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STATISTICAL ESTIMATION OF MUSKRAT ABUNDANCE

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FOTO OMSLAG Jonge muskusrat (foto: Calle Boot)

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TEN GELEIDE

Om de bevindingen uit de studie ook met (model-) experts van buiten Nederland te kunnen delen, en daar eventueel inhoudelijke discussie met hen over te kunnen voeren, is de tekst in het Engels opgesteld.

"Statistical estimation of muskrat abundance. Door Emiel E. van Loon, Ronald C. Ydenberg en Daan Bos. A&W-rapport 2382

Universiteit van Amsterdam/Altenburg & Wymenga ecologisch onderzoek, Amsterdam/Feanwâlden"

De combinatie van velddata en een dynamisch populatiemodel onderbouwen dat de vangstinspanning een van de belangrijkste factoren is om de variatie in gevangen aantallen muskusratten te kunnen verklaren. Bij voldoende inzet zal de bestrijding van muskusratten leiden tot lagere aantallen muskusratten. Het gebruik van het model zal een efficiëntere inzet van bestrijdingsorganisaties tot gevolg hebben.

Dit zijn de belangrijkste resultaten van de veldproef muskusratten die onder de auspiciën van de Unie van Waterschappen in de periode 2013-2015 is uitgevoerd en de ontwikkeling van een dynamisch populatiemodel in opdracht van STOWA. Hierbij is voortgebouwd op eerdere statistische analyses van de gegevens uit de landelijke vangstregistratie van de muskusratbestrijding. Alles wijst erop dat het aantal muskusratten in Nederland momenteel relatief laag is.

Om een populatie stabiel te houden is het zaak om de natuurlijke aanwas af te vangen. Die aanwas is afhankelijk van het aanwezige populatieniveau. Het is om die reden aannemelijk dat er minder inspanning nodig is om een lage populatie stabiel te houden dan een middelgrote of grote populatie. De modeluitkomsten zijn hiermee in overeenstemming. De parameterschattingen in deze studie wijzen er verder op dat uitwisseling (migratie) tussen atlasblokken (5*5 km) niet verwaarloosd kan worden.

Het ontwikkelde model kan de bestrijding voorzien van een gedetailleerd stuk gereedschap om op gebiedsniveau de gevolgen van een verandering in de bestrijdingsintensiteit van bestrijding op het populatieniveau te bepalen. Daarnaast kunnen de objectieve aantalsschattingen gebruikt worden om de relatie te onderzoeken tussen aantallen muskusratten en schade door graverij. Gezamenlijk is deze informatie niet alleen buitengewoon nuttig in het publieke debat over de bestrijding, maar ook bij een beter onderbouwde en meer bedrijfsmatige uitvoering daarvan.

Het onderzoek dat STOWA, Unie, de waterschapslaboratoria en de bestrijdingsorganisaties samen uitvoeren naar het mogelijke gebruik van eDNA in het oppervlaktewater zal die onderbouwing nog beter maken.

Joost Buntsma
Directeur STOWA

SAMENVATTING

Vanuit maatschappelijk, bestuurlijk en biologisch oogpunt, is het wenselijk om inzicht te krijgen in de ontwikkelingen van populaties Muskusratten onder verschillende scenario's van beheer. De Unie van Waterschappen voert daarom een onderzoeksprogramma uit waarin op wetenschappelijke wijze noodzakelijke (veld-)kennis wordt verzameld. Als onderdeel van dit programma is in deze deelstudie een populatie dynamisch model gemaakt, waarbij is voortgebouwd op een eerdere statistische analyse van de gegevens uit de vangstregistratie van de muskusrattenbestrijding.

De modelstudie waarvan in dit document verslag wordt gedaan moet ook in het licht worden gezien van de Landelijke Veldproef Muskusratten. Deze veldproef is uitgevoerd van 2013-2015 door de Unie van Waterschappen samen met ecologisch adviesbureau Altenburg & Wymenga, WUR, de Zoogdiervereniging en H&k Waterkeringbeheer. De gewenste modeluitkomsten uit deze studie helpen om de metingen aan schade uit de veldproef nader te interpreteren en daarmee de waarde van de veldproef verder vergroten.

De model studie beoogde de data uit het vangstregistratiesysteem te benutten om:

1. het effect van bestrijding op populatieomvang te schatten,
2. de inspanning te bepalen die nodig is om een populatie omlaag te brengen of op een bepaald niveau te behouden, en
3. de populatieniveaus voor een groot aantal gebieden, ten minste de 117 atlasblokken uit de landelijke veldproef, objectief te bepalen.

De methode berust op een vergelijking van een viertal modellen die de populatie-dynamiek van de Muskusrat beschrijven en in complexiteit van elkaar verschillen. Gezocht is naar het best passende model bij de beschikbare gegevens, de landelijke vangstregistratiedata. Hierbij is een schattingsprocedure benut die bekend staat als het Kalman filter. In vergelijking met eerdere modellen aan muskusratten populaties in Nederland is in de onderhavige studie een veel groter ruimtelijk en temporeel detail niveau gekozen. Hierdoor zijn de beschikbare gegevens beter benut en is de toepassing voor de praktijk vergroot.

Het model dat uiteindelijk is geselecteerd als best passend bij de data maakt voor de voorspellingen gebruik van gegevens op atlasblok-niveau, tijdstappen van vier seizoenen per jaar en een vangstvergelijking waarbij de vangst toeneemt met de inspanning, maar ook afhangt van populatie dichtheid. Dichtheidsafhankelijkheid speelt een rol in het model.

De belangrijkste bevindingen uit de analyse zijn dat vangstinspanning - in termen van tijd- één van de belangrijkste factoren is om de variatie in vangst te kunnen verklaren. Bestrijding kan leiden tot lagere aantallen muskusratten, mits de inzet voldoende groot is.

Een tweede belangrijke bevinding is dat alles er op wijst dat de aantallen muskusratten in Nederland momenteel relatief laag zijn. Over de gehele studie periode gezien is de omvang van de populatie in 2015 het laagst.

Om een populatie stabiel te houden is het zaak om de natuurlijke aanwas af te vangen. Die aanwas is afhankelijk van het aanwezige populatie niveau. Het is om die reden aannemelijk

dat er minder inspanning nodig is om een lage populatie stabiel te houden dan een middelgrote of grote populatie en de modeluitkomsten zijn daar mee in overeenstemming. De parameterschattingen in deze studie wijzen er verder op dat emigratie en immigratie niet verwaarloosd moeten worden. Dit heeft gevolgen voor de ruimtelijke schaal waarop eventuele bestrijding georganiseerd moet zijn om effectief te wezen.

De uitkomsten van het model dienen met zorg te worden bediscussieerd en beoordeeld, in het bijzonder waar het gaat om de interpretatie en de verdere toepassing er van. Biologisch inhoudelijk levert het aanknopingspunten om de muskusratten populatiedynamica beter te begrijpen. Statistisch gezien is het een stap voorwaarts in het terug-reconstrueren van populatie-omvang bij zoogdieren. De modellering in deze studie is een belangrijke stap vooruit maar is niet het eindpunt. In de aannames en modellen zijn verdere verbeteringen mogelijk, waarbij samenwerking met experts van vanuit de bestrijding en van buiten de wereld van Muskusratten zeer gewenst is.

Twee voor de hand liggende verdere stappen zijn:

a het uitleggen van de modellen en de belangrijkste bevindingen aan bestrijders en management van de waterschappen en bestrijdingsorganisaties, om met hen de sterke en zwakke punten van het model te leren kennen;

b een analyse en interpretatie van de correcties in ruimte en tijd die iedere tijdstap en in ieder atlasblok gemaakt zijn door het Kalman filter.

Het model voorziet de bestrijding van een gedetailleerd gereedschap om op gebiedsniveau de gevolgen van verandering in intensiteit van bestrijding op het populatieniveau te bepalen. Daarnaast kunnen de objectieve aantalsschattingen gebruikt worden om de relatie te onderzoeken tussen aantallen en schade door graverij. Gezamenlijk is deze informatie niet alleen buitengewoon nuttig in het publieke debat over de bestrijding, maar ook bij een beter onderbouwde en meer bedrijfsmatige uitvoering daarvan.

DE STOWA IN HET KORT

STOWA is het kenniscentrum van de regionale waterbeheerders (veelal de waterschappen) in Nederland. STOWA ontwikkelt, vergaart, verspreidt en implementeert toegepaste kennis die de waterbeheerders nodig hebben om de opgaven waar zij in hun werk voor staan, goed uit te voeren. Deze kennis kan liggen op toegepast technisch, natuurwetenschappelijk, bestuurlijk-juridisch of sociaalwetenschappelijk gebied.

STOWA werkt in hoge mate vraaggestuurd. We inventariseren nauwgezet welke kennisvragen waterschappen hebben en zetten die vragen uit bij de juiste kennisleveranciers. Het initiatief daarvoor ligt veelal bij de kennisvragende waterbeheerders, maar soms ook bij kennisinstellingen en het bedrijfsleven. Dit tweerichtingsverkeer stimuleert vernieuwing en innovatie.

Vraaggestuurd werken betekent ook dat we zelf voortdurend op zoek zijn naar de 'kennisvragen van morgen' – de vragen die we graag op de agenda zetten nog voordat iemand ze gesteld heeft – om optimaal voorbereid te zijn op de toekomst.

STOWA ontzorgt de waterbeheerders. Wij nemen de aanbesteding en begeleiding van de gezamenlijke kennisprojecten op ons. Wij zorgen ervoor dat waterbeheerders verbonden blijven met deze projecten en er ook 'eigenaar' van zijn. Dit om te waarborgen dat de juiste kennisvragen worden beantwoord. De projecten worden begeleid door commissies waar regionale waterbeheerders zelf deel van uitmaken. De grote onderzoekslijnen worden per werkveld uitgezet en verantwoord door speciale programmacommissies. Ook hierin hebben de regionale waterbeheerders zitting.

STOWA verbindt niet alleen kennisvragers en kennisleveranciers, maar ook de regionale waterbeheerders onderling. Door de samenwerking van de waterbeheerders binnen STOWA zijn zij samen verantwoordelijk voor de programmering, zetten zij gezamenlijk de koers uit, worden meerdere waterschappen bij één en het zelfde onderzoek betrokken en komen de resultaten sneller ten goede van alle waterschappen.

De grondbeginselen van STOWA zijn verwoord in onze missie:

Het samen met regionale waterbeheerders definiëren van hun kennisbehoeften op het gebied van het waterbeheer en het voor én met deze beheerders (laten) ontwikkelen, bijeenbrengen, beschikbaar maken, delen, verankeren en implementeren van de benodigde kennis.

STATISTICAL ESTIMATION OF MUSKRAT ABUNDANCE

INHOUD

ACKNOWLEDGEMENT

We would like to acknowledge the staff of the muskrat control organisation from the Dutch Water Authorities for the confidence to work with the data from their catch registration system. Especially we thank many of the team leaders and trappers for patiently explaining us how they work and for providing advice in how to interpret the data. Finally, a big thank you to our colleagues at the University of Amsterdam, Wageningen University and Altenburg & Wymenga for engaging in discussions with us about this work.

1

INTRODUCTION

1.1 ESTIMATING MUSKRAT ABUNDANCE FROM CATCH-EFFORT DATA

The estimation of animal abundance from catch-effort data is a difficult but promising field. The method would enable valuable objective estimates for species with specific aims in conservation or pest-management. Efforts for reconstructing population size this way are well known in fisheries biology[1] (Lassen & Medley 2000), and the methodology has to a limited extent been applied to small (Broms et al. 2010; Skalski et al. 2011; Gast et al. 2013) and large game and/or other mammals (Novak et al. 1991; Schmidt et al. 2005; Ueno et al. 2009). In most cases the procedure requires information on age-structure in the harvest. Reed and Simons (1996a; b) suggest a method that is not dependent on age structure and so do Matis et al. (1996; 1999) and Bos et al. (2009, 2010).

Matis et al. (1996) analysed muskrat trapping data from 1969-1991 at the level of whole provinces for the Netherlands, with a stochastic Birth-Death Migration model. Similar data now exist for muskrats in the Netherlands in an even more elaborate dataset, with information on catch and effort by professional trappers on a national scale, but with detailed grain. With these data, aggregated to yearly levels, Bos et al. (2009) tested the hypothesis that muskrat population size could be reconstructed at a local level. The aim is to estimate current population sizes and to judge whether local population levels in the Netherlands are regulated by trapping under the current harvest rates. Bos et al. (2009) indeed managed to do so, but only in about half the number of datasets the models converged. They argued that successful convergence, the precision and the accuracy of the population back-casts will possibly be enhanced by taking into account seasonality, age –structure or spatial context. Besides, they advised to quantify accuracy with more direct methods that estimate population levels.

1.2 MUSKRAT CONTROL IN THE NETHERLANDS

This type of modelling is functional within the applied context of the existing programme for muskrat control in the Netherlands. Details of this control programme are given in Barends (2002) and van Loon et al. (2017). Bos et al. (2016) argue that muskrat control can affect muskrat population size, and provide evidence for this from theory, practice and historical data. They elaborate upon the factors that contribute to effective population control, amongst which the amount of effort. Nonetheless, given the strong public debate on the matter (Zandberg, de Jong & Kraaijeveld-Smit 2011), it would be helpful to have additional information on the effect of catch effort on population size, and the catch effort required to maintain a given population size. Such information may be provided by the models that are subject of this paper.

1 SCA-models statistical Catch at Age; CPUE Catch per Unit Effort; Statistical Population Reconstruction and Virtual Population Analysis.

1.3 LARGE FIELD EXPERIMENT

Recently a large scale management experiment was performed in the Netherlands to study the effect of manipulating harvest intensity of muskrat (catching effort, or time invested trapping,) on potential and actual damage of dikes and waterfronts. The experiment took place during the years 2013-2015 in 117 areas (5*5 km 'atlas squares') selected in a stratified random way. Aim of the experiment was to obtain insight into the costs and benefits of harvesting at different levels of intensity for different seasons, landscapes and population densities, as well as to gauge the publicly acceptable level of damage per region of interest. These aspects are identified as the major gaps in knowledge that hamper proper policy making for muskrat management at the moment. The background of the field experiment is described in a theoretical paper on population dynamics of muskrats in the Netherlands (Bos & Ydenberg 2011). During the study experimental variation was created in possibly one of the most influential independent variables (time invested), and additional information was gathered on sex ratio, age of muskrats caught and –in a limited number of atlas squares- population level. Non-biological data collected within the framework of this field experiment comprise systematic measurements of damage to dikes and banks in the 117 experimental atlas squares. The latter data will have value to illustrate a presumed relation between damage by burrowing and muskrat population density, if objective estimates of density could be obtained. Against this back-ground, the recent field experiment provided additional motivation to elaborate upon the models discussed above: a functional model has the potential to enhance the information gain from the experiment, if only because it would enable us to relate frequency of muskrat damage to muskrat population size.

1.4 AIM

We aim to elaborate upon the Statistical Population Reconstruction initiated for muskrat by Matis et al. (1996) and Bos et al. (2009), by formulating models that capture the essence of the dynamics. On the fundamental side our aim is to move forward with these techniques for estimating animal abundance and other relevant population parameters. On the applied side we aim to quantify to what extent muskrat management is affecting population dynamics, and to estimate the parameters of catching efficiency at different population levels and landscapes that are required for optimising the muskrat control programme with regard to financial, ethical and other (public) considerations.

The work should lead to an enhanced use of the catch-registration system to estimate:

- the effect of catch effort on population size
- the required catch effort to reduce a population size to a prescribed level or to maintain a given population size
- the population size in the 117 experimental atlas squares, in order to relate this to muskrat damage observed during the large scale field experiment.

2

METHODS AND MODELS

2.1 DATA

We have been using the data collected by the Dutch Water Authorities (Unie van Waterschappen, UvW) in their catch-registration system. The available catch-registration data comprises the number of catches, the catch effort (nr of hours spent per km of waterway) per season and 5 by 5 km grid squares (henceforth called atlas squares). These data are used to derive relations between catch effort (hours per km water way), population size, population density (nr individuals per km water way) and number of individuals caught. In this study the data for the period 1987 till 2016 are used. The dataset were split into subsets containing (i) 80% of the atlas squares used to train the model; and (ii) 20% used to evaluate model performance.

2.2 MODELS

A set of models, ranging from simple (essentially without ecological dynamics) to more complex (including ecological dynamics) was developed, parameterised, calibrated, and evaluated on the available data.
The aim of the models is to predict the catch under different levels of effort as implemented by the management. Hence, this relation is explicitly modelled in an observation-equation. The ecological dynamics are modelled by a set of difference equations (i.e. the population size at a certain point in time in a certain atlas square depends on the population size in the previous time period and neighbourhood (i.e. the eight surrounding atlas squares)). The temporal resolution in these equations is the season (four seasons per year: winter, spring, summer and autumn) and the spatial resolution is an atlas square. Within a single time-step redistribution in space is possible from an atlas square to its direct surroundings.

Models of increasing complexity were evaluated against the simpler counterparts and the predictive performance on the evaluation data. The various models evaluated used the same population dynamics, but differed with respect to the observation equation, i.e. an equation describing the relation between population state variables, model forcing (like effort) and catch. The following observation equations were compared:

1. constant catch rate (independent of effort)
2. catch increasing with population density (independent of effort) to a ceiling
3. catch proportional to effort (independent of population density)
4. catch both increasing with population density to a ceiling and proportional to effort

The corresponding equations are:

$$y_k = ccr\ pd_{k-1} \quad (1)$$

$$y_k = cm\ pd_{k-1} / \left(hcd + pd_{k-1}\right) \quad (2)$$

$$y_k = cpe\ eff_k \quad (3)$$

$$y_k = eff_k\ crm\ pd_{k-1} / \left(hcd + pd_{k-1}\right) \quad (4)$$

Where y_k is the predicted catch, pd_k the muskrat population density (pd_k is the population size by the suitable habitat (the length of the water-edges in km): $pd_k=p_k/sh$), ccr the constant catch rate parameter, cm the maximum catch (disregarding effort) at high densities, crm the maximum catch rate per unit effort at high densities, hcd the density at which half the catch rate per unit effort is reached, cpe is the average catch rate per unit effort and eff_k the catch effort. The parameters are specified globally, i.e. constant for all atlas squares. The cpe parameter was derived by averaging over the term $crm\ pd_{k-1}/(hcd + pd_{k-1})$, and the ccr parameter was derived by linearising over $crm\ pd_{k-1}/(hcd + pd_{k-1})$.

The population model that provides the estimated population size per season and atlas square (p_k) is unchanged under these different observation equations and was calibrated while using the most extensive equation (4).

The details of the population model are given in Appendix 1. Birth rate and survival both depend on population density and are modelled by second order polynomials.

2.3 LINKING POPULATION MODEL AND OBSERVATION EQUATION TO REALITY

A state estimation procedure is used to generate predictions with the population model and observation equations. The specific framework applied here is the ensemble Kalman filter (EnKF). This framework allows integration of the information from the realised catch with the knowledge about population dynamics in a flexible yet structured manner, and has been implemented in comparable ways by e.g. Reed and Simons (1996), Bolker (2007) and Buckland et al. (2007).

The EnKF works with an ensemble of predictions from the population model. At the point where observations on catch are available, the predicted catch is compared to the realised catch and used to update the predicted values. The variability among the ensemble members is used to quantify the model prediction uncertainty, which directs the degree to which the model results are corrected by the realised catch. The exact implementation of the algorithm is described in Appendix 2.

2.4 MODEL CALIBRATION AND EVALUATION

The population model and observation equation are calibrated by using the data from the period 2000 to 2010. Initial parameter ranges have been specified based on information from other modelling studies on muskrat population dynamics (Bos et al. 2009; Bos & Ydenberg 2011). These ranges are given in Table 1.

TABLE 1 INITIAL PARAMETER RANGES, USED FOR MONTE CARLO BASED MODEL CALIBRATION AND FINAL PARAMETER RANGES, USED IN THE MODEL SIMULATIONS. ACRONYMS AND MEANING OF EACH PARAMETER IS GIVEN IN TABLE 2, BUT IS ALSO EXPLAINED IN THE MAIN TEXT OR IN APPENDIX 1

	Initial parameter ranges		Final parameter ranges		
Parameter	Lower bound	Upper bound	Lower bound	Upper bound	Chosen value for prediction runs
Catch:					
crm	1	10	6.3	9.6	7.1
hcd	10	50	10.6	14.7	12
Birth rate:					
brmax	3	12	5.5	7.3	6.2
brdec	0.005	0.02	0.008	0.014	0.01
bropt	10	60	16	21	18
Survival rate:					
sjmax	0.3	0.8	0.56	0.64	0.6
sjdec	0	0.001	0	0.00016	0.0001
sjopt	10	60	34	41	38
sa	0.6	0.9	0.81	0.84	0.83
Spatial exchange:					
erm	0	0.3	0.16	0.23	0.19
hed	0	60	7	16	12

TABLE 2 ACRONYMS, MEANING AND UNITS OF THE MODEL PARAMETERS GIVEN IN TABLE 1 OR IN APPENDIX 1

Parameter	meaning	unit
ccr	constant catch rate	fraction
cm	maximum catch at high densities	n
crm	maximum catch rate per unit effort at high densities	n/h
hcd	density at which half the catch rate per unit effort is reached	n/km
cpe	catch per unit effort	n/h
eff	effort spent on catching	h
brmax	maximum value for birth rate at optimum density	n/km
brdec	decline in birth rate under suboptimal densities	n/km
bropt	population density at which birth rate is maximal	n/km
sjmax	maximum value for juvenile survival at optimum density	fraction
sjdec	decline in juvenile survival under suboptimal densities	fraction
sjopt	population density at which juvenile survival is maximal	n/km
sa	adult survival rate	fraction
erm	maximum exchange rate of animals moving between patch and surrounding cells	fraction
hed	population density at which half the maximumexchange rate is reached	n/km

2.5 SELECTING THE MOST ADEQUATE MODEL FROM THE ALTERNATIVE OBSERVATION EQUATIONS

The most suitable observation equation (see eq. 1 to 4) is selected based on a comparison between realised and predicted catch for the twenty hold-out atlas squares. These were squares in which catches were made during the period 1987-2016. The model with the smallest root mean squared difference between realised and predicted catch is selected as the model best describing the system.

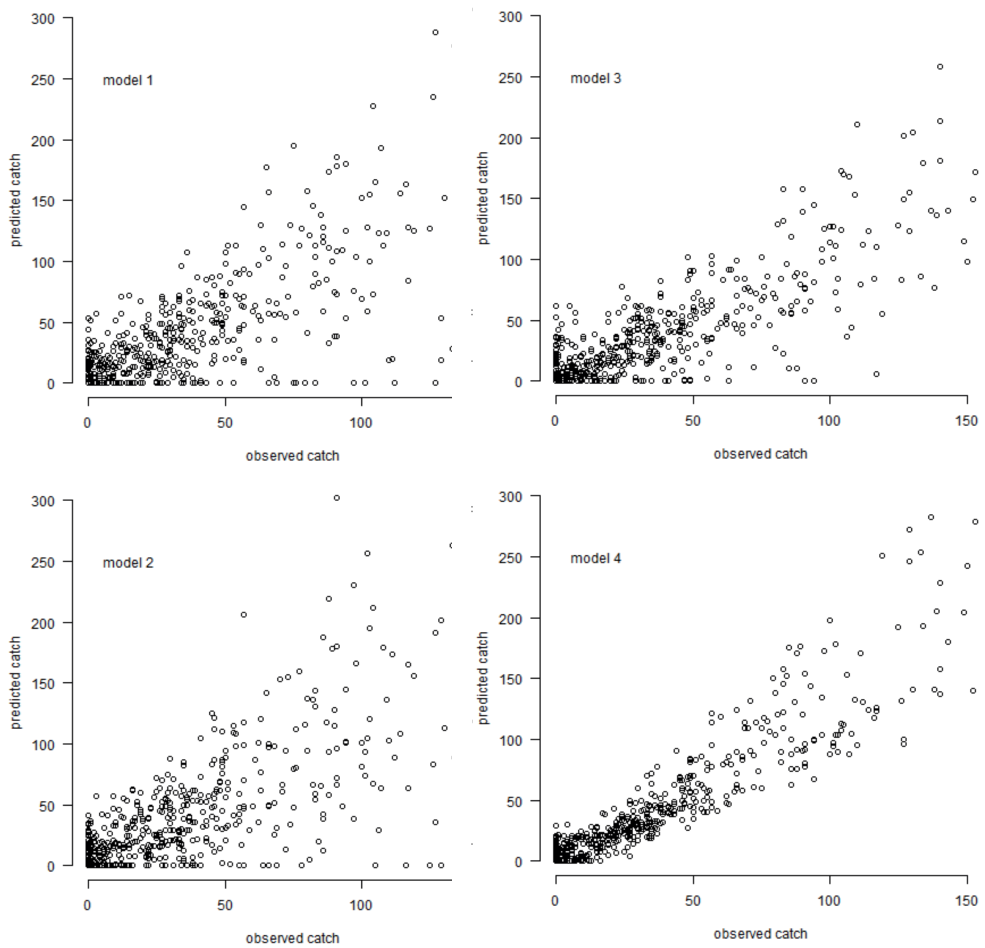
3

RESULTS

3.1 THE PERFORMANCE OF DIFFERENT MODELS

The models with the four different observation equations were compared with respect to their ability to predict realised catches in the hold-out atlas squares. The results of this comparison are shown in Figure 1. The figure shows a tighter relation between predicted and observed catch for the model using measurement equation 4 (see the scatter plots as well as the RMSE and explained variance). Using this model, 96% of the variance in the catch is explained (RMSE: 36), while the next best model (equation 3) explains 87% (RMSE: 37). Applying the model involving only density explains 81% of the variance (RMSE: 49). Omitting effort from the equation and assuming a constant catch rate leads to a considerable drop in predictive power: with model 1, only 66% of the variance can be explained (RMSE: 53).

FIGURE 1 PREDICTED VERSUS OBSERVED CATCH FOR HOLD-OUT DATA FOR FOUR MODELS. EACH POINT REFERS TO THE CATCH IN ONE SEASON FOR ONE OF THE 20 ATLAS-SQUARES. RELATIVELY FEW POINTS FALL OUTSIDE THE RANGE SHOWN HERE (BUT RANGES ARE RESTRICTED TO SHOW SUFFICIENT DETAIL IN THE SMALLER END



Based on this result, we will apply the model with equation 4 as observation equation to generate predictions and further evaluation.

3.2 POPULATION RECONSTRUCTION

By applying model 4 to the complete data period (1987 – 2016), we obtained an estimate of the population size and a confidence interval around these estimates. Figure 2 shows a time-series of the predicted total muskrat population. The estimated population size in 1987 was 2.4 million (averaged over the 4 seasons). It increased to a maximum of 2.9 million in 1993. From that year onwards, the numbers declined to reach a level of 0.47 million in 2016. At the point where the field experiment started in 2013, the population size was estimated to be 0.56 million muskrats. The inset demonstrates that the correlation between population size and catch is strong below a population size of 0.7 million muskrat (the most recent decade), but was much weaker at high population levels (in the early phase of the data-set).

FIGURE 2 PREDICTED MUSKRAT POPULATION SIZE FOR THE NETHERLANDS WITH 0.95 CONFIDENCE BOUNDS. IN THE UPPER-RIGHT PANEL THE RELATION BETWEEN POPULATION SIZE AND CATCH IS SHOWN

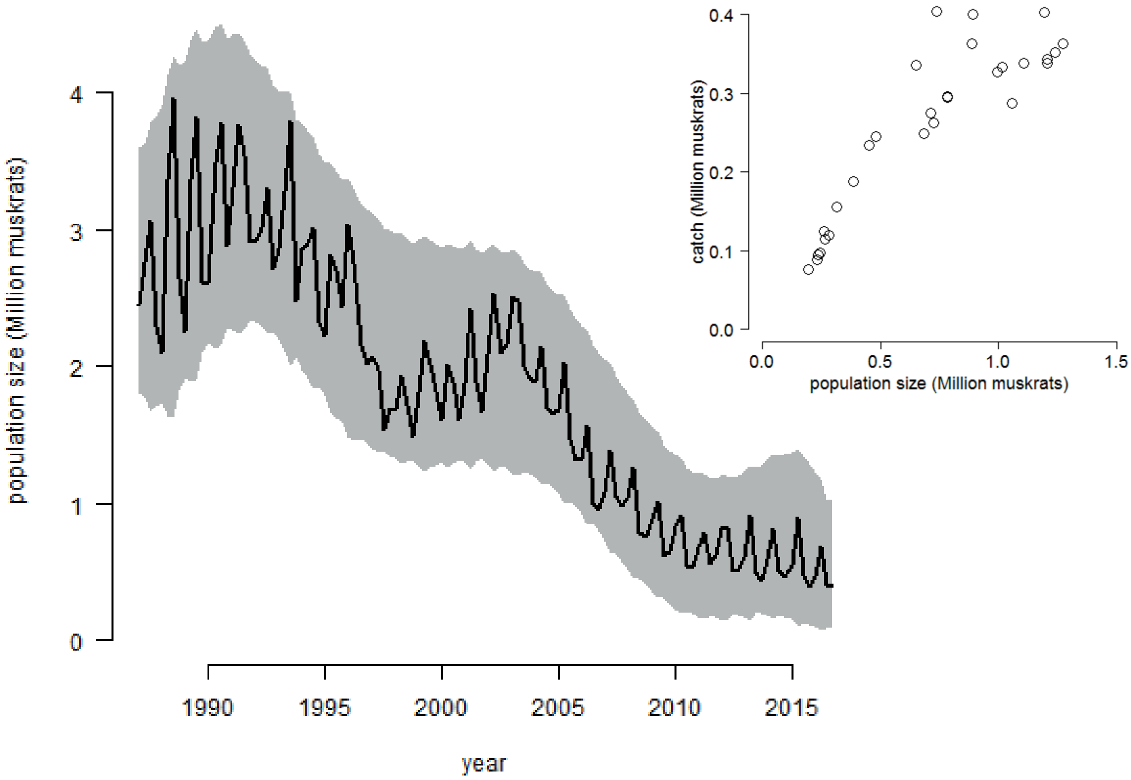


Figure 3 shows the seasonal variation of catch (3A) and relative population size (3B) averaged over the Netherlands. It shows that the catch peaks in winter and autumn. In contrast, estimated population numbers tend to peak in spring while having a low in the autumn (this seasonal pattern is an artefact caused by our implementation of the Kalman filter; we will briefly comment upon it in the discussion).

FIGURE 3 SEASONAL VARIATION IN CATCH (A) AND RELATIVE POPULATION SIZE (B). THE RELATIVE SEASONAL POPULATION SIZE IS THE POPULATION SIZE IN A SEASON DIVIDED BY THE AVERAGE POPULATION SIZE OVER THE ENTIRE YEAR

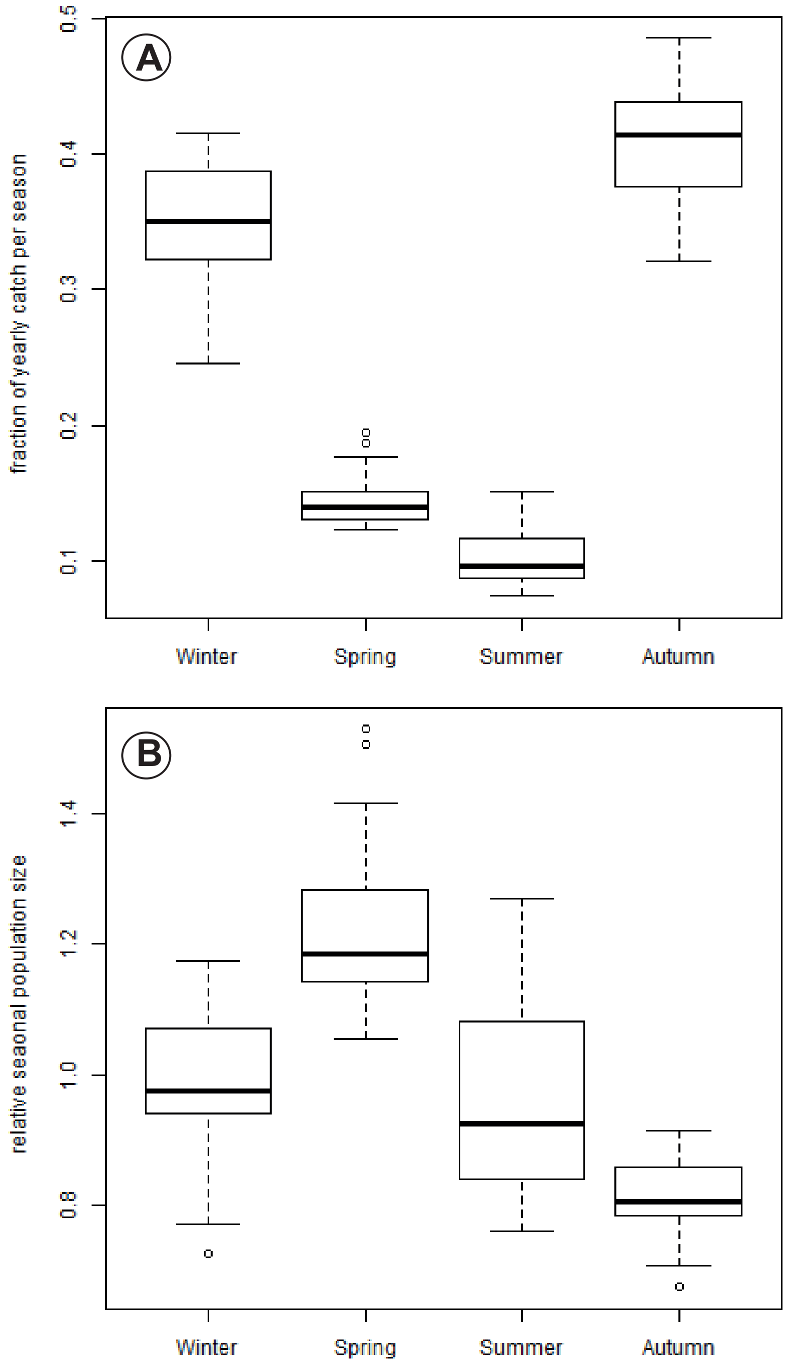
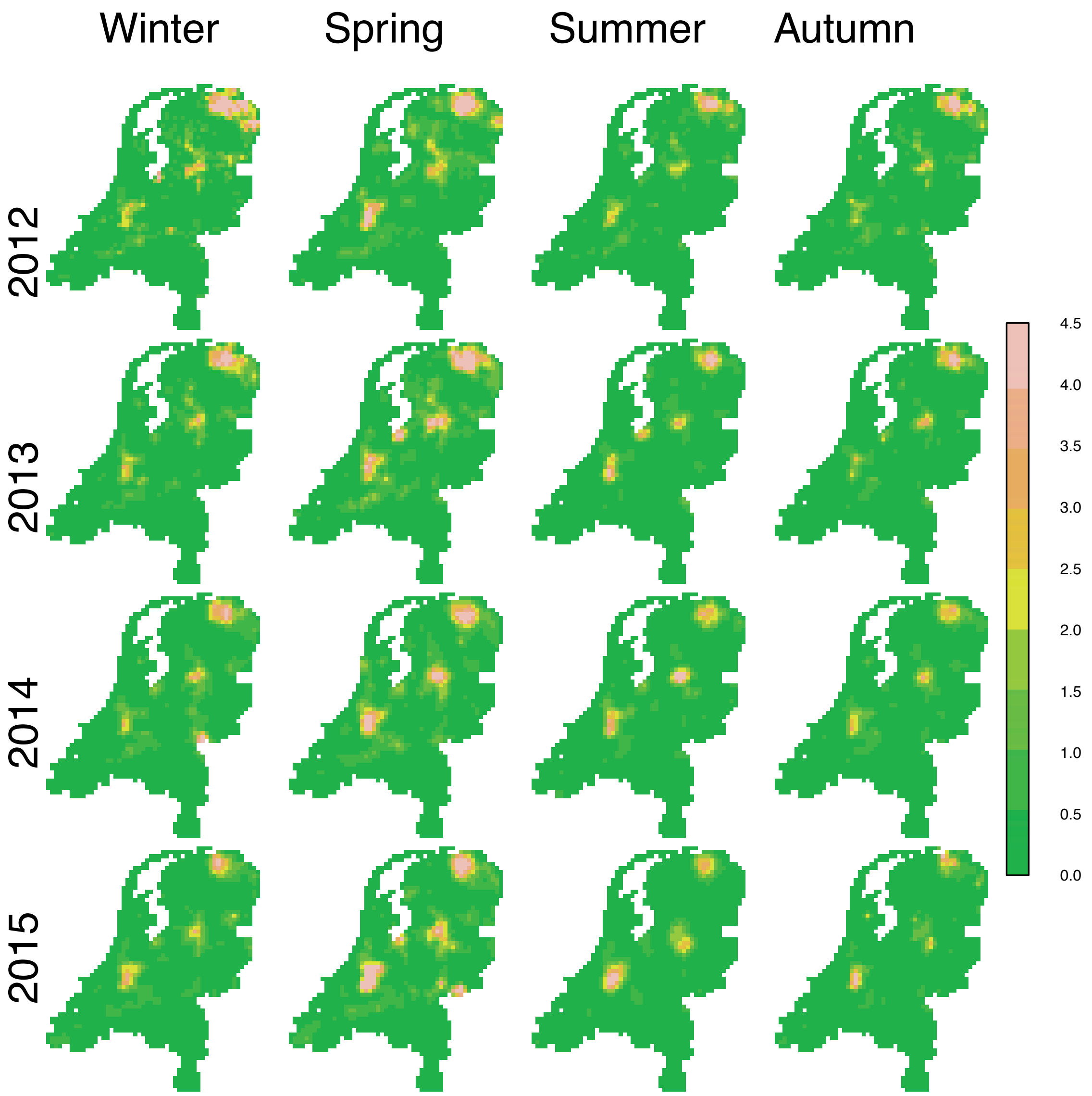


Figure 4 highlights the developments in the years 2012 to 2015. It shows very pronounced local highs, which are sometimes persistent over long periods (south-west of the country), but also decline within a relatively short period (e.g. the region around Zwolle, east of lake IJssel). The population predictions at the level of the atlas squares and seasonal time steps are available digitally (https://surfdrive.surf.nl/files/index.php/s/Cxu6W2dVaZqNyfC).

FIGURE 4 POPULATION MAPS OF MUSKRATS IN THE NETHERLANDS FOR THE PERIOD 2012 TO 2015 (VALUES IN 1000 MUSKRATS PER ATLAS SQUARE). THE WHITE PATCHES ARE PEAK-VALUES ABOVE THE MAXIMUM VALUE OF THE COLOUR SCALE, WHICH REPRESENTS LESS THAN 10% OF THE POPULATION IN THE SPRING PERIOD AND LESS THEN 2% IN THE OTHER SEASONS

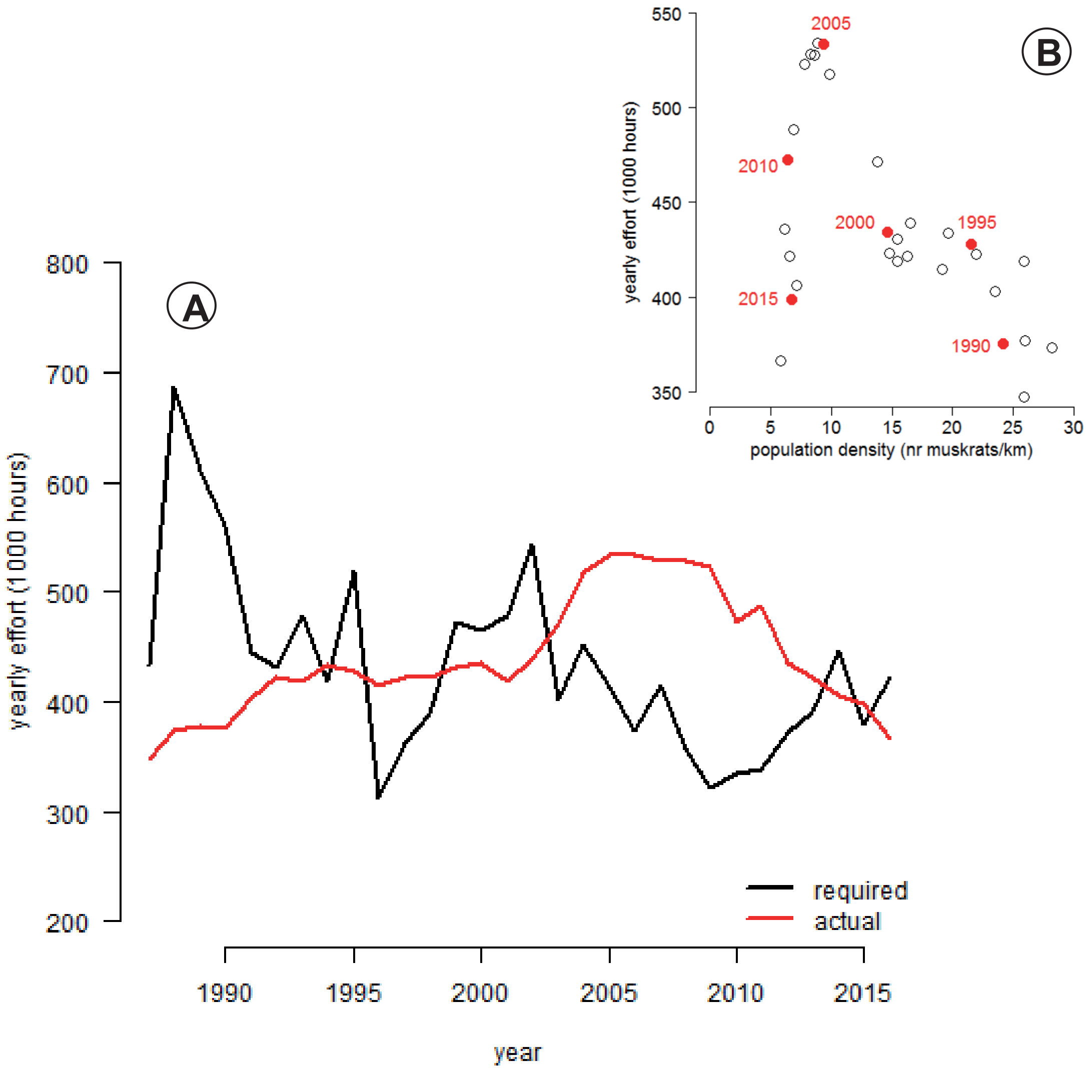


3.3 TRAPPING EFFORT REQUIRED TO COMPENSATE FOR GROWTH

The model allows estimation of the required trapping effort to compensate for net population growth (i.e. the increment caused by birth and survival, not including spatial exchange and catch, step; see Appendix 1, eq. 7b). This required trapping effort is not constant over time as it depends, amongst other things, on the population density. In Figure 5 the historical time series of trapping effort ('actual') is presented in comparison to what was required. It can be seen that from 1995 till 1998, and especially from 2003 until 2014 the trapping effort has been considerably higher than what was required for compensation. This has, on average, led to the more or less continuous population decline presented in figure 2.

Figure 5 also shows the actual trapping effort and population densities for all years in the upper right panel of the graph (panel B, selected years 1990, 1995, 2000, 2005, 2010 and 2015 have been labeled). Panel B emphasizes that -in practice- at low estimated population density, a lower effort is required than what was needed to bring the population down.

FIGURE 5 THE REQUIRED EFFORT FOR COMPENSATION OF NATURAL GROWTH ('REQUIRED') AND ACTUAL YEARLY EFFORT ('ACTUAL'), AVERAGED OVER THE NETHERLANDS. IN THE UPPER-RIGHT PANEL THE RELATION BETWEEN ESTIMATED POPULATION DENSITY AND ACTUAL YEARLY EFFORT IS SHOWN

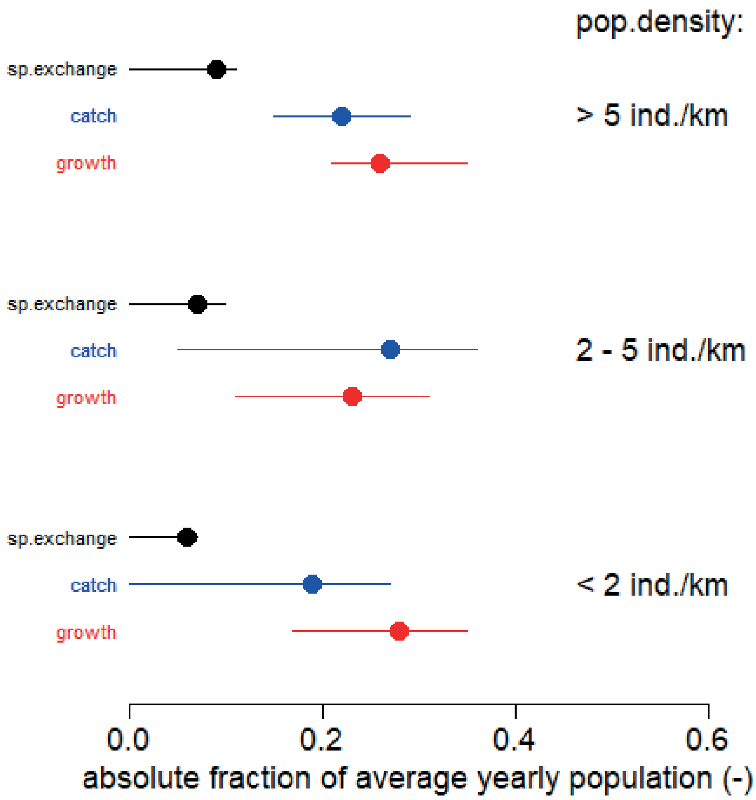


3.4 THE RELATIVE IMPORTANCE OF THE VARIOUS COMPONENTS IN RELATION TO SPATIAL EXCHANGE

Apart from natural growth and catch, the model includes a component describing spatial exchange. The size of this term is driven by the gradient in local population density (focal atlas square relative to its surroundings, appendix 1, eq. 6). Figure 6 shows how the sizes of these three components relate to each other. The values of the components were calculated by dividing the absolute average yearly value of the components by the average yearly population size per atlas square.

The figure shows that the three components have comparable magnitudes, but do nonetheless vary considerably over population density. Striking patterns are the relative importance of catch: it is the largest component at intermediate population densities but considerably smaller than natural growth at low densities. Furthermore, spatial exchange is the smallest component – it increases slightly from 0.06 to 0.07 – but still represents around one third of the size of the natural growth.

FIGURE 6 SIZE OF DIFFERENT COMPONENTS LEADING TO POPULATION CHANGE AT THE LEVEL OF AN ATLAS SQUARE (FOR THOSE SQUARES WHERE ANIMALS WERE PRESENT) DUE TO NATURAL GROWTH (RED), TRAPPING (CATCH, BLUE) AND SPATIAL EXCHANGE BETWEEN ATLAS SQUARES (BLACK). THE HORIZONTAL LINES GIVE THE SPREAD OF THE COMPONENTS AT THE LEVEL OF THE INDIVIDUAL ATLAS SQUARES AND THE CIRCLES GIVE THE AVERAGES FOR THE NETHERLANDS. THE COMPONENTS ARE SHOWN AT THREE LEVELS OF POPULATION DENSITY: ATLAS SQUARES WITH LESS THAN 2 ANIMALS PER KM (37% OF THE CASES), 2 – 5 ANIMALS PER KM (23% OF THE CASES) AND MORE THAN 5 ANIMALS PER KM (40% OF THE CASES)



4

DISCUSSION

This section discusses the main findings, the reliability of the models presented, the use of the models in management, and what needs to be done next.

4.1 MAIN FINDINGS

The modelling exercise has resulted in a certain number of steps forward:

1. we now have independent and objective estimates on muskrat numbers per season at a high spatial resolution;
2. we have obtained insight in the degree to which local population levels are regulated by trapping; and
3. we have estimated the relative importance of immigration and emigration (together, 'migration').

It appears that trapping indeed regulates numbers: Models that assume catch to be dependent upon effort result in a better fit than the same models in which catch is assumed to be independent of effort. This is highly relevant since it is one of the basic premises behind the muskrat control programme, the other ones being that higher muskrat numbers are associated with higher risks for public safety and that these risks can best be averted by reducing numbers. The finding is consistent with those in van Loon et al. (2017).

Migration may be quite substantial. The component describing spatial exchange between atlas squares is clearly smaller than catch or natural growth, but still represents around one third of the size of natural growth (see Figure 6) when differences in population density are high. The process of migration is of interest because of its consequences for spatially differentiated management of muskrat. The greater the role of migration, the more costly it will be to allow local exceptions to an otherwise uniform strategy of eradication or control in space.

The estimated muskrat numbers are themselves valuable in several ways: they serve to evaluate costs of management under different intensities of control, they may be linked to frequency of damage by muskrat to dikes and banks (as measured by van Hemert, in Bos et al. 2016), and they may be linked to other biological processes such as vegetation development in relation to herbivory (c.f. Vermaat, Bos & Van Der Burg 2016). With regard to costs of management it is highly interesting that the population continued to decline over the years 2005-2015, in spite of a decline in actual effort. Generally, the required effort was estimated to decline parallel to a declining population (Figure 5). This corroborates the finding by van Loon et al. (2017) that maintaining control becomes progressively cheaper at lower population density. Such knowledge of the relationship between costs and population size is a prerequisite for the proper calculation of an optimal control strategy (Clark 2010). The model itself can be an important tool in the planning of future muskrat control.

In comparison to previous population back-casts for the same population of muskrat (Matis & Kiffe 1999; Bos et al. 2010), the current model is biologically more apt, because it includes spatial context, seasonality and age structure. The model is more precise in terms of space and time and makes better use of the detailed data available. With regard to age, no field data are available as yet at the national scale, so the added value of including it in the model is quite limited. However, the inclusion of age structure makes the model better prepared for a future situation in which muskrat control is monitored with greater precision.

4.2 RELIABILITY OF MODELS

Technically there are an infinite number of alternative model formulations possible. This number is of course greatly reduced by restricting the options to those that are considered 'biologically relevant' based upon current knowledge of the system. We have tested many different alternatives, varying options at parameter level, varying choice of formulae, and varying seasonal structure. Out of those we have presented a selected subset in the above[2]. However, given the work process chosen, we have not arrived at systematic evaluation of all those model alternatives that we consider relevant. Another reason is that some model alternatives did not converge, which means that the calibration procedure did not arrive at a suitable set of parameters. There is one relationship in particular that would require more rigorous testing in our view. This is the relation describing the nature of density dependence in population growth. Therefore, an uncertainty remains whether, perhaps, alternative model formulations exist that might have predicted the patterns in realised catch, and the underlying parameters and population size, more precise or more accurate than the best model presented above.

The reliability of the models that converged has been judged by comparing observed and predicted values for a subset of data. This procedure allowed us to rank the models in terms of predictive performance. The models clearly differed in that sense, showing that including migration, and taking into account trapping effort results in models that better fit the data. Nonetheless, the different models all yield similar patterns in space and time in the sense that the peak in muskrat numbers in the Netherlands is predicted to coincide with the peak in catches and that recent years are characterised by much lower muskrat numbers than the previous four decades.

A qualitative evaluation of the pattern of catches over time results in a strange inconsistency. The number of animals is predicted to peak in spring, while numbers should actually build up over summer and peak in autumn instead. This phenomenon is the result of the Kalman-filter. As is explained in appendix 2, the Kalman filter produces an updated matrix of model states each subsequent time-step. The difference between the initial expected values and the updated values are called 'innovations'. It manifests itself, amongst others, as an 'immigration' from abroad. Under the current implementation of the model and this filter these innovations tend to artificially affect relative population sizes in the different seasons. In our view the innovations are key to a better understanding about those factors or boundary conditions that are not yet included in the model. Proper interpretation of the innovations should lead to further model improvement.

2 We learned, for example, that a sub-division into four seasons resulted in models that were easier to both parameterize and calibrate than a subdivision in 13 periods (the resolution of the original data).

A strong correlation was observed between population size and catch below a population size of 0.7 million muskrat (the most recent decade), while a much weaker correlation was present at high population levels (in the early phase of the data-set). This may entirely be related to the fact that the capture process is modelled by a Holling II function (eq. 4, a line increasing towards a ceiling), although this is confounded with the possibility that the muskrat control organisations were less consistent in data administration or less effective in the early phase of the data-set.

According to the estimated parameter values the movements of muskrat between atlas squares is substantial in comparison to net population growth. This is in apparent contrast to findings by LaHaye et al. in Bos et al. 2016, who studied muskrat movements in the landscape using marked individuals and radio-telemetry. They found that most muskrat were live-trapped and finally kill-trapped within their own territory. Less than 30% of the individuals was trapped over a distance of more than 500 meter. This is probably to be explained by the fact that the time available for marked individuals to actually move before being re-captured was limited to less than three months and the majority of individuals in their study were adults that had settled already. It is however highly consistent with results obtained from theoretical analysis by Matis et al. 1996 and Matis & Kiffe (1999). These authors, when modelling the spread of muskrats in 11 provinces in the Netherlands during their invasion from 1968 to 1991, showed that stochastic birth-death-migration (BDM) models with migration typically fit the catch data better than the corresponding models without migration.

4.3 THE USE OF THE MODELS IN MANAGEMENT

The general findings of the modelling exercise are of direct relevance for application in muskrat management. As mentioned above, they underpin one of the basic premises behind the muskrat control programme, that muskrat control leads to lower muskrat numbers. The model results are furthermore consistent with the idea that the required trapping effort to maintain a given population size declines with population density. This can be interpreted as an incentive to strife for very low population sizes or even eradication, rather than intermediate population levels in those regions where muskrat population control is chosen as the prevalent management tool to maintain public safety.

Ideally, the best models are to be used to compare different scenario's of management. This can and should be done, because it will help to think quantitatively and support management decisions in a transparent way. The value of the comparisons will however be much higher if the model has been subject to rigorous inspection for validity and robustness first. Especially at the extremes of population density, the realm of specific extrapolations and comparisons of management scenarios, model results can be quite different depending on the nature of the density dependent relationship in population growth that is assumed. There are two main alleys for such rigorous inspection. The first is to explain the models and their main results to trappers and other staff of the Dutch Water authorities, especially the muskrat control organisations. Together with them an inventory of strengths and weaknesses should be made as well as a decision which weaknesses are too important to ignore. The second is to analyse and interpret the corrections that are made to the model in each time step in each atlas square by the Kalman filter (these are the so-called 'innovations'). The innovations point directly at times and places where the model goes wrong, which will surely lead to greater understanding.

4.4 RECOMMENDATIONS

Carefully study the nature and the size of the 'innovations', i.e. the corrections made to model predictions by the Kalman filter. Try and identify systematic patterns that may be used to improve upon the model.

Compare predictions for 2016 made by the current model, calibrated with data until 2015, with predictions made by staff of the UvW for that same year.

Use the model to compare scenario's of management. Design scenario's that are relevant for muskrat control in practice, such as a 'uniform' versus a 'guided' allocation of effort. Illustrate what will happen when effort is diminished too soon and how much effort would be required for complete removal.
It would also be of interest to show the correlation between CPUE (catch per unit effort, in Dutch vangsten/uur shortened as v/u) and population size to settle an old discussion about the value of the parameter 'vangsten per uur'.

Acquire technical input (in terms of ICT knowledge) to further optimise the software and its design in such a way that multiple biologically relevant models can be compared amongst each other in a systematic way. It is also desirable that other people than the designer-group can evaluate alternative model formulations.

Quantify which relation between population density and population growth provides the best model predictions and identify those models that overall perform best.

Evaluate robustness of the models (are the differences relevant from ecological or management perspective?) and perform sensitivity analyses on the best ones (are the model predictions particularly sensitive to certain parameters or relationships?

Improve the monitoring of muskrat control by incorporating the age class of animals captured. Use the data to both calibrate the model and follow the population developments in the field more closely.

4.5 CONCLUSIONS

In this study, several models were formulated to reconstruct the development of the Dutch muskrat population. These models were validated and compared to each other. The results from this model validation and comparison yields the following conclusions:

1 Using Statistical Population Reconstruction we succeeded in quantifying muskrat abundance and relevant population parameters. The results indicate that current muskrat population size is lower than it was in previous decades. The output needs to be judged with caution. This is because the measures of error accompanying the output are conditional upon the assumption that the underlying models is valid.

2 The results of the modelling exercise are promising, but a systematic comparison of all relevant model alternatives has not been achieved. This is because some of the model alternatives we tested failed to converge. Nevertheless, global inferences can be made using the model which are highly relevant for the policy regarding muskrat control.

3 The comparison of models indicates that muskrat control affects muskrat numbers: Models that assume a dependency of catch on effort result in a better fit than the same models in which catch is assumed to be independent of effort [3].

4 The model results are consistent with the idea that the required catch effort to maintain a given population size declines with population density.

5 According to the estimated parameter values, the movements of muskrat between atlas squares cannot be neglected in comparison to net population growth.

6 Further development of the models is certainly possible and worthwhile from a management and a scientific point of view. It will however require technical input to formalise biological hypotheses and embed the current knowledge in an adequate e-science infrastructure which allows to further enhance our understanding.

3 To provide more robust evidence, the remaining parameters need to be estimated separately for models in- and excluding effort, which has not been done here.

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APPENDIX 1

MODEL DESCRIPTION

The muskrat population model is set up as a model is defined on a rectangular grid of 5 by 5 km, which coincides with the spatial observation units in the muskrat-catch registration system (atlas-squares). The model operates with seasonal time-steps, based on a subdivision of a year into winter, spring, summer and autumn (denoted by k with values 1 to 4 respectively). The model distinguishes two state variables: the number of adults (a_k) and juveniles (j_k) and keeps track of these numbers in each cohort for each seΩason k and each spatial unit. In the equations that follow, the spatial units are not explicitly denoted (they apply to both state variables, while the parameters in the model are the same for all spatial units, except for one: the suitable habitat (*sh*). The suitable habitat for the muskrat is given by the length of the water-edges in km.

The year starts in the winter season, when the cohort with juveniles is transferred to the cohort of adults.

$$j_k = 0 \qquad \text{1a}$$

$$a_k = sa\, a_{k-1} + j_{k-1} + se_k\, j_{k-1} - ca_k \qquad \text{1b}$$

here a and j refer to the number of adults and juveniles in the respective season, sa is the adult survival rate (a constant), se_k is the spatial exchange, which depends on the density of the focal spatial unit and its eight surrounding patches. The term ca_k gives the number of adults that are being caught by trapping.

In the spring and summer seasons (k=2 and 3), the equations change due to birth and the absence of migration.

$$j_k = sj_k\, j_{k-1} + br_k\, a_{k-1} - cj_k \qquad \text{2a}$$

$$a_k = sa\, a_{k-1} - ca_k \qquad \text{2b}$$

With sj_k as the juvenile survival rate (density dependent and therefore not constant in space and time), br_k the birth rate (also density dependent) and cj_k the number of juveniles that are being caught by trapping.

In the autumn season (k=4), the system switches again:

$$j_k = sj_k\, j_{k-1} + se_k\, j_{k-1} - cj_k \qquad \text{3a}$$

$$a_k = sa\, a_{k-1} + se_k\, a_{k-1} - ca_k \qquad \text{3b}$$

With all parameters as previously explained. Note there is spatial exchange modelled in autumn for juveniles and adults

The total population size in each period is the sum of the number of juveniles and adults (p_k=a_k+j_k) and the population density is calculated by dividing the population size by the suitable habitat (the length of the water-edges in km): pd_k=p_k/sh.

The birth rate at any given time depends on the population density by a second order polynomial:

$$br_k = -brdec\left(pd_{k-1} - bropt\right)^2 + brmax \quad (4)$$

where the parameters are set to $brdec = 0.01$, $bropt=20$, and $brmax=6$. The parameter $bropt$ specifies the density at which the maximum birth rate occurs, $brmax$ is the maximum birth rate at optimum density and $brdec$ is the decline in birth rate under suboptimal densities.

The survival rate for juveniles is also given by a second order polynomial:

$$sj_k = -sjdec\left(pd_{k-1} - sjopt\right)^2 + sjmax \quad (5)$$

where the parameters are set to $sjdec = 0.0001$, $sjmax=40$, and $sjmax=0.6$. The parameter $sjopt$ specifies the density at which the maximum survival rate occurs, $sjmax$ is the maximum survival rate at optimum density and $sjdec$ is the decline of survival rate (a general mechanism for this at low levels may – for example – be due to increased predation pressure, at higher levels this may be due to competition and disease). Note that the survival rates are defined per season, so a survival on a yearly basis is $0.6^4=0.13$ at best for a juvenile, the value for seasonal survival for adults (*sa*) is fixed at 0.85.

The spatial exchange is given by a rectangular hyperbola (saturation curve):

$$se_k = erm\left(pd_{k-1} - Apd_{k-1}\right)/(hed + \left(pd_{k-1} - Apd_{k-1}\right)) \quad (6)$$

with erm a fixed exchange rate, specifying the fraction of individuals that can move between a patch and its surroundings. This exchange rate is achieved at very high differences in density between a focal patch and the average population density in its surrounding patches ($pd_{k-1}-Apd_{k-1}$). The parameter hed specifies the population density gradient at which 0.5 *er* is reached.

Finally, the estimated catch is described by the models given in the main text (equations 1-4, in model 4 it is a rectangular hyperbola:

$$y_k = eff_k\, crm\, pd_{k-1}/\left(hcd + pd_{k-1}\right) \quad (7a)$$

with y_k the predicted catch, based on pd_{k-1} and a number of parameters. The term eff_k is the effort spent on catching (field hours), crm the maximum catch rate per unit effort at high densities, and hcd the density at which half the catch rate per unit effort is reached. A value of 0.8 was used for crm and a value of 40 for hcd.

Ultimately, the predicted catch is compared to the realised (observed) total catch c_k. The realised catch c_k is distributed over ca_k and cj_k proportionally to the relative amounts a_k and j_k.

To determine the trapping effort that would be required to compensate for natural growth ($ceff_k$), the net population increment after survival and birth without catch can be calculated (see e.g. eq. 2a and 2b) and substituted for y_k in equation 7a. Reorganising this equation leads to an expression for $ceff_k$ (see eq. 7b)

$$ceff_k = max\left(br_k\, a_{k-1} + sa\, a_{k-1} - a_{k-1} + sj_k\, j_{k-1} - j_{k-1}; 0\right) \left(hcd + pd_{k-1}\right)/(crm\, pd_{k-1}) \qquad \text{7b}$$

The term $max(\ldots;0)$ specifies that only population increments are considered. In case of a population decline, the result is set to zero. In that case there is no effort required to compensate for natural growth[4].

4 Note that this algorithm may be a biased estimator since it does not integrate effort over the year.

APPENDIX 2

STATE CORRECTION WITH AN ENSEMBLE KALMAN FILTER

The implementation of the Ensemble Kalman filter largely follows Burgers et al. (1998) and Evensen (2003; 2007).

The equations with a_k and j_k as output (eqs 1 to 3, supported by equations 4 to 6), are combined in a single set of equations to form a population model (also called the state-transition function) which predicts the population at a given time step for every spatial unit (pd_k, equation 8a). This model is linked to a second equation (equation 7), describing the predicted catch under the actual effort if this population density would be present. The latter equation is also called the observation function, and is for clarity repeated as equation 8b.

$$pd_k = f\left(j_{k-1}, a_{k-1}, \dots.\right) \quad \text{8a}$$
$$y_k = eff_k \, cpm \, pd_{k-1}/\left(hcd + pd_{k-1}\right) \quad \text{8b}$$

Both the population model and the observation function as specified by eq. 8a and b give an expected value for a given spatio-temporal unit. A stochastic version of the model adds an error term due to misspecification of the population model, q_k ('model error'); and a combined error due to misspecification in the observation function and sampling error, r_k ('observation error'):

$$x_k = pd_k + q_k \quad \text{with } q_k \sim N(0, \mathbf{Q}) \quad \text{9a}$$
$$y_k = h(x_k) \quad \text{where } h(..) \text{ is the righthand side of 8b} \quad \text{9b}$$
$$c_k = y_k + r_k \quad \text{with } r_k \sim N(0, \mathbf{R}) \quad \text{9c}$$

The covariance matrix **Q** describes the estimate of the model error, and the covariance matrix **Q** describes the error in the observations. The value y_k is what the value of the data would be for the state x_k in the absence of observation errors.

The values for all the spatial units can be combined in a single column vector for all x_k into $\mathbf{x}_k$ (a vector is denoted by a bold non-italic symbol) and for all y_k into $\mathbf{y}_k$. In what follows we will omit the subscript for time (k) for readability (still each of the calculation steps are referring to a single time instant). In addition, we assume that there are *m* spatial units, so that vectors $\mathbf{x}_k$ and $\mathbf{y}_k$ have a length of *M*.

Given an initial estimate of **Q**, an ensemble of N vectors with model errors ($\mathbf{q}_i$) is generated, which give N vectors $\mathbf{x}_i$. The vectors $\mathbf{x}_i$ are used to form the matrices **X** and **XA**

$$\mathbf{X}[:, i] = \mathbf{x}_i \quad \text{10a}$$
$$\mathbf{XA}[:, i] = \mathbf{x}_i - \bar{\mathbf{x}} \quad \text{10b}$$

where the i-th column of **X** consists of the vectors $\mathbf{x}_i$ and **XA** consists of ensemble member i minus the average over all ensemble members ($\overline{\mathbf{x}}$). Both **X** and **XA** have dimension (*N x M*).

Based on the vectors $\mathbf{x}_i$, N ensemble members $\mathbf{y}_i$ are generated via equation 9b. These ensemble members make-up the matrix **H**, and **HA** is built-up column-wise by taking the difference of each individual ensemble member with the average over all ensemble members ($\overline{\mathbf{y}}$).

$$\mathbf{H}[:,i] = \mathbf{y}_i \qquad \text{11a}$$
$$\mathbf{HA}[:,i] = \mathbf{y}_i - \overline{\mathbf{y}} \qquad \text{11b}$$

A matrix **D** is formed by assigning to each column in **D** (denoted by $\mathbf{D}[:,i]$) the vector with observations **c** plus a random vector $\mathbf{r}_i$ from the M-dimensional Normal distribution $N(0, \mathbf{R})$.

$$\mathbf{D}[:,i] = \mathbf{c} + \mathbf{r}_i \qquad \text{12}$$

Subsequently the matrix **P** is calculated by

$$\mathbf{P} = \frac{1}{N-1}\mathbf{HA}\,\mathbf{HA}^{T} + \mathbf{R} \qquad \text{13}$$

with **R** the covariance matrix for the error in the observation equation (as before).

Next, a matrix with updated model states is calculated by

$$\mathbf{X}^{p} = \mathbf{X} + \frac{1}{N-1}\,\mathbf{XA}\,\mathbf{HA}^{T}\mathbf{P}^{-1}(\mathbf{D} - \mathbf{H}) \qquad \text{14}$$

The matrix $\mathbf{X}^{p}$ forms the new starting point of the model over a subsequent time-step, providing values the best estimate of *pd* for all M spatial units, over N ensemble members. To each of these values *pd* equations 9a and 9b are applied again, after which the various matrices are rebuilt (equations 10 to 13) for a next estimation step (equation 14).

APPENDIX 3

POPULATION SIZE IN THE 117 EXPERIMENTAL ATLAS SQUARES

VALUES OF ESTIMATED ANNUAL MEAN POPULATION SIZE OF MUSKRAT PER ATLAS SQUARE

Atlas	year					
square	2010	2011	2012	2013	2014	2015
351	643	891	2340	1711	1870	3100
357	562	980	529	326	229	96
547	476	75	1	9	18	0
621	1066	245	232	178	98	163
643	601	279	146	137	17	41
644	835	436	467	153	36	61
713	3365	3773	4533	3507	2768	3392
714	2194	3188	4867	4363	2989	2901
722	3915	4338	4244	3197	3139	3891
724	3142	5838	8104	5942	3738	3155
727	1629	2121	2160	1787	1105	763
736	2011	3591	3681	2899	1955	1148
757	577	1084	1515	978	659	434
831	741	1302	2920	1817	952	826
853	868	838	1396	948	806	836
1016	893	672	344	100	48	17
1024	929	532	252	570	70	82
1047	1286	1028	667	523	264	313
1048	1348	695	284	279	146	165
1141	1379	630	307	282	175	161
1225	570	393	434	716	597	594
1257	51	53	96	95	46	25
1341	758	964	1342	657	463	263
1435	249	238	739	237	157	144
1456	222	121	567	275	1059	930
1528	2271	1245	589	296	135	79
1616	492	310	160	187	90	53
1622	1802	1533	1775	1076	838	319
1632	2016	2010	1911	1488	856	431
1635	971	426	188	192	303	191
1645	1673	1241	943	583	564	494
1727	115	13	19	22	33	77
1734	104	81	29	77	116	212
1933	439	289	62	112	221	31
2113	1090	728	463	485	685	441
2116	2909	2161	1280	1097	803	744
2125	3586	2810	2090	2312	2237	1777

Atlas	year					
square	2010	2011	2012	2013	2014	2015
2133	1792	1799	1548	2585	3249	1660
2136	2934	2636	2381	2309	2338	1272
2142	2269	2581	2573	2410	1905	1481
2143	2753	2732	2530	3235	3728	2110
2144	2668	2626	2431	3058	5111	2786
2153	2611	2673	1996	2074	2422	1881
2154	2212	1972	1653	1796	3090	2031
2552	262	304	749	804	1097	838
2638	106	528	225	255	367	188
2642	90	133	325	636	459	429
2718	328	94	171	242	413	463
2725	551	1501	1652	869	1216	1968
2738	222	70	209	459	677	951
2745	665	729	863	1024	998	1646
2748	58	11	21	189	282	421
2812	324	230	295	251	168	283
2836	235	366	140	109	56	50
2847	176	224	196	109	96	73
3114	793	476	368	567	489	511
3131	249	276	565	690	1044	1212
3133	1975	1609	2093	3143	2387	2578
3135	4678	2599	2101	1631	1768	2690
3137	1941	1731	1194	1007	1210	1025
3142	1274	936	1667	2119	2802	2844
3145	3875	2426	2072	1260	1624	2469
3146	2725	1420	1032	887	1377	1998
3153	2179	1678	2678	2546	3515	5126
3154	2502	1869	2066	1362	1963	3478
3233	346	232	255	270	22	22
3346	203	235	213	241	511	386
3358	37	243	21	232	221	61
3437	210	174	192	172	297	219
3723	188	66	169	87	136	115
3813	3031	1687	2681	2825	3536	5933
3814	2731	1487	1630	1479	1876	3582
3816	1118	363	38	149	295	620
3817	582	217	13	226	175	236
3821	1379	693	954	1290	1556	2215
3822	3682	1684	2831	3204	3444	5178
3825	1596	662	415	605	750	1246
3826	930	343	96	370	367	410
3833	2679	1587	2001	1795	1997	3467
3834	1791	1124	1089	996	1285	2056
3842	885	661	1006	1022	1087	1882
3845	966	865	664	563	802	562
3846	995	862	1021	1009	1022	505
3848	879	943	690	764	855	647
3945	493	844	599	347	238	263
3947	437	836	1033	654	259	318

Atlas	**year**					
square	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**
3954	308	255	231	464	277	241
4016	128	238	225	253	513	517
4041	161	176	112	110	265	387
4042	113	72	103	189	341	527
4043	92	89	189	506	594	812
4054	128	169	491	420	841	517
4311	117	101	51	49	74	58
4348	570	443	501	471	403	586
4354	808	908	688	405	266	256
4415	371	795	930	709	610	248
4433	398	585	629	788	714	502
4451	1973	1308	1216	854	677	523
4537	0	0	0	0	11	0
4544	15	21	29	44	49	88
4558	1	28	1	0	0	0
4641	12	75	7	9	26	10
5028	13	3	0	1	0	2
5045	0	0	0	0	0	0
5124	70	39	72	127	154	120
5133	10	2	7	11	94	11
5141	2	17	2	0	5	0
5157	3	3	0	0	0	1
5252	13	8	35	67	82	110
5711	0	0	0	0	0	0
5723	41	27	3	7	0	0
5724	121	41	17	18	4	3
6042	15	15	8	7	11	18
6051	13	2	12	5	25	23
6053	1	8	1	0	15	3
6224	20	29	8	3	78	12
6233	2	55	5	6	79	39