Figure 0-4: Relation between the fraction of prey eliminated with respect to the prey in the Vlie tidal basin at the start of the year and the red knot months in the Vlie tidal basin. Each sample point indicates one year, the horizontal lines represent the mean fraction of prey eliminated. A) *C. edule*. B) *L. balthica*.

APPENDIX VII – Prey elimination and prey densities

The prey depletion increased slightly with increasing prey biomass for both prey species. With increasing prey densities, the prey elimination increased strongly. See Figure 0-5 for a visual of this increase with increasing prey densities as observed in the Vlie tidal basin during the study period.

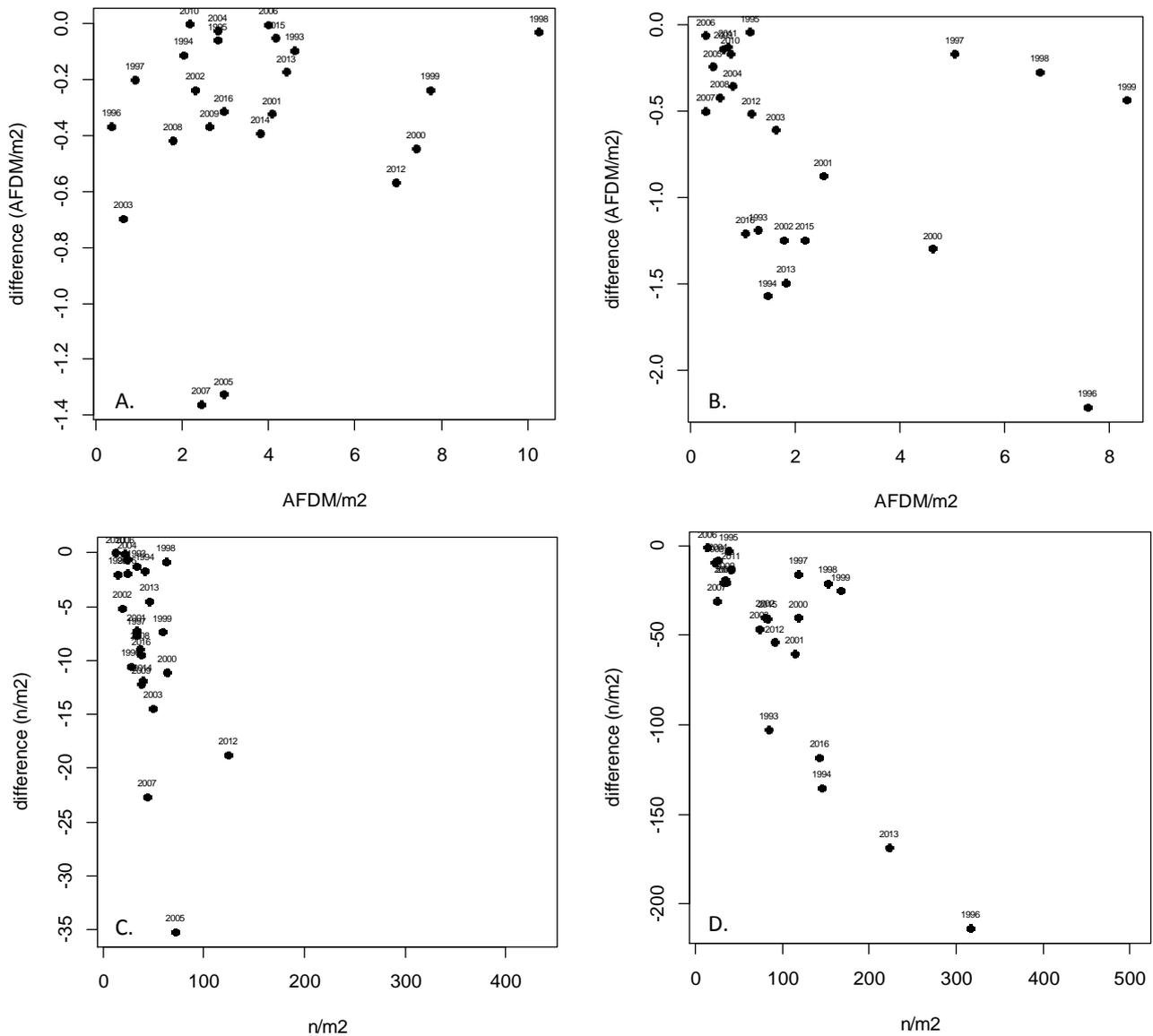


Figure 0-5: The prey elimination as a function of prey density. A-B) prey elimination in biomass per square meter with increasing prey biomass. A) *C. edule*, B) *L. balthica*. C-D) prey elimination in individuals per square meter with increasing prey densities in individuals per square meter. C) *C. edule* D) *L. balthica*.

APPENDIX VIII – Red knot energy requirements

The biomass required by all red knots in the Vlie tidal basin was higher than the edible biomass of *C. edule* that was present in most sample years (Figure 0-6A). For *L. balthica* the amount of biomass available in the tidal basin generally was more in accordance with the amount of energy required by all red knots each year (Figure 0-6B). The energy requirements of all red knots was higher than the amount of *C. edule* biomass that was eliminated in the Vlie tidal basin most years (Figure 0-6C). The energy requirements of all red knots and the elimination of *L. balthica* matched relatively well (Figure 0-6D). The number of red knots predicted to be in the Vlie tidal basin based on the amount of edible *C. edule* biomass did not match the amount of red knots that were observed (Figure 0-6E). The number of red knots predicted in the Vlie tidal basin based on the amount of *L. balthica* biomass present matched relatively well with the number of red knots observed each year (Figure 0-6F).

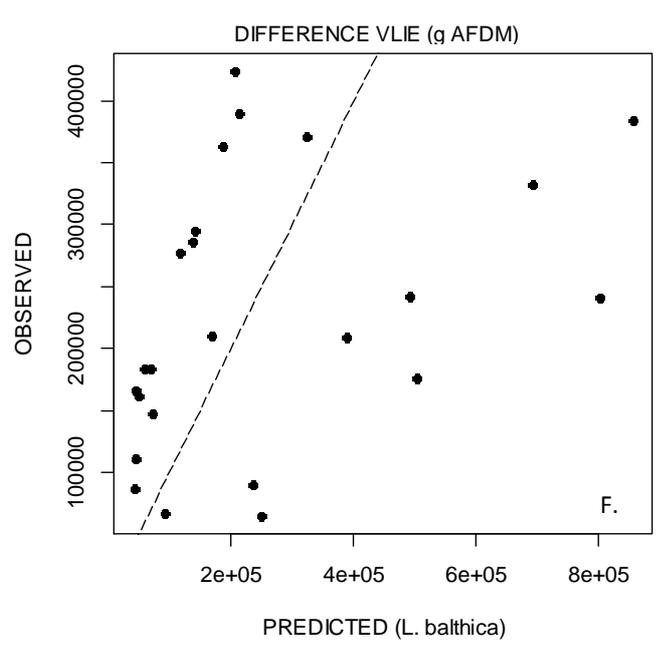
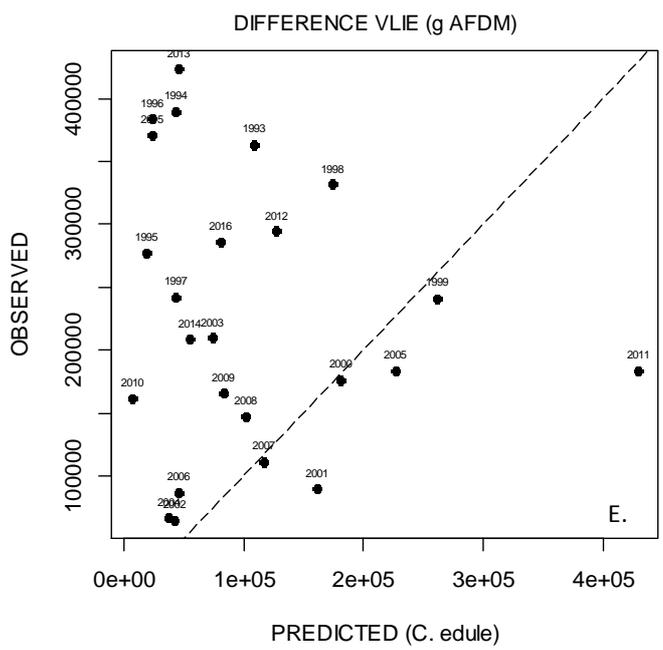
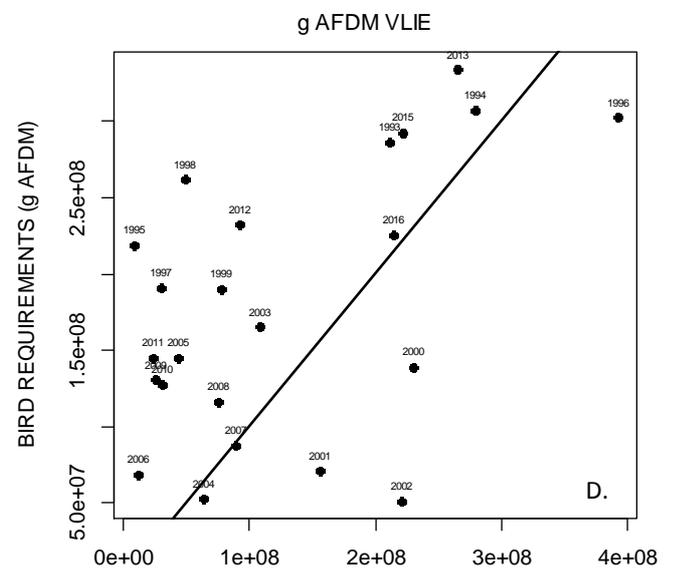
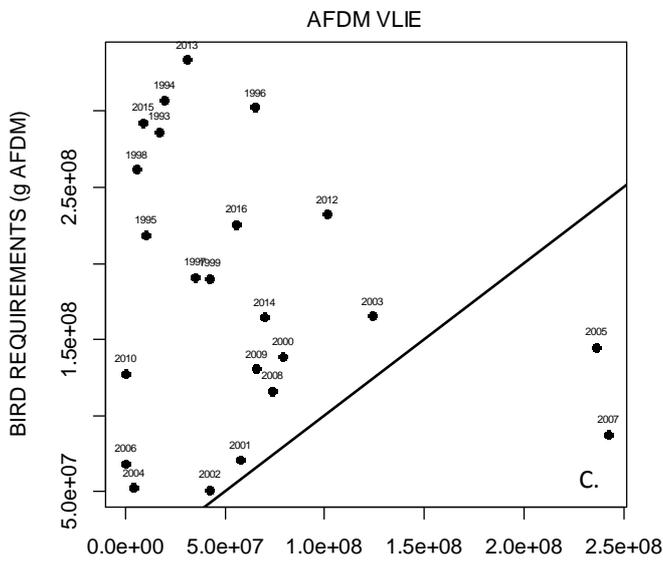
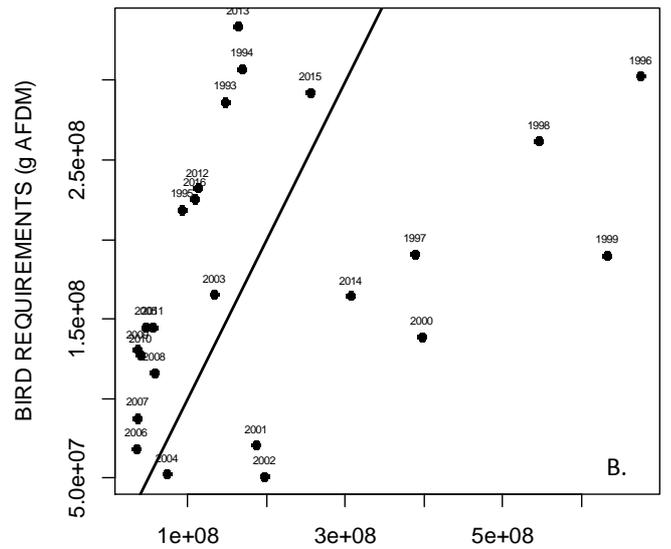
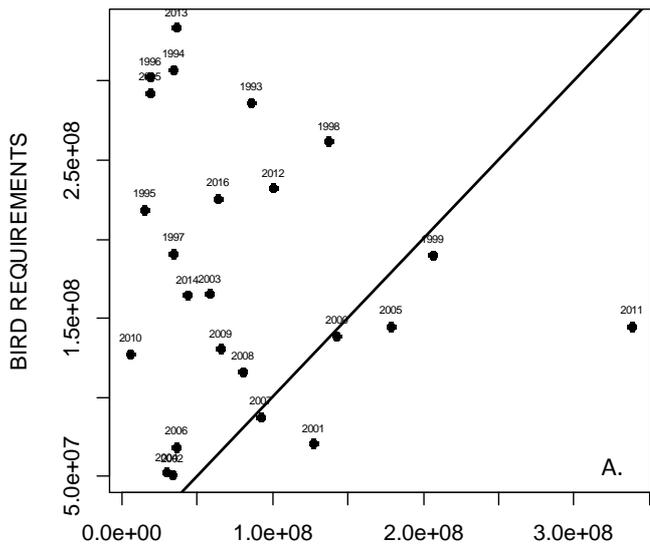


Figure 0-6: A-B) Energy requirements of all red knots in g biomass compared to the total available prey biomass in the Vlie tidal basin. The solid line is the x=y line. A) *C. edule* B) *L. balthica*. C-D) Energy requirements of all red knots in g biomass compared to the total elimination of prey biomass in the Vlie tidal basin. The solid line is the x=y line. C) *C. edule*. D) *L. balthica*. E-F) Number of red knots predicted based on the total edible prey biomass in the Vlie tidal basin compared to the observed number of red knots. The dashed line is the x=y line. E) *C. edule*. F) *L. balthica*.