An individual-based model for the migration of pike (*Esox lucius*) in the river Yser, Belgium

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a b s t r a c t

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*Keywords:*

Individual-based model Migration

Northern pike Rivers

For many decades, pike populations in Belgium have been suffering from a decline of the environmental quality due to habitat deterioration, water pollution and many other degrading phenomena. Since past attempts to rehabilitate the pike populations had only limited success, it is of importance to gain insight into the spatio-temporal dynamics of pike such that more effective restoration programs can be effectu- ated in the future. Ideally, this can be accomplished by relying on telemetry data, but since the collection of such data is both labour-intensive and costly, researchers often resort to a simulation-based approach, which on its turn requires a sound spatio-temporal model. Therefore, and as a ﬁrst step towards an integrated individual-based model (IBM) for describing pike dynamics in rivers, an IBM mimicking the movement of pike in the river Yser, Belgium, is proposed in this paper. This model considers the speci- ﬁcities of pike, such as its seasonally dependent migration, swimming speed and habitat preference, and is based upon environmental data from the river Yser. It is shown that the *in silico* spatio-temporal dynamics coincides with the one that is typically inferred from *in situ* observations. Amongst other things, the proposed model may be relied upon to identify the most appropriate management and restoration measures through a scenario analysis.

### Introduction

Taking into account its role as a top predator in aquatic ecosys- tems throughout the northern hemisphere on the one hand (*e.g.* [Craig,](#_bookmark49) [1996;](#_bookmark49) [Berg](#_bookmark49) [et al.,](#_bookmark49) [1997),](#_bookmark49) and its commercial and recre- ational value on the other hand ([Crossman](#_bookmark50) [and](#_bookmark50) [Casselman,](#_bookmark50) [1987;](#_bookmark50) [Raat,](#_bookmark50) [1988),](#_bookmark50) the spatio-temporal distribution of pike (*Esox lucius* L.) in both rivers and still waters received considerable attention throughout the last decade (*e.g.* [Cook](#_bookmark48) [and](#_bookmark48) [Bergesen,](#_bookmark48) [1988;](#_bookmark48) [Diana,](#_bookmark48) [1980;](#_bookmark48) [Koed](#_bookmark48) [et al.,](#_bookmark48) [2006;](#_bookmark48) [Masters](#_bookmark48) [et al.,](#_bookmark48) [2002;](#_bookmark48) [Ovidio](#_bookmark48) [and](#_bookmark48) [Philippart,](#_bookmark48) [2005;](#_bookmark48) [Rosell](#_bookmark48) [and](#_bookmark48) [Macoscar,](#_bookmark48) [2002;](#_bookmark48) [Vehanen](#_bookmark48) [et al.,](#_bookmark48) [2006).](#_bookmark48) Such stud- ies were further motivated by an increasing need for adequate rehabilitation and restoration programs as pike populations in Europe and North America have been suffering from eutrophication and habitat loss since the ﬁfties of the previous century ([Casselman](#_bookmark42)

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[and](#_bookmark42) [Lewis,](#_bookmark42) [1996).](#_bookmark42) Also in Belgium, pike populations suffered sig- niﬁcantly from the overall decrease of the environmental quality in general ([Maes](#_bookmark43) [et al.,](#_bookmark43) [2004),](#_bookmark43) and habitat destruction in particu- lar ([de](#_bookmark57) [Nie,](#_bookmark57) [1996).](#_bookmark57) Therefore, several attempts were undertaken to reintroduce pike, but a rehabilitation of the concerned pike popula- tions was mostly not attained since the primary causes leading to a relapse of the Belgian pike populations, such as poor water quality and habitat deterioration, largely remained ([Knaepkens](#_bookmark77) [et al.,](#_bookmark77) [2004;](#_bookmark77) [Vandenabeele](#_bookmark77) [et al.,](#_bookmark77) [1998).](#_bookmark77) In spite of the growing number of data sets on the spatio-temporal dynamics of pike, the investigation of such data has largely been restricted to statistical analyses ([Kobler](#_bookmark78) [et al.,](#_bookmark78) [2008a,b;](#_bookmark78) [Koed](#_bookmark78) [et al.,](#_bookmark78) [2006;](#_bookmark78) [Masters](#_bookmark78) [et al.,](#_bookmark78) [2002;](#_bookmark78) [Vehanen](#_bookmark78) [et al.,](#_bookmark78) [2006),](#_bookmark78) whereas, to this day, no efforts have been spent to the development of a spatially explicit model that explains the observed patterns of movement, and which might be parametrized using such data sets. This is rather surprising since numerous such attempts have been undertaken to gain insight into the distribution of other ﬁsh species such as, among others, brook char (*Salvelinus fontinalis*) ([Clark](#_bookmark47) [and](#_bookmark47) [Rose,](#_bookmark47) [1997),](#_bookmark47) bullhead (*Cottus gobio*) ([Charles](#_bookmark45) [et al.,](#_bookmark45) [2008),](#_bookmark45) rainbow trout (*Oncorhynchus mykiss*) ([Clark](#_bookmark47) [and](#_bookmark47) [Rose,](#_bookmark47) [1997),](#_bookmark47) striped bass (*Morone saxatilis*) ([Rose](#_bookmark66) [et al.,](#_bookmark66) [1993),](#_bookmark66) but also seaﬁsh ([Hubbard](#_bookmark72) [et al.,](#_bookmark72) [2004)](#_bookmark72) and even water-bound arthropods ([O’Callaghan](#_bookmark55) [and](#_bookmark55) [Gordon,](#_bookmark55) [2008).](#_bookmark55)

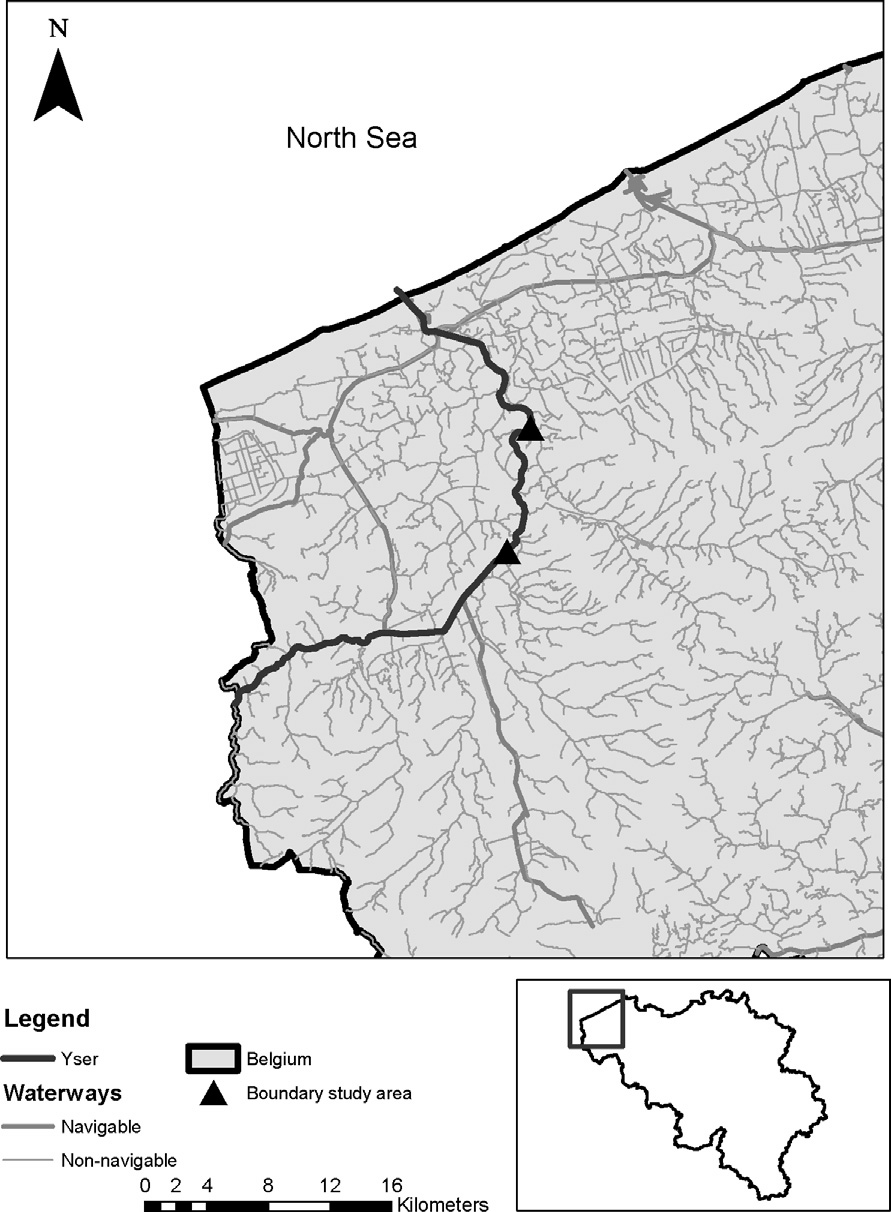
Indeed, in ecology the use of spatially explicit models in gen- eral and individual-based models (IBMs) in particular, which often involve ﬁsh populations, is manifold ([Chen](#_bookmark46) [et al.,](#_bookmark46) [2011;](#_bookmark46) [Grimm,](#_bookmark46) [1999)](#_bookmark46) and their contribution to a full understanding of the spatio- temporal dynamics of ﬁsh has long been considered promising ([Van](#_bookmark69) [Winkle](#_bookmark69) [et al.,](#_bookmark69) [1993).](#_bookmark69) Essentially, the development of spatially explicit models complies with the earliest recordings on species diversity by, among others, [Darwin](#_bookmark53) [(1859),](#_bookmark53) who states that “*each organic being is either directly or indirectly related in the most impor- tant manner to other organic beings*”, and, as such, emphasizes the importance of space-time relationships. Acknowledging this interconnection, few other research groups have endeavoured the development of IBMs for mimicking the *in situ* dynamics of pike. Yet, the IBM put forward by [McDermot](#_bookmark52) [and](#_bookmark52) [Rose](#_bookmark52) [(2000)](#_bookmark52) presumes a spatial compartment of the accessible space and is speciﬁcally designed for mimicking the dynamics of lake ﬁsh. On the other hand, the IBM proposed by [Farrell](#_bookmark63) [et al.](#_bookmark63) [(2006)](#_bookmark63) is restricted to the early-life history of pike and it is also based upon a spatial compartment of the water body at stake, being the St. Lawrence River.

Recently, a next hurdle towards the establishment of a full- ﬂedged spatially explicit model for describing the dynamics of pike populations has been taken by [Arlinghaus](#_bookmark36) [et al.](#_bookmark36) [(2009),](#_bookmark36) who pro- posed a deterministic Leslie-matrix population for mimicking the temporal density ﬂuctuations of an age-structured pike popula- tion (see also [Arlinghaus](#_bookmark37) [et al.,](#_bookmark37) [2010).](#_bookmark37) Yet, their model neglects the spatial variability of the environmental factors inﬂuencing the structure of the pike population and can neither take into account undirected movement nor migration, which is deﬁned as a con- sistent directional movement ([Quinn](#_bookmark64) [and](#_bookmark64) [Deriso,](#_bookmark64) [1999).](#_bookmark64) Certainly, the latter plays an important role in the dynamics of pike since this ﬁsh species may cover tens of kilometres during the spawning season ([Harvey,](#_bookmark71) [2009;](#_bookmark71) [Ovidio](#_bookmark71) [and](#_bookmark71) [Philippart,](#_bookmark71) [2005),](#_bookmark71) although adult pike are generally considered as solitary predators that adopt an ambushing strategy for hunting their preys ([Raat,](#_bookmark65) [1988;](#_bookmark65) [Maitland](#_bookmark65) [and](#_bookmark65) [Campbell,](#_bookmark65) [1993;](#_bookmark65) [Webb](#_bookmark65) [and](#_bookmark65) [Skadsen,](#_bookmark65) [1980)](#_bookmark65) and often have dis- tinct home ranges (*e.g.* [Donnely](#_bookmark62) [et al.,](#_bookmark62) [1998;](#_bookmark62) [Malinin,](#_bookmark62) [1969,](#_bookmark62) [1970).](#_bookmark62) In addition, pike are highly dependent on vegetation as (densely) vegetated areas make up ideal habitats during the earliest growth stages and provide cover for hunting individuals ([Bry,](#_bookmark44) [1996).](#_bookmark44)

Motivated by the lack of a spatially explicit model for describing both undirectional and directional movements of pike, we propose an IBM for evolving reliable spatial-temporal distributions of pike within one of Belgium’s principal rivers, namely the river Yser. This IBM takes inspiration from the one developed by [Hubbard](#_bookmark72) [et al.](#_bookmark72) [(2004),](#_bookmark72) but this paper extends their work in the sense that (1) the IBM is adapted to mimic the dynamics of a solitary ﬁsh species,

1. it is calibrated by means of collected ﬁsh trajectory data, and
2. a methodology for setting up a realistic initial condition is out- lined. Although the main focus of this paper is on a description of pike populations in the river Yser, it should be emphasized that the developed IBM is generic in the sense that it may be relied upon for mimicking the *in situ* dynamics of other ﬁsh species in differ- ent regions after tuning its location- and species-speciﬁc model parameters.

This paper is structured as follows. Following a brief description of the study area in [Section](#_bookmark6) [2,](#_bookmark6) we present the mathematical con- structs upon which the proposed IBM is built in [Section](#_bookmark10) [3.](#_bookmark10) Thereby, particular attention is spent to a quantiﬁcation of the most crucial model parameters using data that were gathered in the frame- work of a telemetry study that was conducted in the study area. Moreover, the assessment of a reasonable initial distribution of the *in silico* individuals within the considered waterway and the incorporation of the migratory behaviour are given considerable attention. Simulation results afﬁrming the usability and soundness of the developed model are presented in [Section](#_bookmark25) [4,](#_bookmark25) together with a



**Fig. 1.** Location of the river Yser and its main tributaries in Belgium together with the location of the study area.

validation of the proposed IBM using the collected telemetry data. Finally, these results are elaborately discussed in [Section](#_bookmark31) [5.](#_bookmark31)

### Study area

Although the river Yser springs in France, the largest part (44 km) of its course is located in northwest Belgium where it drains into the North Sea through a tidal sluice that protects it from tidal ﬂuctuations ([Fig. 1).](#_bookmark5) The river is rain-fed and has an aver- age discharge of 1.44 m3 s−1, while its average water depth is 2.5 m notwithstanding it is relatively shallow (0.4 m) at locations where the man-made spawning grounds are located ([Mouton](#_bookmark54) [et al.,](#_bookmark54) [in](#_bookmark54) [press).](#_bookmark54) The actual study area covers a 10 km stretch of the river that is located almost halfway the Belgian river part ([Fig. 1),](#_bookmark5) has an aver- age width of 20 m and contains three artiﬁcial spawning grounds that are located at 158 m, 8225 m and 8896 m upstream from the downstream boundary of the study area, respectively, and which are denoted in the remainder of this paper as SG1, SG2 and SG3. Upon making abstraction of meandering, this stretch was repre- sented by a rectangular region measuring 1000 m × 20 m in which the position of the individuals could be identiﬁed unambiguously by means of a Cartesian coordinate system centred halfway the river at the downstream boundary of the study area.

As the hydraulic and physicochemical properties showed only a negligible variability along the considered river stretch ([Fig. 2),](#_bookmark7) whereas the variation in vegetation types in the shallow zones, as well as the naturalness of the bank reinforcements, which both strongly inﬂuence the habitat suitability for pike ([Bry,](#_bookmark44) [1996),](#_bookmark44) was more pronounced, the habitat suitability along the concerned river stretch was assessed by surveying the latter characteristics at a spa- tial resolution of one meter along both river banks (see [Mouton](#_bookmark54) [et al.,](#_bookmark54) [in](#_bookmark54) [press).](#_bookmark54) This survey distinguished between ﬁve vegetation types, namely reedy, scrubby, pioneer, sparse and no vegeta- tion, whereas four bank types were considered, being natural,

*4*



*Water level and river bed m*

*3*

*2*

*1*

*0*

*1*

*0 2000 4000 6000 8000 10 000*

*x m*

(a)

*25*

*Water temperature*

*°C*

*20*

*15*

*10*

*5*

*0*

*0 2000 4000 6000 8000 10 000*

*x m*

(b)

*25*

*Concentration dis solved oxygen mg l*

*20*

*15*

*10*

*5*

*0*

*0 2000 4000 6000 8000 10 000*

*x m*

(c)

**Fig. 2.** Average water level (a), water temperature (b) and dissolved oxygen concentration (c) *versus* the distance from the northern inlet of the study area during the spring season. The dashed lines demarcate the envelope that encloses all measurements.

**Table 1**

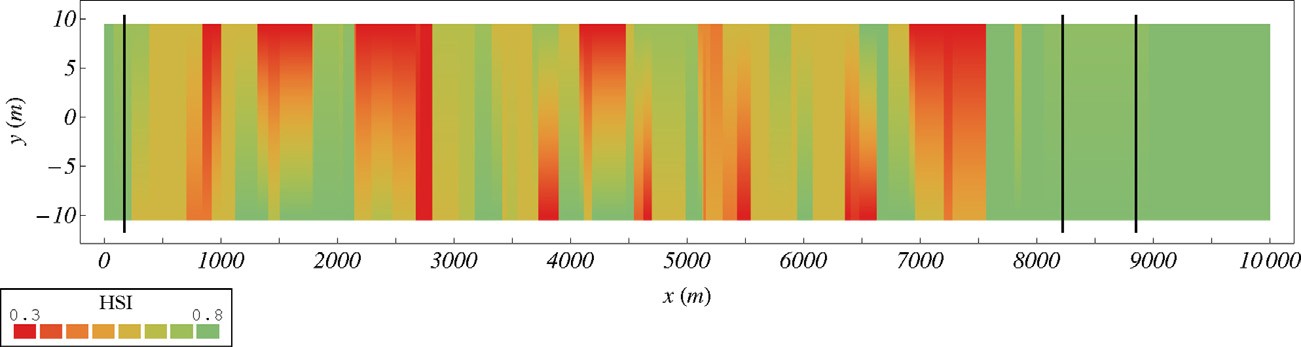
Proportion of the total bank length of the study area indicated in [Fig. 1](#_bookmark5) that is covered by each of the considered vegetation and bank types.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Bank type vegetation | Vertically reinforced | Natural | Foreshore | Semi-natural | None |
| None | 0.15 | 0.13 | 0.011 | 0.034 | 0 |
| Sparse | 0.082 | 0.027 | 0.0035 | 0.001 | 0 |
| Reedy | 0.18 | 0.16 | 0.067 | 0.020 | 0.002 |
| Scrubby | 0.040 | 0.084 | 0 | 0.00 | 0 |
| Pioneer | 0 | 0 | 0 | 0 | 0 |

semi-natural and vertically reinforced banks, and foreshores. [Table 1,](#_bookmark8) listing the relative importance of the different vegetation and bank types within the study area, clearly shows that the ripar- ian vegetation mainly consisted of reedy plants, whereas natural and vertically reinforced banks made up the largest part of the river stretch. As a means to quantify the habitat suitability, a habi- tat suitability index (HSI), denoted *17*, was employed, which has been widely used to build ecological models upon ([US](#_bookmark68) [Fish](#_bookmark68) [and](#_bookmark68) [Wildlife](#_bookmark68) [Service,](#_bookmark68) [1981)](#_bookmark68) and ranges from zero (unsuitable habitat) to one (suitable habitat) ([Mouton](#_bookmark54) [et al.,](#_bookmark54) [in](#_bookmark54) [press;](#_bookmark54) [Pauwels](#_bookmark54) [et al.,](#_bookmark54) [in](#_bookmark54) [press).](#_bookmark54) Since the left and right bank were surveyed separately, the HSI often differed between the facing river banks, such that it was opted to linearly interpolate the HSI between the left and right bank in order to obtain a unique HSI at every location in the study area. [Fig. 3](#_bookmark9) visualizes the spatial distribution of the HSI within the study area together with the man-made spawning grounds and clearly shows that the best habitats are located in the most upstream part

of the study area. For comprehensiveness, it should be mentioned that the artiﬁcial spawning grounds were assigned a HSI of 1 as these were considered to provide the optimal conditions for pike spawning and development.

Between November 2010 and December 2011 a telemetry study was carried out in the river Yser during which 15 tagged adult pike were tracked and their position was registered using dedi- cated antennas at daily, two- or three-daily or weekly intervals, depending on the season. It was opted to track not more than 15 individuals because their *in situ* localization is very time-consuming and labour-intensive, while fewer pike were tracked in the frame- work of most former pike telemetry studies (*e.g.* [Diana,](#_bookmark58) [1980;](#_bookmark58) [Kobler](#_bookmark58) [et al.,](#_bookmark58) [2008b;](#_bookmark58) [Ovidio](#_bookmark58) [and](#_bookmark58) [Philippart,](#_bookmark58) [2005).](#_bookmark58) Since this data set is used merely to assess the most crucial parameters of the proposed IBM, such as the swimming speed and the limits of the subsequent behavioural seasons, we refer to [Pauwels](#_bookmark60) [et al.](#_bookmark60) [(in](#_bookmark60) [press)](#_bookmark60) for an elaborate discussion of the telemetry campaign and



**Fig. 3.** Spatial distribution of the HSI within the study area together with artiﬁcial spawning grounds SG1 , SG2 and SG3 , which are located at 158 m, 8225 m and 8896 m upstream from the downstream boundary, respectively.

for a record of the biometric data of the tagged individuals. Data will be reported here only if they are required for a good understanding of this paper.

### Model development

* 1. *Equations of motion*

Basically, the spatio-temporal dynamics of a pike individual *i* is governed by a vector equation that was proposed originally by [Vicsek](#_bookmark75) [et al.](#_bookmark75) [(1995)](#_bookmark75) to simulate the motion of interacting parti- cles in a plane, but which has been used thereafter to describe the formation and migration of seaﬁsh schools ([Barbaro](#_bookmark38) [et al.,](#_bookmark38) [2009;](#_bookmark38) [Hubbard](#_bookmark38) [et al.,](#_bookmark38) [2004),](#_bookmark38) as well as the movements of pedestrians ([Vicsek](#_bookmark76) [et al.,](#_bookmark76) [1999).](#_bookmark76) This vector equation allows to describe the position *pi*(*t*) = (*xi*(*t*), *yi*(*t*)) of the *i*th pike that belongs to a popula- tion of size *N* through time and is given by

**W***i* (*t*)

[2005),](#_bookmark71) and is further provided by studies indicating considerable ﬂuctuations of their degree of activity ([Koed](#_bookmark44) [et al.,](#_bookmark44) [2006).](#_bookmark44)

Finally, it should be emphasized that the selection of a trust- worthy initial condition from which the dynamics of a *in silico* pike population can be evolved using Eqs. [(1)–(3)](#_bookmark11) deserves particu- lar attention because not all initial spatial distributions within the river stretch at stake are equally likely as pike preferentially occupy (densely) vegetated areas ([Bry,](#_bookmark44) [1996)](#_bookmark44) and are often tied to a given home range (*e.g.* [Donnely](#_bookmark62) [et al.,](#_bookmark62) [1998;](#_bookmark62) [Malinin,](#_bookmark62) [1969,](#_bookmark62) [1970).](#_bookmark62) In the remainder of this section we elaborate on each of the aforemen- tioned issues and, as such, show how the model of [Hubbard](#_bookmark72) [et al.](#_bookmark72) [(2004)](#_bookmark72) can be extended in order to describe the *in situ* dynamics of solitary river ﬁsh in general, and the one of pike in a Belgian river more in particular.

* 1. *Seasonal migratory behaviour*

Following a literature review on the migratory behaviour of pike, three periods during which adult pike show distinct migra-

**x***i* (*t* + *�t*) = **x***i* (*t*) + *vi* (*t*)

∗**W***i* ∗

*�t,* (1)

tory behaviour were distinguished in one annual cycle. Firstly, the spawning season during which, as mentioned already in [Section](#_bookmark3)

where **x***i*(*t*) = [*xi*(*t*), *yi*(*t*)]T (the location) and *vi* (*t*) is the swimming

speed of the *i*th individual. Further, **W***i*(*t*) is a weighted average, *i.e.*

**W***i* (*t*) = (1 − *˛i* (*t*))**P***i* (*t*) + *˛i* (*t*)**Q***i* (*t*)*,* (2)

of two unit vectors **P***i* and **Q***i* that steer the direction in which pike *i* moves depending on the presence of other individuals in its neighbourhood and the season (**P***i*), and the (seasonal) attrac- tion to spawning grounds (**Q***i*). Using these vectors, the swimming direction *Bi* of a given pike *i*, which is deﬁned by the angle between the horizontal axis of an orthogonal coordinate system centred in (*xi*(*t*), *yi*(*t*)) and the vector of motion, can be obtained from

[1,](#_bookmark3) pike cover big distances in order to ﬁnd eligible spawning grounds ([Harvey,](#_bookmark71) [2009;](#_bookmark71) [Inskip,](#_bookmark71) [1982).](#_bookmark71) Secondly, the passive seden- tary period that runs from the end of the spawning season until the start of the winter and during which pike displays its typical sit- and-wait strategy, *i.e.* long stationary periods that are sporadically interchanged with sudden and short-lasting movements to catch its preys ([Koed](#_bookmark44) [et al.,](#_bookmark44) [2006).](#_bookmark44) Finally, the active sedentary season covering the winter months and lasting until the start of the spawn- ing season. The latter clearly differs from the second one because the individuals have to look for their potential preys more actively ([Koed](#_bookmark44) [et al.,](#_bookmark44) [2006),](#_bookmark44) which is further reinforced by the higher pike abundance that can be reached during these months owing to the absence of cannibalism ([Craig,](#_bookmark49) [1996).](#_bookmark49)

cos *Bi* (*t*)

=

sin *Bi* (*t*)

**W***i* (*t*)

∗**W***i* (*t*)∗

*.* (3)

Taking into account the existence of distinct behavioural sea- sons, it is natural to assume that exists a gradual transition between the behaviour tied up with the spawning season and the one dis-

Essentially, the weighing coefﬁcient *˛i*(*t*) in Eq. [(2)](#_bookmark12) allows to alter

the relative contribution of **P***i*(*t*) and **Q***i*(*t*) in the determination of **W***i*(*t*), which is particularly useful to mimic the dynamics of orga- nisms that display distinct types of behaviour throughout the year. Hence, it enables a species-speciﬁc periodization of the individuals’ behaviour through time.

To this day, Eqs. [(1)–(3)](#_bookmark11) have been used formerly to simulate the migration of school ﬁsh ([Hubbard](#_bookmark72) [et al.,](#_bookmark72) [2004),](#_bookmark72) such that, upon assuming that such species align their swimming direction and velocity to each other, **P***i* follows from

cos *ϕi* (*t*)

played during either the active or passive sedentary season. This progression was described using fuzzy sets ([Adriaenssens](#_bookmark39) [et al.,](#_bookmark39) [2004;](#_bookmark39) [Zadeh,](#_bookmark39) [1965,](#_bookmark39) [1975a,b,c),](#_bookmark39) the weighing function *˛i*(*t*) in Eq.

[(2)](#_bookmark12) can be contemplated as a trapezoidal fuzzy set (*E*1, *E*2, *E*3,

*E*4), where *E*2 and *E*3 denote the day numbers between which the movement of the individuals is completely driven by the attrac- tion to the spawning grounds, and *E*1, respectively *E*4, represents the beginning and the end of the transient, respectively. For com- prehensiveness, it should be mentioned that the ﬁrst of January

is labelled as day number one, so that the 31st of December 2011 was assigned day number 365. Similarly to the weighing function

*˛* (*t*) for discriminating between the spawning season on the one

**P***i* (*t*) =

sin *ϕi* (*t*)

*,* (4)

*i*

hand, and the sedentary seasons on the other hand, a weighing function that grasps the transition periods in which pike individ-

where *ϕi*(*t*) represents the average swimming direction of the ﬁshes in the neighbourhood of an individual *i*, and similarly for *vi* (*t*).

Yet, as pike is a solitary predator ([Raat,](#_bookmark65) [1988;](#_bookmark65) [Maitland](#_bookmark65) [and](#_bookmark65) [Campbell,](#_bookmark65) [1993;](#_bookmark65) [Webb](#_bookmark65) [and](#_bookmark65) [Skadsen,](#_bookmark65) [1980)](#_bookmark65) that exhibits cannibal- ism if the competition with its congeners is too strong ([Craig,](#_bookmark49) [1996),](#_bookmark49) it is clear that the determination of **P***i* must be altered in order to account for these speciﬁcities. Indeed, for such a species it would be erroneous to assume that an individual aligns its movement with nearby individuals. Besides, modifying the determination of *vi* (*t*) and *ϕi*(*t*) is further motivated by the fact that pike cover great distances during the spawning season, whereas they tend to be sedentary throughout the rest of the year. Evidence of such a dichotomous behaviour has been furnished by studies reporting substantial differences between the recorded swimming distances throughout one annual cycle ([Harvey,](#_bookmark71) [2009;](#_bookmark71) [Ovidio](#_bookmark71) [and](#_bookmark71) [Philippart,](#_bookmark71)

uals display distinct degrees of activity was deﬁned as a trapezoidal fuzzy set (*</*1, *</*2, *</*3, *</*4), where *</*2 and *</*3 denote the day numbers between which pike is passively sedentary, and *</*1, respectively

*</*4, represents the beginning and end of the transient, respectively. [Fig. 4](#_bookmark14) visualizes an example of both transition functions in case that

*˛i*(*t*) = (45, 73, 104, 134) and *ˇi*(*t*) = (104, 104, 304, 334).

To account for the discrepancies that naturally exist between individual pike, every *in silico* individual *i* was assigned a so-called biological clock *˚i* at the beginning of an annual cycle, which indi- cates the day number at which the spawning season of individual *i* starts during the considered annual cycle, and which was drawn from a discrete uniform distribution that covers the period during which *in situ* pike individuals commence their migratory quest. In order to identify this spawning season, as well as the sedentary seasons, [Fig. 5](#_bookmark17) visualizes the average minimal daily displacement

*1.0*

*0.8*

*Membership degree*

*0.6*

*0.4*

*0.2*

*0.0*

*Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Date*

that the majority of pike in the Flemish rivers are retrieved at less than hundred meters from the site where they are ﬁrst captured. On the other hand, a preliminary analysis of the telemetry data set allowed to infer a considerably higher home range during the active sedentary season, namely *ri* = 2000 m. During the spawning season pike are not bound to their territory (*˛i* = 1), such that no *ri* had to be chosen. Further, disregarding intraspecies variability, the home range was assumed the same for all individuals within the population, such that we may write *r* = *ri* for all *i*.

*3.3.2. Swimming direction*

**Fig. 4.** Transition functions *˛i* (*t*) and *ˇi* (*t*) deﬁned as trapezoidal fuzzy sets (45, 73, 104, 134) and (104, 104, 304, 334), respectively.

(MDD) of the tracked pike during the 13-month telemetry cam- paign together with the corresponding standard deviation. From this plot it was inferred that the tracked pike covered the largest distances between February 1 and May 1, so that this period was

Taking into consideration that pike exhibit territorial behaviour outside the spawning season, *ϕi*(*t*) in Eq. [(4)](#_bookmark13) could not be computed by averaging the speed of nearby individuals, which is plausible for school ﬁsh, but rather using

*ϕi* (*t*) = *ˇi* (*t*)*ϕl* (*t*) + (1 − *ˇi* (*t*))*ϕa*(*t*)*,* (5)

*i* *i*

which, basically, is a *ˇ*-weighted sum of the behaviour during the passive sedentary season, *i.e.*

identiﬁed as the spawning season, whereas their degree of activity

was minimal from May 1 on until December 1 (passive sedentary

( *E*(*p* (*t*))*,* if *d*(*p* (*t*)*, c* ) *>* 50 or (∃*j*)(*d*(*p* (*t*)*, p* (*t*)) ≤

*ϕ*2

10)*,*

season). Further, the period between December 1 and February 1

*i* (*t*) =

*i i i i j*

*Bi* (*t*) + *�i,* else*,*

(6)

was identiﬁed as the active sedentary season. Taking into account that [de](#_bookmark56) [Laak](#_bookmark56) [and](#_bookmark56) [van](#_bookmark56) [Emmerik](#_bookmark56) [(2006)](#_bookmark56) point out that pike are

where *d*(*pi*(*t*), *pj*(*t*)) denotes the Euclidean distance between

*pi*(*t*) and *pj*(*t*) and similarly for *d*(*pi*(*t*), *ci*), *E*(**x***i* (*t*)) = arctan(*xi* (*t*) −

residing about fourteen days near their spawning grounds and *xr r*

introducing 15-day transition periods between every two consec- utive behavioural seasons, we chose *˛i*(*t*) = (*˚i*, *˚i* + 15, *˚i* + 15 + 14,

*˚i* + 15 + 2 ×14), and accordingly *ˇi*(*t*) = (*˚i* + 15 + 14, *˚i* + 15 + 14, 318,

334), where 334 refers to the start of the active sedentary season (December 1).

*i , yi* (*t*) − *yi* ) + *˛* expresses that a pike *i* ﬂees in the direction of its

territory centre if it encounters a congener or crosses the outskirts

of its territory, and *�i* denotes a random perturbation of *Bi*(*t*) for which it holds that *�i* ∼ *U*(− *˛*/4, *˛*/4), and the one observed during the active sedentary season, *i.e.*

# (

*ϕ*3(*t*) =

*E*(*pi* (*t*))*,* if *d*(*pi* (*t*)*, ci* ) *>* 2000*,*

(7)

* 1. *Homing, swimming direction and speed*

*i*

*Bi* (*t*) +

*�i,* else*.*

* + 1. *Homing*

Since numerous papers report that pike exhibit territorial behaviour and have a certain home range (*e.g.* [Donnely](#_bookmark62) [et al.,](#_bookmark62) [1998;](#_bookmark62) [Malinin,](#_bookmark62) [1969,](#_bookmark62) [1970),](#_bookmark62) every *in silico* individual *i* was assigned such a home range, which was contemplated as the radius *ri* of its circular territory *ri* centred at *ci* = (*xr , yr* ) through which pike *i* can swim

Informally, Eq. [(6)](#_bookmark15) expresses that an *in silico* individual will not change its swimming direction deliberately during the passive sedentary season unless it encounters a congener at less than 10 m (*d*(*pi*(*t*), *pj*(*t*)) ≤ 10) or it crosses the boundary of its territory (*d*(*pi*(*t*), *ci*) > 50). Similarly, Eq. [(7)](#_bookmark16) governs the behaviour of the *in silico* indi- viduals during the active sedentary season in such a way that they

*i i*

freely. It was opted to resort to literature and a preliminary analy-

sis of the telemetry data set in order to pin down the home ranges during the consecutive behavioural seasons because their direct assessment would have required an advanced method of analy- sis due to the irregularity of the sampling intervals ([Katajistoa](#_bookmark76) [and](#_bookmark76) [Moilanen,](#_bookmark76) [2006),](#_bookmark76) which was considered beyond the scope of this paper that is of a more generic nature. During the passive seden- tary season *ri* was chosen 50 meters, being the lower bound of the interval of home ranges reported by [Donnely](#_bookmark62) [et al.](#_bookmark62) [(1998)](#_bookmark62) and in agreement with the ﬁndings of [Goethals](#_bookmark67) [et al.](#_bookmark67) [(2006)](#_bookmark67) who report

will only change their swimming direction intentionally if they

cross the boundaries of their territories (*d*(*pi*(*t*), *ci*) > 2000). Besides the intended and directed changes, Eqs. [(6)](#_bookmark15) [and](#_bookmark15) [(7)](#_bookmark15) capture the stochasticity of the swimming process by perturbing the swimming direction in absence of an external stimulus.

Since *˛i* = 1 during the spawning season, the swimming direc- tion will then be determined completely by the attraction towards the spawning grounds that is embodied in **Q***i*(*t*). The attraction to a spawning ground SG was described by means of a potential func- tion *˚*(*x*, *y*) that quantiﬁed this attraction at each location in the

study area, such that **Q***i*(*t*) in Eq. [(2)](#_bookmark12) was obtained from a potential gradient ∇*˚*(*x*, *y*) *i.e.*:

*˚*(*xi* (*t*)*, yi* (*t*))

**4000**

**Q***i* (*t*) = ∇

*.* (8)

**3000**

**2000**

**MMD (m)**

**1000**

**0**

∗∇*˚*(*xi* (*t*)*, yi* (*t*))∗

Naturally, if there are multiple spawning grounds SG*s* in the study area, *in silico* individuals will be partially attracted to each of them, which can be expressed mathematically by aggregating individ- ual potential functions *˚s*(*xi*(*t*), *yi*(*t*)), *i.e.* one for every spawning ground SG*s*. As such, *˚*(*xi*(*t*), *yi*(*t*)) in Eq. [(8)](#_bookmark18) should be replaced by

*ˇ* [*˚s*(*xi* (*t*)*, yi* (*t*))], where *ˇ* represents an aggregation function.

*s s*

In order to express the attraction of pike towards a spawning

**1000**

**Jan Apr Jul Oct Date**

ground SG*s* in the river Yser during the spawning season, a potential function *˚s*(*x*, *y*) as proposed originally by [Magnússon](#_bookmark46) [et al.](#_bookmark46) [(2004)](#_bookmark46)

was deﬁned as

**Fig. 5.** Average minimal daily displacement (MDD) of the tracked pike *versus* time.

The area enclosed between the dashed lines corresponds to the average MDD plus/minus the standard deviation.

*m*

*˚s*(*x, y*) = − 2*˛*

ln *d*((*x, y*)*,* (*xs, ys*))*,* (9)

**SG 1 SG 2 SG 3**

**1**

*v*˜3(*t*)∼*W*3(0*.*60*,* 262*.*23). In order to account for the vague transition between the subsequent behavioural seasons, which is formalized by the fuzzy sets *˛i*(*t*) and *ˇi*(*t*), the effective swimming speed of

**0.0**

*i*

**2**

**3**

**max *k***

an individual *i* was obtained from:

*vi* (*t*) = *˛i* (*t*) *v*˜1(*t*) + (1 − *˛i* (*t*))[*ˇi* (*t*) *v*˜2(*t*) + (1 − *ˇi* (*t*))*v*˜3(*t*)]*.* (10)

**0.5 *k***

**Potential function**

*i i* *i*

**1.0**

**1.5**

**0 2000 4000 6000 8000 10 000**

*i*

**Distance from northern boundary m**

This equation stipulates that the effective swimming speed of an *in silico* individual was determined as a weighted sum of its swimming speed during the spawning season *v*˜1(*t*) and the one in the two other seasons, where the latter was computed as a weighted sum of the swimming speeds during the active and passive sedentary seasons. The outcome of this methodology is illustrated in [Fig. 7,](#_bookmark22) which shows the effective swimming speed of an individual during

**Fig. 6.** Potential functions *˚*1 , *˚*2 and *˚*3 corresponding with the spawning grounds SG1 , SG2 and SG3 together with the overall potential function max*˚k* (shaded area).

*k*

in which (*xs*, *ys*) denotes the centre of SG*s*, and *m* is the total attrac- tion to the spawning grounds that was assumed to be one. Taking into account the presence of multiple spawning grounds in the

one annual cycle upon replacing *v*˜*j* (*t*) in Eq. [(10)](#_bookmark20) by the average recorded MMD during the corresponding behavioural season, being 613, 122 and 404 m day−1, respectively.

*3.4. Initial and boundary conditions*

*i*

As mentioned before, every *in silico* pike *i* had to be assigned

concerned river stretch ([Fig. 3),](#_bookmark9) *in situ* individuals will be partially

attracted to each of them. Yet, it is likely that an individual will

a territory *ri*

with centre **c***i*

located within the concerned river

prefer the spawning ground that is located the closest since this requires the smallest energy loss due to migratory movements, such that the overall potential function was written as max*˚k* .

*k*

The potential functions *˚*1, *˚*2 and *˚*3 corresponding with the spawning grounds SG1, SG2 and SG3, respectively, as well as the overall potential function max*˚k* along the river stretch at stake

*k*

are sketched in [Fig. 6.](#_bookmark19)

*3.3.3. Swimming speed*

Since an analysis of the telemetry data gathered during the spawning season revealed that the MMD obeyed a Weibull dis- tribution, the swimming speed, expressed in meter per day, of every individual *i* and at every consecutive time step was drawn from a Weibull distribution *W*(*À*, *k*), where *À* represents the shape parameter and *k* is the scale parameter, which were determined using the maximum likelihood method (see *e.g.* [Harris](#_bookmark70) [and](#_bookmark70) [Stocker,](#_bookmark70) [1998).](#_bookmark70) As such, we assessed that *À* = 0.60 and *k* = 406.03, such that  *v*˜1(*t*)∼*W*1(0*.*60*,* 406*.*03), where *v*˜1(*t*) denotes the swimming speed

stretch because pike are solitary, homing, and sporadically canni-

balistic beings ([Craig,](#_bookmark49) [1996;](#_bookmark49) [Donnely](#_bookmark49) [et al.,](#_bookmark49) [1998;](#_bookmark49) [Malinin,](#_bookmark49) [1969,](#_bookmark49) [1970).](#_bookmark49) Once these territories were pinned down, it was assumed that **x***i*(0) = **c***i* to initiate model simulations. As such, we had to allo- cate the territories realistically across the study area in order to set up a lifelike initial pike distribution from which the *in silico* dynamics could then be evolved using the proposed IBM.

Essentially, the allocation of territories may be envisaged as an optimization problem since it is natural to assume that a pike indi- vidual will try to minimize the overlap between its own territory and the one of individuals in its vicinity because it is a solitary and sporadically cannibalistic species ([Craig,](#_bookmark49) [1996),](#_bookmark49) while at the same time it will try to maximize the area of its *ri* that is located in parts of the river that are well suited for sustaining pike. The latter was quantiﬁed by means of a habitat suitability index, denoted *17*. By relying on the methodology proposed by [González](#_bookmark68) [et al.](#_bookmark68) [(2003)](#_bookmark68) for ﬁnding the optimal distribution of wireless sensors, the minimi- zation of the overlap between different individuals was expressed mathematically as the minimization of

*i* *i*

of an individual *i* at a given *t* during the spawning season. Simi- larly, the individual swimming speeds during the passive and active sedentary season, denoted as *v*˜2(*t*) and *v*˜3(*t*), respectively, were

2

*O*1 = \\*e*−*d*(*ci,cj* ) *r*− *,* (11)

2

*i j* =*/ i*

*i* *i*

drawn from Weibull distributions that were parametrized using

data on the MMD that were collected during these behavioural seasons in the framework of the aforementioned telemetry study.

*i*

where *d*(*ci*, *cj*) denotes the Euclidean distance between *ci* and *cj*.

The contribution of each of the exponential terms in the right-hand side (RHS) of Eq. [(11)](#_bookmark21) can be at most one if and only if *ci* = *cj*, and

More precisely, it was found that

*v*˜2(*t*)∼*W*2(0*.*45*,* 48*.*82) and

approaches zero if *d*(*ci*, *cj*) ≥ 2 *r*. This is illustrated more clearly in

**600**

**1**

**500**

**Swimming speed m day**

**400**

**300**

**200**

**Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Date**

**Fig. 7.** Effective swimming speed of a pike individual during one annual cycle as given by Eq. [(10)](#_bookmark20) in which ˜*j* (*t*) is replaced by the average MMD of the corresponding

*v*

*i*

behavioural season.

**1.0**

**0.8**

**0.6**

***O*1**

**0.4**

smaller than *e*−(2−2 *f* ) , *j* will accept this overlap. Of course, such a trade-off only arises if all stretches within the river where the HSI is maximal are already occupied prior to the introduction of *j*.

In the remainder of this paper, it is assumed that a pike opts for a maximization of its *17*(*ri*) as long as the overlap this might bring forth is smaller than one halve of its territory’s radius (*f* = 1/4).

2

Further, it was opted to exclude the artiﬁcial spawning grounds as

(2−2 *f* )2

**0.2**

possible territories, such that the factor (*e*−

of Eq. [(13)](#_bookmark26) was approximately 1/5.

*/17* − *17*) in the RHS

**0.0**

**0 1 2 3 4 5**

**d *c i* ,*c j r* 1**

**Fig. 8.** Penalty function *O*1 (Eq. [(11))](#_bookmark21) *versus d*(*ci* , *cj* )*r*−1 .

Finally, it is clear that boundary conditions had to be imposed to avoid individuals from leaving the river stretch if their posi- tion at *t* + *�t* given by Eq. [(1)](#_bookmark11) would be located outside the study area. Within the framework of this paper, reﬂecting bound- ary conditions were used to mimic the movement of pike that were approaching the river banks as faithfully as possible. This

[Fig. 8,](#_bookmark23) which shows *O*1 as a function of *d*(*ci*, *cj*)*r*−1 in the case the ﬁsh population consists of only two individuals *i* and *j*.

The second constraint on the allocation of the territories, namely the maximization of their habitat quality or, equivalently, the mini- mization of the territories’ area that is located in regions with low HSI, could simply be formulated as the minimization of

*O*2 = \1 − *17*(*ri* )*,* (12)

*i*

where *17*(*ri*) represents the HSI at *ci*.

Finally, the objective functions *O*1 and *O*2 were merged in one integrated objective function that was then relied upon for allocat- ing the territories among the ﬁsh within the population at stake. Yet, attention had to be paid to the relative weight that was assigned to each of the constraints. More speciﬁcally, this traced back to assessing how much overlap 2 *f r* (*f* ∈ [0, 1]) an individual *j* will tol- erate with an other *ri* if this overlap maximizes *17*(*rj*). This was assessed by taking into account that the term in the RHS of Eq.

[(11)](#_bookmark21) increases by exp(− (2 − 2 *f*)2) as the overlap between *ri* and *rj* increases from zero to 2 *f r*, whereas the RHS of Eq. [(12)](#_bookmark24) decreases by *17* − *17*, where *17* and *17* represent the maximum and minimum HSI in the study area, respectively, if the territory of *j* is located in a region that maximizes its HSI but also entails an overlap 2 *f r*. Hence, nor-

malization of the RHS of Eq. [(12)](#_bookmark24) by (*17* − *17/* exp(−(2 − 2 *f* )2)) entails

that an individual will tolerate an overlap of 2 *f r* as long as this leads to *17*(*rj* ) = *17*, such that the integrated objective function could be written as

kind of boundary conditions dictates that such individuals were reﬂected at the boundaries of the study area, which either rep- resented the river bank or the in- or outlet of the concerned river stretch, if **x**(*t* + *�t*) was located outside the study area. More precisely, the line connecting *pi*(*t*) and *pi*(*t* + *�t*) that intersects with the study area’s boundary was reﬂected on this boundary at the point of intersection in such a way that the incoming angle equalled the outgoing one. It can be shown that the swimming direction of reﬂected individuals becomes *˛* − *Bi*(*t*) or 2*˛* − *Bi*(*t*) if the reﬂection occurred at a vertical or horizontal boundary, respectively.

1. ***In silico* experiments**
   1. *Initial condition and spawning grounds*

It was supposed that *N* = 50 as this agrees with the lower bound of the carrying capacity range that is mentioned in literature ([Craig,](#_bookmark49) [1996).](#_bookmark49) Further, Eq. [(13)](#_bookmark26) was minimized using simulated annealing ([Cˇ erny´ ,](#_bookmark71) [1983;](#_bookmark71) [Kirkpatrick](#_bookmark71) [et al.,](#_bookmark71) [1983),](#_bookmark71) which is a well-established algorithm for numerically optimizing functions. As this optimiza- tion procedure can be time-consuming if the *in silico* population consists of a relatively large number of individuals, we opted to minimize Eq. [(13)](#_bookmark26) by successively adding one individual to the population, allocating its territory such that Eq. [(13)](#_bookmark26) was mini- mized under the condition that the position of already allocated territories remained unchanged and repeating this procedure until

# ⎛

\ 2 2

2 ⎞

*e*−(2−2 *f* )

each individual in the populations was assigned a territory. It was veriﬁed that the allocation of the territories by relying on this

*O* = \ ⎝

*i*

*j* =*/ i*

*e*−*d*(*ci,cj* ) *r*−

+ (1 − *17*(*ri* ))

*17* − *17*

⎠ *.* (13)

approach did not signiﬁcantly differ from the one obtained by assigning them concurrently. Comparing [Fig. 9,](#_bookmark27) which shows the

To clarify the above reasoning, consider a pike *j* of which the terri- tory should be located in a river stretch where *17* = 0*.*8 and *17* = 0*.*3, and which is already occupied by another pike *i*. Hence, it is clear

2

that the second term in Eq. [(13)](#_bookmark26) decreases by *17* − *17* (*e*−(2−2 *f* ) */17* −

2

location of the territories that were assigned to the individuals within the *in silico* population at stake, and the spatial distribution of the HSI clearly unveils that the majority of them were situated in those stretches of the river that are characterized by a high HSI. This is further conﬁrmed by [Fig. 10,](#_bookmark28) which depicts the rela-

*17*) = *e*−(2−2 *f* )

if *rj* can be assigned to a part of the river stretch

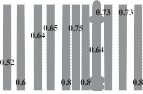
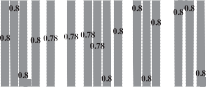
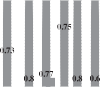
tive frequency distribution of both the number of territories and

where the HSI is maximal as opposed to an allocation to a region where *17*(*rj* ) = *17*. Accordingly, as long as the additional contribution of the ﬁrst term in the RHS of Eq. [(13)](#_bookmark26) due to a possible over-

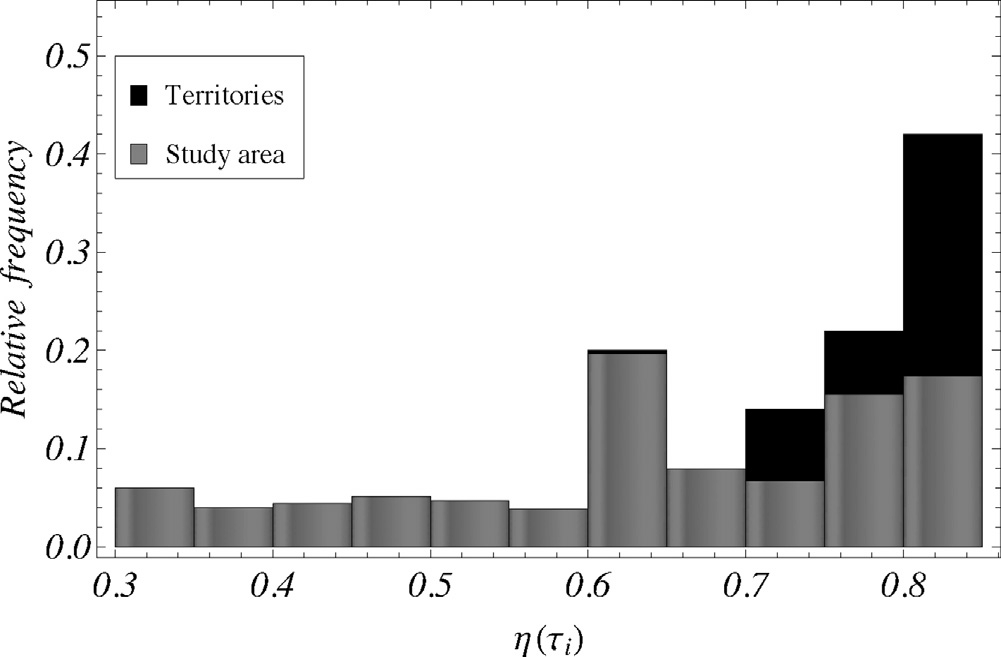
lap between *ri* and *rj* that is required to maximize *17*(*rj*), remains

the surface area within the concerned river stretch *versus* the HSI,

as the distribution of the former is patently shifted towards the higher end of the HSI range compared to the one of the surface area.



**Fig. 9.** Location of the territories of the 50 pike within the considered population, which is optimized numerically according to Eq. [(13).](#_bookmark26)



**Fig. 10.** Relative frequency distribution of the number of territories (black) and the surface area (gray) within the concerned river stretch *versus* the HSI.

* 1. *An annual cycle*

Within the framework of the *in silico* experiments reported in the remainder of this paper, we chose *�t* = 3600 s. [Fig. 11](#_bookmark29) shows snapshots of the *in silico* spatial pike distribution within the study area at the beginning of six different days during an annual cycle. The dates at which snapshots are shown, were selected such that the movement patterns during both the sedentary and spawn- ing season can be inferred from [Fig. 11.](#_bookmark29) From the ﬁrst snapshot, which was taken at the very beginning of the spawning season, it is obvious that all members of the population were residing within their territory, whereas, at March 2, some pike (colored gray) were already migrating towards the spawning grounds nonetheless most individuals could still be found within their territory. During the next weeks, the number of pike that started its journey towards the spawning grounds gradually increased and by May 2 most of them could be retrieved near one of the artiﬁcial spawning grounds. Finally, as the migration season ended, all individuals returned to their territories where they could be retrieved during the summer months and the remaining part of the year.

Of course, the simulated spatio-temporal distribution depicted in [Fig. 11](#_bookmark29) is just one possible realization brought forth by simula- tion of the developed IBM from the given initial condition (*cf.* [Fig. 9)](#_bookmark27) owing to the stochasticity that is involved through the assessment of the swimming direction and speed by means of Eqs. [(6)](#_bookmark15) [and](#_bookmark15) [(7),](#_bookmark15) and Eq. [(10),](#_bookmark20) respectively. Hence, in order to acquire a reli- able understanding of the individuals’ spatio-temporal dynamics it was imperative to generate a predeﬁned number of realizations by repeatedly simulating the spatio-temporal species distributions and draw conclusions on the *in silico* time series of macroscopic characteristics that were computed afterwards over both the real- izations and the individuals within the *in silico* population at stake. Throughout the remainder of this paper, 100 realizations of the established IBM are underlying the discussion and conclusions.

[Fig. 12](#_bookmark30) visualizes the average distance between *ci* and *pi*(*t*) during an annual cycle together with the average speed of the indi- viduals within the population at stake, which were calculated over both the 100 realizations of the IBM and the individuals. The shaded area always illustrates the envelope in which 95 % of the realiza- tions was retrieved. From the former it can be inferred that the average distance remained approximately 1000 m until the begin- ning February, which can be understood by recalling that pike move almost randomly within their territory with radius 2000 m during the active sedentary season. Yet, as soon as the migration seasons commenced the average distance increased to about 1100 m. Fur- thermore, during the latter season the distance between *ci* and *pi* was highly variable between the populations’ individuals, which

can be attributed to the fact that some individuals were already migrating, whereas others were still residing in their territories ([Fig. 13](#_bookmark32)). Besides, the territory of some *in silico* individuals was centred in the direct vicinity of an artiﬁcial spawning ground, so that these individuals had no incentive to cover a large distance in pursuit for a suitable spawning ground, as opposed to individ- uals whose territory was located at a greater distance from such an artiﬁcial spawning ground. Clearly, this variability vanished almost completely once the pike returned to their territories since they then entered the passive sedentary season during which they were highly sedentary. Similar observations were made with regard to the swimming speed that is depicted in [Fig. 12](#_bookmark30)(b). In case of this quantity, the variability relates to the different degrees of activity that pike tend to show throughout one annual cycle (*cf.* Eq. [(10)).](#_bookmark20)

In order to gain insight into the variability of a given individ- ual’s characteristics across the 100 realizations, which gets blurred by representing averages over both the realizations and individ- uals, [Fig. 14](#_bookmark33) shows the average distance between two given *in silico* individuals and their territory during one annual cycle, as well as their average swimming speed, which are both obtained by aver- aging only over the IBM realizations. Although the average distance between *ci* and *pi*(*t*) during the spawning season was considerably small for one of the tracked individuals due to relatively limited distance between its territory and a spawning ground, this ﬁgure clearly shows that the overall behaviour of the two tracked individ- uals coincides with the tendencies that have been observed with regard to the entire *in silico* population ([Fig. 12).](#_bookmark30) This is particularly true for the swimming speed.

* 1. *Validation of the individual-based model*

Here, we will show the similarity between the outcome of the *in silico* experiments and the *in situ* movements of pike that were registered in the river Yser between November 2010 and December 2011. As such, we grant the usability of the proposed IBM in the framework of similar settings. Taking into consider- ation the stochastic nature of the IBM, which is caused by drawing the swimming speed of an *in silico* ﬁsh at every time step from the parametrized Weibull distributions *W*1, *W*2 and *W*3, and fur- ther by perturbing the swimming direction (Eqs. [(6)](#_bookmark15) [and](#_bookmark15) [(7)),](#_bookmark15) it should be clear that there can never be a one-to-one correspon- dence between the real-world trajectory of a given pike individual and its *in silico* counterpart. Indeed, in such a stochastic setting the trustworthiness of the IBM should not be evaluated by assessing the discrepancies between an *in situ* trajectory and an *in silico* one, but rather by showing that the former constitutes a possible and plausible outcome of an *in silico* experiment. Since a series of *in silico* experiments yields a probability distribution of the occupied locations for every *in silico* individual and every time step, one can show the validity of the proposed IBM if one is able to show that the trajectory of its *in situ* counterpart could have been drawn from a contiguous series of such distributions. More speciﬁcally, taking into account the homing behaviour of pike, the observed trajectory of a pike individual that has its territory at **c***i* should constitute a possible realization of the distributions of an *in silico* individual that has its territory centred near **c***i* throughout an annual cycle.

[Fig. 15](#_bookmark34) depicts the average position and the corresponding con-

ﬁdence interval of an *in silico* individual of which the territory is centred near the one of an *in situ* individual for which the registered positions during 2011 are depicted as black dots. Two conclusions can be drawn immediately from this ﬁgure. Firstly, it is clear that the observed positions throughout the annual cycle are not located on the curve that connects the average position of the corresponding *in silico* individual, but nonetheless they are often located relatively close to that line or to the dashed lines that indicate the limits of the 95% conﬁdence interval. Secondly, it is obvious that the overall



**Fig. 11.** Simulated spatial distribution of the individuals (arrowheads) within the study area at the beginning of six different days during an annual cycle together with the territories (dotted lines) determined by minimization of Eq. [(13).](#_bookmark26) The individuals, of which two are shown by large arrowheads for telemetry purposes, are represented by black arrowheads if *˛i* (*t*) = 0 and gray arrowheads if *˛i* (*t*) > 0. The spawning grounds are indicated as SG*k* .

patterns that can be inferred from the positional data of the real- world individual, such as the relatively steady position during the passive sedentary season and the signiﬁcantly more pronounced positional ﬂuctutations during the active sedentary and spawning seasons, are also inherent to the dynamics of the *in silico* individual,

which comes forward by the much wider/broader conﬁdence inter- val during the latter seasons, as opposed to their width in the former one. The latter similarity indicates that the proposed IBM captures the differences in pike dynamics between the distinct behavioural seasons. Moreover, in agreement with the telemetry data, the

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**Fig. 12.** Average distance between *ci* and *pi* (*t*) (a) and average swimming speed (b), which are obtained by averaging over both the realizations of the IBM and the individuals. The shaded area illustrates the envelope in which 95% of the realizations is retrieved.

simulation experiments indicate that the concerned individual did not undertake a migratory quest, which can be attributed to the presence of a spawning ground near the centre of its territory or to persistent homing behaviour ([Vehanen](#_bookmark73) [et al.,](#_bookmark73) [2006).](#_bookmark73) The agreement between the *in silico* and *in situ* dynamics was further conﬁrmed by means of the washer method ([Venturini,](#_bookmark74) [2011),](#_bookmark74) which indicated for the real-world individual at stake that only 19% of the observa- tions constituted outliers of the corresponding *in silico* distribution. Similar ﬁndings were made with regard to the agreement between the simulated and observed dynamics for other individuals that spent the largest part of their annual cycle in the modelled river stretch. Of course, it may be expected that this agreement will be even more pronounced if also the size of the home range during the sedentary seasons would be deduced from the telemetry data, but, as mentioned before, this is considered beyond the scope of this paper.

Aside from the fact that the IBM should yield an ensemble of tra- jectories that encloses the real-world one, it is also important that it somehow grasps the *in situ* interaction between *in situ* pike individ- uals. The comparability between the *in situ* and *in silico* interaction is demonstrated in [Fig. 16](#_bookmark35) which shows the normalized pairwise distance, *i.e.* the pairwise distance normalized by the length of the river stretch, between *in situ* and *in silico* pike individuals through- out the considered annual cycle. It is immediately clear from this ﬁgure that the absolute values of this quantity are different from one another, but this can be understood by drawing attention on the unequal number of *in silico* and *in situ* individuals, on the one hand, and the discrepancy between the length of the modelled river stretch and the one through which the tagged pike could freely move, on the other hand. Besides, in the *in silico* experiments one keeps track of the entire pike population in the modelled river stretch, whereas only a small subsample of the *in situ* population

**50**

**40**

**Number of spawning individuals**

**30**

**20**

**10**

**0**

**15 Jan 01 Feb 15 Feb 01 Mar 15 Mar 01 Apr 15 Apr 01 May**

**Date**

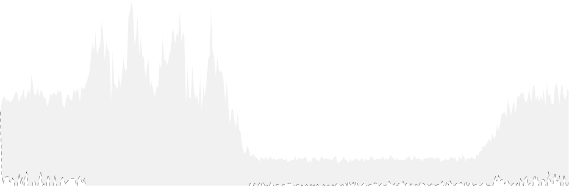
**Fig. 13.** Average cumulative number of pike that started its migratory movement towards one of the spawning grounds, which is obtained by averaging over both the realizations and the individuals. The shaded area illustrates the envelope in which 95% of the realizations is retrieved.

was followed during the telemetry study. Aside from the discrepan- cies between the absolute values of this quantity, [Fig. 16](#_bookmark35) indicates that the increased repulsion between *in situ* individuals during the spawning season is captured by the developed IBM because the pairwise distance between *in silico* individuals is clearly augmented during that season.

### Discussion

Even though the developed IBM is presented in the framework of recent attempts for understanding the spatio-temporal dynamics of pike in the river Yser, Belgium, it is generic in the sense that it can be tuned easily if another ﬁsh species is at stake by tuning its param- eters using species-speciﬁc telemetry data. Especially the transition functions *˛i*(*t*) and *ˇi*(*t*) as well as the speciﬁcities of the species’ territories, *i.e.* the variability of the home range throughout one annual cycle, deserves particular attention if one aims at using this model within for another species. Further, the swimming speeds should be drawn from distributions that are based upon data origi- nating from telemetry or recapturing experiments in the concerned study area, and it should not be forgotten that a HSI map of this area, which takes into account the environmental characteristics that are known to affect the particular species, has to be assem- bled since this is crucial for setting up a trustworthy initial spatial distribution of the individuals. As mentioned before, for the sake of simplicity, the home range during the passive sedentary season was inspired on values that were found in literature ([Donnely](#_bookmark62) [et al.,](#_bookmark62) [1998),](#_bookmark62) whereas the one during the active sedentary season was based upon a preliminary analysis of the telemetry data that were collected in the study area. Yet, within the framework of species- and location-speciﬁc studies, these values should be determined by means of dedicated methods of analysis using telemetry data ([Katajistoa](#_bookmark76) [and](#_bookmark76) [Moilanen,](#_bookmark76) [2006).](#_bookmark76) Analogously, such data should be exploited to obtain the experimental distributions that are under- lying the swimming speed during the consecutive behavioural seasons, as well as to delimit these behavioural seasons.

In spite of the common knowledge that most species tend to occupy those habitats within the ecosystem that are most suited to sustain them, which is particularly true for solitary ﬁsh species such as pike, IMBs are often evolved from a random initial dis- tribution. As such, this compromises the trustworthiness of the IBM simulations from the very beginning of the concerned simu- lation period, which can however be overcome by determining an *in silico* initial condition that reﬂects a realistic distribution of the *in situ* individuals’s positions. Generally, such an approach leads to an optimization problem, such as the one deﬁned by Eq. [(13)](#_bookmark26) for establishing a trustworthy initial pike distribution. The proce- dure adhered to in this paper for minimizing Eq. [(13)](#_bookmark26) and which



**Fig. 14.** Average distance between *ci* and *pi* (*t*) (a and b) and average swimming speed (c and d) for two individuals of the population at stake. The average values are obtained by averaging over the IBM realizations. The shaded area illustrates the envelope in which 95% of the realizations is retrieved.



comprises the stepwise solution of this optimization problem by assigning the territories consecutively as individuals are added to the population, requires signiﬁcantly less computing time than solving it by simultaneously optimizing the allocation of the territo- ries of all individuals within the concerned population. In addition, it is certainly not unlikely that such a stepwise optimization, and hence territory allocation, resembles the real-world situation more naturally since juvenile pike that are trying to establish their new territories will thereby be hindered by pike that already settled theirs.

Since it is presumed that pike is a solitary species that sticks to the same territory throughout its life, a pike’s territory is not reallo- cated once it has been pinned down by minimizing Eq. [(13).](#_bookmark26) Though

this presumption is based upon ﬁndings in literature ([Alessio,](#_bookmark40) [1986;](#_bookmark40) [Karas](#_bookmark40) [and](#_bookmark40) [Lehtonen,](#_bookmark40) [1993;](#_bookmark40) [Malinin,](#_bookmark40) [1969,](#_bookmark40) [1970),](#_bookmark40) a recent study in south Belgium revealed that only three out of six tracked ﬁsh returned at the end of the spawning season to the same territory as the one they occupied before they started their migratory quest ([Ovidio](#_bookmark59) [and](#_bookmark59) [Philippart,](#_bookmark59) [2005),](#_bookmark59) which is in line with the observations of [Diana](#_bookmark61) [et al.](#_bookmark61) [(1977).](#_bookmark61) If future studies would conﬁrm this ﬁnding, a (partial) reallocation of the territories at the end of the spawning season should be incorporated into the model. Similarly, if teleme- try data would reveal a clear relationship between the position of an individual within its territory and the HSI at that particular location, the IBM can be extended easily to take into account such ﬁndings since the current model structure allows them to move



**10 000**

**Position from the northern inlet of the study area (m)**

**9000**

**8000**

**7000**

**6000**

**Jan Apr Jul Oct Jan Date**

**Fig. 15.** Average position of an *in silico* individual (black line) of which the territory is centred near the one of the real-world individual for which the registered positions during 2011 (black dots) are plotted together with the corresponding conﬁdence interval (dashed lines).

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**Fig. 16.** Pairwise distance between *in situ* (a) and *in silico* (b) individuals during an annual cycle in 2011.

freely within their territory. Of course, this would require accu- rate knowledge of the environmental conditions that steer the HSI at a high spatial resolution, which might be difﬁcult to acquire. Finally, it is beyond question that the current IBM merely takes into account the spatio-temporal movements of pike, whereas an integrated population model would require a coupling between the migration module presented in this paper, on the one hand, and a growth model for pike, for which one could rely on a spatial version of a Leslie matrix model that has been proposed only recently for describing temporal density ﬂuctuations ([Arlinghaus](#_bookmark36) [et al.,](#_bookmark36) [2009),](#_bookmark36) on the other hand. Besides, by coupling the developed model with a prey distribution and/or hydrodynamics model, the *in silico* exper- iments will mimic the *in situ* spatio-temporal population dynamics even more closely.

Aside from the quantitative agreement between the *in silico* and *in situ* dynamics that was presented in [Section](#_bookmark25) [4,](#_bookmark25) there are a few other indicators of the trustworthiness of the proposed IBM. For instance, upon closer inspection of the average swimming speed and the average distance between *c**i* and *pi*(*t*), visualized in [Fig. 12](#_bookmark30)(a) and (b), respectively, it is clear that the overall patterns coming forward in these plots coincide with the ones expected tak- ing into account the assumptions underlying the migration model and the used parameter values. The model’s soundness is further conﬁrmed by the plots in [Fig. 14](#_bookmark33) because they indicate that the variability between the *in silico* population’s individuals can be pro- nounced, something which is typically observed between living organisms, irrespective of their species, sex and habitat require- ments ([Koed](#_bookmark44) [et al.,](#_bookmark44) [2006;](#_bookmark44) [Vehanen](#_bookmark44) [et al.,](#_bookmark44) [2006).](#_bookmark44) Furthermore, it was observed that the average *in silico* pike density near SG3 was only one third of the average densities recorded near SG1 and SG2, which is in line with expectation since the former is shielded from migrat- ing pike by SG2 that is encountered ﬁrst by upstream migrating individuals. Naturally, it is likely that pike nonetheless might pre- fer to migrate to SG3 if the carrying capacity near SG2 is exceeded. Yet, this interference can only be incorporated in the proposed IBM if one has insight into the spatial distribution of this carrying capacity, which can only be assessed if one has precise and detailed knowledge of the spatio-temporal distribution of prey ﬁsh across the river Yser. We agree that the distribution of prey ﬁsh might be an important factor inﬂuencing pike migration, but data on such distributions are lacking to this day. Firstly, since it was practically not possible, nor ﬁtting within the scope of the telemetry study to tag and position pike prey species. Secondly, existing gill net and electro ﬁshing data sets on the ﬁsh communities in the river Yser are incomplete, such that they cannot be combined with the telemetry data set, or be used to investigate the effect in a multivariate anal- ysis or ANOVA. Furthermore, there is no information on the diet of pike in the river Yser, which would be needed to gain insight into this species’ diet that is known to vary seasonally and between

water systems and even within the population ([Beaudoin](#_bookmark41) [et al.,](#_bookmark41) [1999;](#_bookmark41) [Flinders](#_bookmark41) [and](#_bookmark41) [Bonar,](#_bookmark41) [2008).](#_bookmark41) Finally, to our knowledge there are no studies on the spatial predation behaviour of pike, which can be attributed to the fact that most studies on pike’s predation behaviour are conducted within the scope of biomanipulation and because such studies would be very time consuming ([Craig,](#_bookmark51) [2008;](#_bookmark51) [Beaudoin](#_bookmark51) [et al.,](#_bookmark51) [1999;](#_bookmark51) [Kahilainen](#_bookmark51) [and](#_bookmark51) [Lehtonen,](#_bookmark51) [2003).](#_bookmark51)

### Conclusions

In this paper, an IBM for describing the spatio-temporal distribu- tion of northern pike is proposed. The established model takes into account the speciﬁcities of the considered ﬁsh species. Although this model is presented within the framework of management- related issues in the river Yser, Belgium, it is nonetheless generic in the sense that it contains only a limited number of model param- eters, which can be determined for the species and river system at stake. In this paper, the model parameters are derived from data collected during a telemetry study in the river Yser. Moreover, it is shown that the registered *in situ* trajectories fall within the envelope of possible *in silico* trajectories, which demonstrates the trustworthiness of the developed model.

In addition to the model, a methodology is proposed that can be relied upon for establishing trustworthy initial conditions from which the spatio-temporal dynamics can be evolved. Future work should aim at a coupling between the here proposed migration model and already existing growth models in order to arrive at an integrated spatio-temporal model for mimicking the dynamics of pike in aquatic ecosystems.

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