A comparison of model structures for the simulation of amphipod (Talitrus saltator) population dynamics.

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Abstract: A dynamic model is proposed in order to simulate sandhopper (*Talitrus saltato*r) population dynamics under various scenarios. It was built under the Stella simulation software and so far it has attained the calibration and verification stages. The basic structure of the model depends on the simulation of the number of animals in each age class (45 days). A von Bertalanffy growth curve has been adjusted to the treated field data. From this equation another one expressing the instantaneous growth rate was extracted and used to calculate the growth. The number of individuals in each age class increases due to the ageing process i.e. new individuals coming from the previous age classes. The number of animals in the first age class increases due to recruitment. Fertility is related to the weight of females, therefore the recruitment is predicted by knowing the average weight and the number of females present. The outputs from each age class are the ageing and mortality. Three types of recruitment were tested: 1. A single and long reproduction period only dependent on the day of the year. 2. More than one reproduction period but also dependent on the day of the year. (2 and 3 periods). 3. Reproduction dependent on the temperature and day length. Each of these types involved a different set of equations therefore the comparison of the results of each type acts (sensu lato) as a form of sensitivity analysis. Satisfactory results were accomplished by some of the model variants described above. A simple alternative approach to these model variants was also tested with the best results. No size dependent fertility and no parallel structures to simulate growth in size or weight were considered. In addition the use of shorter age classes (28 days) was also experimented.

Keywords: sandhopper; recruitment; population density; photoperiod; temperature.

1. INTRODUCTION

In the literature some studies on *T. saltator* mention reproductive biology and population dynamics. These studies are absolutely fundamental but with few exceptions [e.g. Williams, 1985] the causality of the processes affecting population dynamics is not thoroughly studied. Ecological models lead to a higher degree of self-conscience in what concerns the gaps in our knowledge. Moreover they allow us to test some hypothesis regarding the mechanics behind the observed processes. By building a population dynamics model of *Talitrus saltator* we are not only building a tool for predictions under various scenarios but we are also forced to produce a state of the art on factors affecting its population dynamics. It was therefore our purpose that the model would accomplish the following goals: a) a correct simulation of the population dynamics of *Talitrus saltator* b) incorporation in the model of the most important ecological processes involved in the population dynamics of the species and c) indications on the relative importance of each parameter or process on the dynamics of the population. This will aid the use of the species as a possible indicator of beach disturbance.

2. DATA BACKGROUND

The calibration of the model was performed using data from *Talitrus saltator* population structure on the coast of Lavos obtained by Marques et al. [subm.]. Data used included, life span, density (per m coast), recruitment periods, growth, sex ratio and age of sexual maturation. Mortality rates were calculated by fitting exponential decay equations to the data of the densities of each cohort during the period when it was identified. This procedure assumes a constant value for the mortality of each cohort throughout its entire life. No consistent length or weight dependent daily mortality rates were found, therefore an average value of 0.00993 (S.D. of 0.00757) and a median value of 0.00638 were found for the cohorts identified. Other important information, such as fertility, was obtained from previously published papers [e.g. Williams, 1978] and then checked for model performance. In the case of the fertility some of the versions of the model used a weight vs. fertility regression but the final one relied on an average value of 13 per female.

3. CONCEPTUALISATION OF THE MODEL

Sandhopper (*T. saltator*) population was subdivided into age classes, each one constituting a state variable. This division would account for differences on the fertility of the females and would allow us to calculate the number of individuals in each age class, their average weight and the biomass of the entire population. Air temperature, lunar periodicity and day length are the main forcing functions for the model (Figure 1). The moisture content of the sand seems to affect only the spatial distribution of the animals and therefore it was not considered a relevant forcing function.

4. MODEL STRUCTURES

Each sandhopper entering an age class takes 45 or 28 days to reach the next one depending on the model version. At the end of the final age class sandhoppers are considered to have reached the maximum possible life duration. Recruitment happens during one or more than one period of the year depending on the version of the model being used.

4.1 First approach

Average sandhopper weight was calculated for each of eight age-class time intervals as described by Anastácio et al. [1999]. The increase in weight for each 45-day period was considered dependent on the temperature. At very low winter temperatures [David, 1936] but also at extremely high summer temperatures [Scapini et al., 1992], sandhoppers retreat to burrows therefore it was assumed that growth was arrested. Fertility was considered dependent on the weight and several mechanisms to start recruitment were tested.

4.2 Second approach

Considerably simpler than the previous one. Eleven, instead of eight, age classes, were used lasting 28 days each. This value was chosen taking into account the need to test smaller intervals in the age classes and also the lunar influence [Williams, 1979] in the life cycle of the animal. The weight of the animals was not calculated and therefore fertility was considered as a constant value per female, independently of its age. This approach uses a minimum and a maximum temperature and a minimum day length to proceed with the recruitment. Recruitment takes place on a semi-lunar periodicity and it was considered that maturity is attained only near the end of age class 4. This was accomplished by considering age classes 1 to 3 as totally constituted by juveniles (or immatures) and age class 4 as having only a small percentage of adults capable of reproduction.

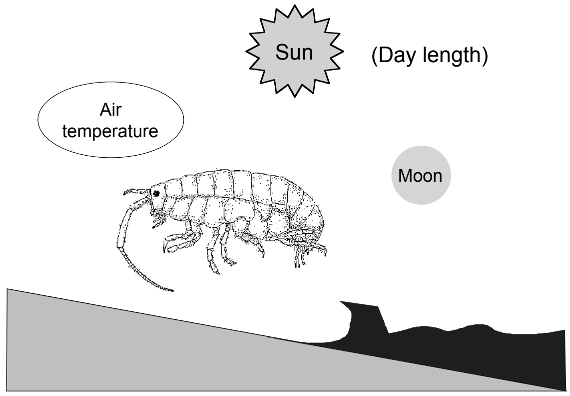

Figure 1. Conceptual model for Talitrus saltator population dynamics.

Table 1. Components of the model and their values when applicable. [a] - initial values are presented. F.F.=Forcing function. Par.=Parameter. S.V.=State Variable. C.R.=Calculated rate. C.V.=Calculated value

Type	Name	Value	Units
F.F.	temperature	time series	ºC
F.F.	daylength	time series	hours
F.F.	timenew	1 to 364	dimensionless
Par.	mortality_rate	0.178	per 28 days
Par.	pctg_age 4	0.9	proportion
Par.	fertility	13	recruits/female
Par.	max_recruit temp	27	ºC
Par.	min_recruit_dayl	13	hours
Par.	min_recruit temp	14	ºC
Par.	recruit_pulse_period	14	days
Par.	sex_ratio	0.455	females/total
S.V.	age 1	0[a]	ind./m coast
S.V.	age 2	0[a]	ind./m coast
S.V.	age 3	0[a]	ind./m coast
S.V.	age 4	0[a]	ind./m coast
S.V.	age 5	253[a]	ind./m coast
S.V.	age 6	0[a]	ind./m coast
S.V.	age 7	193[a]	ind./m coast
S.V.	age 8	235[a]	ind./m coast
S.V.	age 9	153[a]	ind./m coast
S.V.	age 10	0[a]	ind./m coast
S.V.	age 11	0[a]	ind./m coast
C.R.	recruit	variable	ind./m coast/ day
C.V.	juveniles	variable	ind./m coast
C.V.	adult_females	variable	ind./m coast
C.V.	total_number	variable	ind./m coast

5. EQUATIONS

Stella (version 5.1.1) with Euler integration method was used as software to run the model.

5.1 First approach

a) Growth:

The daily increase in dry weight was determined and used to fit Equation 1:

$$\frac{d_w}{d_t} = 0.002496 \cdot DW^{\frac{2}{3}} - 0.006845 \cdot DW \qquad (1)$$

Having a series of values, W1 to W8, corresponding to the weights after each 45 days period (age class) it is possible to calculate the dry weight by keeping track of the value of the previous W, 45 days ago (Equation 2):

$$Wi = W(i-1)_{(-45)} + T_{eff} \cdot days \cdot (0.002496 \cdot W(i-1)_{(-45)}^{(2/3)} - 0.006845 \cdot W(i-1)_{(-45)}) \qquad (2)$$

Wi - dry weight at the end of age class “i”

$W(i\text{-}1)_{(-45)}$ - dry weight at end of age class “i-1”

T_{eff} - temperature regulator for growth, dependent on the average temperature during growth

days - number of the previous 45 days in which growth was possible

The temperature regulator for growth, “T_{eff}” ($f_{(T)}$ in the equation) was calculated with the aid of the following equation from Lehman et al. [1975 in Bowie et al., 1985], which has the shape of a skewed normal distribution (Equation 3):

$$f_{(T)} = e^{\left(-2.3\left(\frac{T - T_{opt}}{T_x - T_{opt}}\right)^2\right)} \qquad (3)$$

T_{opt} - temperature for maximum growth

T_x - $=T_{min}$ when $T<=T_{opt}$

$=T_{max}$ when $T>T_{opt}$

T_{min} - Minimum temperature for growth.

T_{max} - Maximum temperature for growth.

In the model the following values were used according to unpublished results from Collombini and Chellazi: Maximum temperature 28.8ºC, minimum temperature 9ºC and optimum temperature 24.7ºC. This is in accordance with data showing that the species was active from 10 to 28.8ºC [Scapini et al., 1992].

b) Mortality:

Analysis of field data did not demonstrate any age, size or weight dependent mortality rates. For this reason a common value was used for all the age classes.

c) Fertility and recruitment:

Fertility is known to depend on the size of *T. saltator*. The equation from Williams [1978] was used in which we have (Equation 4):

"number of embryos per brood" =
= -2.58 + 1.17 * "body length" (4)

Three types of recruitment were tested. 1. A single and long reproduction period only dependent on the day of the year. 2. More than one reproduction period but also dependent on the day of the year: 2a) two periods or 2b) three periods. 3. Reproduction dependent on the temperature and day length

Each of these types involved a different set of equations therefore the comparison of the results of each type will act (*sensu lato*) as a form of sensitivity analysis. Type 1 used Equation 5 for the regulation of recruitment:

$$\text{Fert reg} = e^{\left(-2.3\left(\frac{\text{Timenew} - \text{Max\_day}}{\text{Phase} - \text{Max\_day}}\right)^2\right)} \qquad (5)$$

The variable “Phase” will assume different forms when the following conditions are met:

IF Timenew >Max_day THEN Phase = End_day ELSE Phase = Start_day

Variables in Equation 5 are: Fert reg = regulator for recruitment. Timenew = Julian day. Max_day = day when the highest recruitment happens. Start_day = day when recruitment starts. End_day = day when recruitment ends.

This equation provides an adequate shape of the recruitment curve but it needs to be multiplied by two other values in order to obtain the number of new recruits each day. These are the number of new recruits that would be released if all the mature females were giving birth and the maximum percentage of mature females releasing new recruits.

Type 2 (a and b) used Equation 6 modified from the normal distribution curve presented in Sokal and Rohlf [1987] for each wave of recruitment:

$$\text{Wave} = a \cdot \frac{0.39894}{\text{sd}} \cdot e^{\left(-0.5\left(\frac{\text{Timenew} - \text{day}}{\text{sd}}\right)^2\right)} \qquad (6)$$

In which:

Wave = Recruitment wave. a = correction factor for the adjustment of the curve. sd = standard deviation. Timenew = Julian day. day = day of the maximum recruitment value.

“Wave” multiplied by the number of new recruits that would be released if all the mature females were giving birth will provide the value for the new recruits at each day.

In case 2a for the first recruitment wave a = 1.9, day = 140 and sd = 20 and for the second recruitment wave, a = 0.15, day = 223 and sd = 21.0236. In case 2b for the first recruitment wave a = 0.8, day = 110, sd = 6, for the second recruitment wave, a = 1.3, day = 160, sd = 4 and for the third recruitment wave, a = 0.3, day = 235 and sd = 6.
Recruitment type 3 used the following logic (7) to produce recruits:

IF (Temperature > min_recruit_temp AND Temperature < max_recruit_temp AND Daylength>min_recruit_dayl) THEN PULSE(1, 1, recruit_pulse_period) ELSE 0

It means that if the temperature is within the limits for recruitment and if the day length is long enough to start reproduction then we will have recruitment on a periodical basis e.g. based on a lunar cycle. Otherwise recruitment will be zero. The model used a value of 14ºC for the minimum temperature for recruitment, 27ºC for the maximum temperature for recruitment, and 13 for the minimum day length.

5.2 Second approach

Equations defined in the previous approach for Growth (and its temperature regulation), female fertility and recruitment do not apply in the present case. Recruitment i.e. the number of recruits being added to the population each day at age class 1 is defined by Equations 8, 9, 10 and 11:

recruitment = recruitment_pulse _ adult_females _ fertility (8)

recruitment_pulse =
IF (temperature > min_recruit_temp AND temperature <max_recruit_temp AND daylength>min_recruit_dayl) THEN PULSE(1, 1, recruit_pulse_period) ELSE 0 (9)

adult_females = sex_ratio _ (total_number - juveniles) (10)

juveniles = age_1 + age_2 + age_3 + pctg_age4 _ age_4 (11)

The average number of eggs produced by each female ("fertility"=13) was determined by Williams [1978]. The equation for "recruitment_pulse" uses an IF THEN ELSE logical statement and it means that a minimum and a maximum temperature and a minimum day length are needed to produce a certain output value. If these conditions are met then a value of one will be produced at a periodicity defined by "recruit_pulse_period" if they are not met then zero is the output value.
In the equations most of the names of the components are self-explanatory. Table 1 provides the values used in each parameter, the initial values of each state variable and also an explanation for the meaning of each model component.

6. SENSITIVITY ANALYSIS

Table 2. Sensitivities of the density of *Talitrus saltator* (total number) to several model parameters.

	Sensitivities of "total number"			
	+50%	+10%	-10%	-50%
mortality rate	-1.041	-1.460	-1.764	-2.678
pctg age 4	-0.228	-1.028	-1.028	-1.028
fertility	0.810	0.765	0.742	0.696
max recruit temp	0.000	0.000	0.847	1.278
min recruit dayl	-1.278	-3.038	-45.036	-44.113
min recruit temp	-1.031	-2.748	-11.261	-2.252
recruit pulse period	-0.397	13.962	-12.159	-2.868
sex ratio	0.810	0.765	0.742	0.696

Table 3. Sensitivities of the density of *Talitrus saltator* (total number) to several initial values.

	Sensitivities of "total number"			
	50%+	10%+	10%-	50%-
age 5	0.708	0.708	0.708	0.708
age 7	0.172	0.172	0.172	0.172
age 8	0.082	0.082	0.082	0.082
age 9	0.036	0.036	0.036	0.036

The method described by Jorgensen [1988] and by Haefner [1996] was used to perform a sensitivity analysis. The effects caused on the density by ±10% and ±50% changes in the parameters and initial values values were tested (Table 2 and 3). When initial values were zero it was impossible to use the formula.
The total densities of *Talitrus saltator* are deeply affected by variations in the minimum recruitment day length (min_recruit_dayl), the minimum temperature for the recruitment (min_recruit_temp), and the period between each recruitment wave (recruit_pulse_period). These parameters have a strong influence in the timing of reproduction and population density as opposed to the maximum temperature for recruitment (max_recruit_temp), which seems rather unimportant for model performance. Also very important is the "mortality rate", showing also an inverse reaction pattern to changes in the parameter.

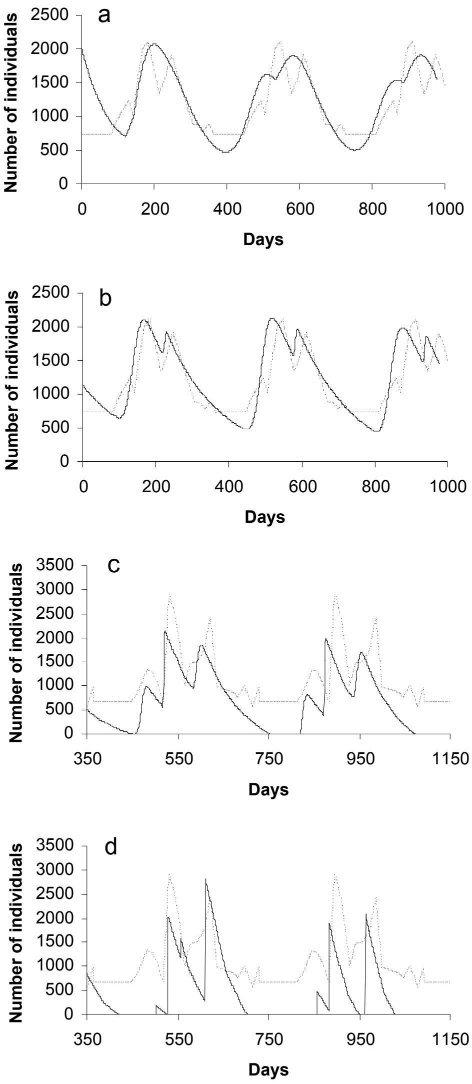

Figure 2. Field data and simulations results (dark line) obtained under the first approach using four different model versions to simulate recruitment: a) one long reproduction period dependent on the day of the year b) two reproduction periods dependent on the day of the year. c) three reproduction periods dependent on the day of the year. d) reproduction dependent on the temperature and day length. “a” and “b” use smoothed field data. “c” and “d” present simulation results after an initiation run of ca. one year.

The sensitivity of the population densities to each initial value of the state variables was equal for all the levels of change. The density of *T. saltator* was most sensitive to the initial number of individuals in age class 5 and least sensitive to the initial number in age class 9.

7. SIMULATION RESULTS

7.1 First approach

From the different types of recruitment chosen different results were obtained (Figure 2). In situation a and b the observed densities are smoothed data, calculated as an average of three points in order to eliminate abnormal density oscillations in consecutive sampling dates. Situation a corresponds to a simulation of a single and long recruitment period, and we can see that two bumps in the density line appear spontaneously. Situation b corresponds to the simulation of two recruitment waves and therefore the smoothed densities field data and the simulated density present a closer resemblance in behaviour.

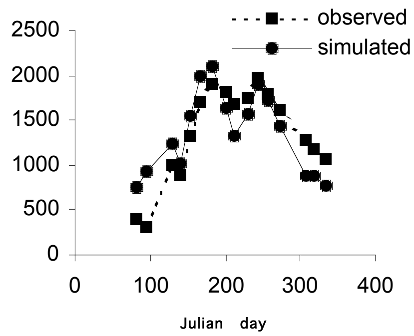

Figure 3. Results obtained from the final model version (second approach). Plot of the observed and simulated data vs. time for each sampling date only.

Situations c and d in Figure 2 represent a comparison of simulated density data and non-smoothed field data. This last type of data presents big oscillations and therefore it is more difficult to model such behaviour. Situation c represents the simulation obtained by the model in which three different periods of reproduction were used. One can see that in this case both the behaviour and the values simulated closely match the field data. Finally in the last situation (d) a dependence on both the temperature and the day length was used, and recruitment takes place on a lunar periodicity. From the figure it seems that the behaviour of the simulated data is close to the real data. Unfortunately the model presented a very weak long-term stability and therefore only the data from two consecutive years are presented.

7.2 Second approach

This approach is in our opinion the best one. It shows a good fit between the observed and simulated densities of *Talitrus saltator* (Figure 3) by using temperature and day length dependencies for recruitment. There is a slight tendency to overestimate the number of individuals at small densities and this will probably occur during the cold season.

8. DISCUSSION

Two main approaches were used: the first one with four different versions and the second one with a single and successful version. Although the first approach resulted generally in a reasonable match between simulated and observed data it had some serious inconvenients. The first 3 model versions (section 5.1c) were insufficient for the model purposes; in fact recruitment was simply started by the day of the year. This has no biological meaning although the same photoperiod is found at the same Julian day. The fourth model version considered mechanisms for the start of reproduction in which day length and temperature were now considered important. Nevertheless the model had a poor long-term stability. The use of continuous reproduction during a period of the year or during a few different periods provided non-satisfactory results. In all the four cases in order to obtain a good match between simulated and observed values mortality rates had to be unrealistically high. The consequence of this is the indication that recruitment would be discontinuous and therefore a different model structure had to be tested. This is what led us to the implementation of the second approach. This is in fact a simpler but also an explanatory model. We believe that the processes taking place in this model correspond to mechanisms observed in nature. Therefore this approach is the model being discussed in the following paragraphs.

There is high model sensitivity to changes in the structure and parameters of the recruitment mechanism. This is notorious when several model versions were sequentially tested using different approaches for the recruitment process. Also, as expected, the value of the mortality rate is very important for the stability of the model. A rate of 0.178 per 28 days was determined by calibration and it is equivalent to 0.00726 per day, which is close to both the average (0.00993) and the median (0.00638) values for the field data cohorts.

So far the model attained the calibration phase and the question to be posed is if it will make correct predictions under a different situation. This could mean another year in the same or a nearby location or a totally different and remote *T. saltator* population. If one of the above is achieved then the model can be considered validated i.e. tested with an independent data set [Jorgensen, 1988]. Nevertheless the process of model building clarified some issues and some gaps in the knowledge were identified.

9. ACKNOWLEDGEMENTS

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