Social interactions can affect feeding behaviour of fish in tanks

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Fish from the same clutch of eggs, so of the same age and family, can differ substantially in size after some time in a tank as result of social interactions. On the basis of computer simulation studies I here demonstrate that it is possible to mimic this empirical observation using the rules of the standard Dynamic Energy Budget (DEB) model, supplemented with a simple stochastic module for interaction between individuals that have identical parameters. The remarkable result is that length-at-age of two individuals in a tank where the number of food particles is kept constant closely follows von Bertalanffy growth curves with very different parameters, while in reality the individuals have identical parameters. The empirical observation demonstrates that fish are close to the supply end of the supply–demand spectrum and that age-based models for growth don’t apply to supply systems. The significance of the result is discussed.

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1. Introduction

Visual interaction is known to affect growth in fish (Jobling, 1994), but (Wirtz, 1975) could not demonstrate effects of size differences in blennius. Fig. 1 shows two fish from the same brood, which have lived in the same five-litre aquarium. (Insland et al., 1998) concluded that size-dependent growth alone fails to explain size variation in turbot populations. Cohorts of equally sized artic char have been found to grow faster than cohorts of varying size (Seppä et al., 1999) due to suppressed aggression. This probably relates to the present situation. The mechanism behind the size difference is in this case probably the way of feeding, which involved a limited number of relatively big food chunks for the whole brood supplied once each day. Initially, the size differences were very small, but the largest animal always took priority over its smaller siblings, which amplified the size differences. This mechanism is further supported by the experiment to select a small individual and place it in a separate tank. Now having access to a much larger amount of food, it rapidly grew and the size difference with the largest fish in the first tank almost disappeared. So the small individuals had the metabolic capabilities to grow at the rate of the large individuals.

Although I have no detailed measurements that quantify the effect of social interaction on feeding, the qualitative observation is important enough to wonder if the standard Dynamic Energy Budget (DEB) model can mimic the phenomenon, if supplemented with rules for the interaction between individuals. Two further motivations for this effort are the importance of stochasticity in energetics and the role of interactions between individuals in the maintenance of diversity. I discuss these reasons in a bit more detail.

The coupled processes of substrate (food, nutrients) uptake and use have behavioural and metabolic components, and most stochastic effects are in the behavioural components. Behavioural stochasticity in population dynamical models does much more than just adding noise, it can affect the asymptotic behaviour in a qualitative way. It is well-known, for instance, that most simple deterministic prey–predator models for closed systems show the paradox of enrichment (Gurney and Nisbet, 1998): at small amounts of nutrient, the prey–predator system has a point attractor, but if we increase the amount of nutrient, the system suddenly starts to oscillate with a substantial amplitude. The nutrient level at which this occurs is called a Hopf bifurcation point in bifurcation theory (Kooi and Kelpin, 2003). It is a mathematical property of such models, that has hardly empirical support. We showed that the incorporation of stochasticity in the searching of the predator dramatically affects this behaviour of the prey–predator system (Kooijman et al., 2007). The effect of an increase of the amount of nutrient is a gradual increase of the deviations from the mean and they become gradually more regular, i.e. the variance in the amplitude and period decreases. Every now and then the systems spend some time close to the mean value (i.e. the unstable attractor of the deterministic model). No sudden changes in the behaviour of the stochastic system occurs at the Hopf bifurcation point, and the increase in deviations from the mean start at a lower amount of nutrients, namely at the focal point, i.e. the point where the deterministic models starts to show overshoot behaviour (i.e. the population first exceeds its carrying capacity, and then settles down in a damped oscillatory way). This latter behaviour is temporary only, and the long-term behaviour is still a stable point attractor. On the approach to the Hopf bifurcation point, the overshoot behaviour become more intense and it takes longer to damp, which explains why just after the Hopf, the amplitude is substantial. Stochastic perturbations force the system in the overshoot behaviour continuously. This qualitative

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difference between stochastic and deterministic population models applies to a rather large class of models (Nisbet and Gurney, 1982).

Most simple competition models, where food or nutrient uptake is monotonously increasing with food (nutrient) density, have an unrealistic property: the species with the lowest resource needs out-competes all other species. In nature we can observe a bewildering species diversity, but this diversity is extremely hard to mimic in simple models. A rather general theorem states that the number of competing species that can co-exist in the long run in a spatially and temporarily homogeneous environment cannot exceed the number of types of nutrient (food) in the case the system has a point attractor (Gurney and Nisbet, 1998). In the case of limit cycles, a rather general theorem states that the out-competes all other species. In nature we can observe a basis of many forms of symbioses (Kooijman et al., 2003). A third and add chemical/metabolic realism). This mechanism is also the products of other species (and so increase the number of resources category. Another is to include (mutual) syntrophy: species live of spatial (and/or temporal) structure, and allow for local, but not global values), but not many more. This well-known problem of simple models can be solved in different ways that can be classified in three categories (which all make models more complex). One is to include spatial (and/or temporal) structure, and allow for local, but not global extinction by choosing appropriate rules for migration. Metapopulation models (Hanski and Gaggiotti, 2004) belong to this category. Another is to include (mutual) syntrophy: species live of products of other species (and so increase the number of resources and add chemical/metabolic realism). This mechanism is also the basis of many forms of symbioses (Kooijman et al., 2003). A third route is to let food uptake not only be a function of food availability, but also a function of the population density. Social interaction can be one of the mechanisms that is known to allow for long-term co-existence of many species that compete for a small number of resources in homogeneous environments in a wide window of parameter values (Kooijman and Troost, 2007).

Having given context to study stochastic models for social interaction, this paper first presents a specification of a simple set of the rules for searching of food particles and social interaction; then follows the presentation of some computer simulations with conclusions and a discussion places the conclusions in a wider context.

2. Behavioural rules

Fig. 1. These talking gouramis, Trichopsis vittatus, come from the same brood and therefore are the same age. They also grew up in the same aquarium. The size difference resulted from competition for a limited amount of food chunks, which amplified tiny initial size differences.

The focus is here on a stochastic model for feeding of a single individual on a single type of food particles of equal size in a spatially homogeneous situation that is consistent with the standard DEB model (Kooijman, 2000). I then extend the model to more individuals and see how social interaction can amplify size differences. The stochastic feeding model is constructed such that the expected feeding rate of an individual of length L is \( J_{\text{AS}} = f \langle \bar{h}_{\text{AS}} \rangle \) with scaled functional response \( f = X/(K + X) \), where \( f \) is quantified as mass of food particles per time and food density \( X \) and saturation constant \( K \) as mass of food particles per volume, as in the standard DEB model; \( \langle \bar{h}_{\text{AS}} \rangle \) is the maximum surface area-specific food uptake rate. The mass of a food particle is \( M_L \) (in C-mole). In number of food particles, we write for the feeding rate in number of particles per time \( \dot{h}_X = \bar{h}_{\text{AS}} \langle \bar{h}_{\text{AS}} \rangle L^2 \) with maximum specific feeding rate \( \bar{h}_{\text{AS}} = \bar{h}_{\text{AS}} M_L \) and \( f = X/(K + X) \), with \( X = X_M K \) and \( K = X_M K \) (Notice that \( \bar{h}_{\text{AS}} < 0 \) and \( \dot{h}_X > 0 \). At high food density \( X_M \), for \( f = 1 \), searching takes a negligible amount of time, and the mean time it takes to handle a single food item is \( t_{\text{h}} = 1/\bar{h}_{\text{AS}} \), where \( \bar{h}_{\text{AS}} \) is the maximum surface area-specific feeding rate. Since \( \dot{h}_X = (t_x + t_0) \), the time for searching is \( t_x = 1/\bar{h}_X - 1/\bar{h}_{\text{AS}} = K f (\bar{h}_{\text{AS}})^{-1} X_M K L^{-2} \).

Suppose that the food particles at a given time are randomly distributed in space with mean density \( X_M \). The probability that the nearest food particle is at a distance larger than \( L \) from an individual at a random site is

\[
\text{Prob} \{ L_d > L \} = \exp \left( -X_M L^{n4} / 3 \right)
\]

see e.g. (Stoyan, 2006). So, the nearest food particle is at mean distance

\[
\epsilon L_d = \int_0^\infty \text{Prob} \{ L_d > L \} dL = (4/3) (X_M L^{n4} / 3)^{-1/3} = a X_M^{-1/3}
\]

with \( a = \Gamma(4/3) (n4/3)^{-1/3} = 0.554 \). Travelling at speed \( S \), the time to reach this particle is \( t_x = \epsilon L_d / S = a X_M^{-1/3} / S \), so the speed is \( S = a X_M^{-1/3} / t_x = a X_M^{-1/3} / (\bar{h}_{\text{AS}} X_M K)^{1/2} = b = a X_M^{-1/3} / (\bar{h}_{\text{AS}}) \).

We now construct a feeding process of a single individual in a unit cube of habitat on the basis of the following rules

Rule 1 a new food particle appears at a random site within the cube at the moment one of the resident particles disappears. It stays on this site till it disappears; the total number of food particles remains constant.

Rule 2 a food particle disappears at a constant probability rate \( \dot{u} \), or because it is eaten by the individual. The moments of disappearance and the sites of appearance of food particles are the only sources of stochasticity in this model, which translate into a stochastic travelling time to the nearest food particle.

Rule 3 the individual travels in a straight line to the nearest visible food particle at speed \( S = b X_M^{1/2} \), eats the particle upon arrival and waits at this site for a time \( t_0 = (\bar{h}_{\text{AS}})^{-1} L^{-2} \). The individual changes direction if the food particle at which it is aiming disappears or a nearer new one appears. It changes speed because of changes in length.

Rule 4 the individual grows following the standard DEB model, i.e. the food particle converts to reserve instantaneously (because the digestion process in not part of the standard DEB model); the scaled reserve density \( e \) of an individual of structural volume \( L^3 \) makes a jump from \( e \) to \( e + (L_x / L^3) e \) upon feeding, where \( L_x \) is a constant length that depends on the size and the nutritional value of a food particle (see below); scaled reserve density is used for metabolism at rate \( d e / dt = e \langle h_{\text{AS}} \rangle L^2 / L \); reserve converts to structure and the length changes at rate \( \delta \) = \( L = \delta L \). At time \( t = 0 \) the length is \( L = L_0 \), and the reserve density \( e = f \).

Rule 5 all food particles are visible. We now extend the rules for \( N \) individuals that interact not only by competition, but also by social intimidation using the following rule that replaces Rule 5:

Rule 5 a food particle becomes invisible for an individual of length \( L_x \), if an individual of length \( L_x \) is within a distance \( L_x (L_y / L_x)^2 \) from the food particle, irrespective of being aimed at.

The interpretation of the food length \( L_x \) is \( L_x^2 = M_L X / M_{\text{AS}} \), which makes that \( L_x = \langle h_{\text{AS}} \rangle L X_{\text{AS}} / M_{\text{AS}} \). Notice that by increasing mass \( M_L \), while keeping \( \langle h_{\text{AS}} \rangle \) constant, the maximum length will increase as well. Keeping \( \langle h_{\text{AS}} \rangle \) constant, however, will result in an increase in variance.
The food density $X$ and the particle disappearance rate $\mu$ are environmental parameters. Although the food particles do not move, the replacement scheme has the effect as if the particles move at infinite speed to another random location at random points in time. The mean distance between two random points on a unit edge is $1/3$, on a unit square it is $0.521405$, and on a unit cube it is $0.65853$. So the mean speed of a food particle in a cube with edge $L_d$ is $0.65853L_d\mu$. If this is in the same order of magnitude as the speed of the organism, it strongly affects the feeding process; if it is much larger, the individuals will starve to death.

We have two different spatial units, that of the individual ($h_{xm}$, $L_b$ and $L_s$) and of the environment (in $X$, $K$ and $L_{Ls}$), here chosen as cm and m, respectively. Speed is primarily controlled by the saturation constant $K$. The social interaction increases with decreasing number of food particles per individual. The variance increases with food length $L_s$, but decreases in time because of the smoothing capacity of the individual increases with size (the catabolic flux is inversely proportional to a length measure).

We have 8 parameters $X_b$, $K_x$, $L_b$, $L_{Ls}$, $h_{xm}$, $k_{sh}$, $g$, $\mu$ for feeding and growth of a single individual with state variables scaled reserve density $e$ and structural length $l$ and one extra parameter, $L_n$, for the feeding and growth of $N$ interfering individuals. Notice that $[h_{xm}]L_b^3$ plays the role of the energy conductance $\dot{V}$ in the standard DEB formulation, which does not account for stochasticity or the discreteness of food particles. This stochastic extension, therefore, does not come with an increase in the number of parameters, while we need a single parameter to introduce social interaction. We can out-scale one parameter, if our interest is in relative length change, $l = L/L_n$ with $L_n = \{h_{xm}\}^{1/3}k_{sh}$, and another one by choosing the spatial scale such that $K_x = 1$, and a final one if we out-scale time, e.g. by choosing the maintenance rate coefficient $k_{sh}$ as unit of time. The core of the problem of how the variance in length builds up as function of time, e.g. by choosing the growth rate simultaneously, such that it can be summarised as a single effect, namely on food availability. This follows from the structure of the DEB model, we don’t need to fit very many parameters to the simulation results. Without these effects we expect $e = X/(K_x + X_b) = 10/(2 + 10) = 0.833$ and observe $e = 0.77$, so the effect is a factor $0.77/0.83 = 0.92$. In the situation with two fish, the behaviour of the scaled reserve density for both individuals shows that one individual first grows slightly faster than the other, then the other individual was more lucky, a length difference developed and social interaction then

3. Results and conclusion

Fig. 2 illustrates simulation results. It is important to remember that both individuals have exactly the same parameter values, all deviations are caused by interaction with their environment, i.e. the food availability, which differentiates between the individuals during the growth period.

The first observation is that reserve smoothes out stochastic fluctuations in food availability very effectively and the growth curves hardly reveal the stochastic nature of the feeding process. The scaled reserve density shows erratic behaviour when the fish is small, but this rapidly damps when it grows. This result follows from the fact that the relaxation time for the scaled reserve density is proportional to body length, i.e. $L/L_n$.

The second observation is that for the single fish stochastic growth is retarded relative to the deterministic expectations because of the border effects (which reduces local food density near the edges and especially in the corners), and the stochastic displacements of food particles (which increase the travelling distances). After an erratic start of the scaled reserve, it settles to a constant value; no obvious trend is visible. This means that, despite the fish is growing, and so travelling faster, the border effect hardly depends on size. The consequence of the standard DEB model is that, at constant reserve density, length-at-age is growing as a von Bertalanffy curve with inverse von Bertalanffy growth rate

$$r^{-1} = 3/k_{sh} + 3L_{Ls}/e$$

with $L_n = eL_{Ls}$

So the inverse von Bertalanffy growth rate is linear in the ultimate length, which means that the border effect, in combination with the displacements of food particles, changes ultimate length and the von Bertalanffy growth rate simultaneously, such that it can be summarised as a single effect, namely on food availability. This follows from the structure of the DEB model, we don’t need to fit von Bertalanffy growth curves to the simulation results. Without these effects we expect $e = X/(K_x + X_b) = 10/(2 + 10) = 0.833$ and observe $e = 0.77$, so the effect is a factor $0.77/0.83 = 0.92$. In the situation with two fish, the behaviour of the scaled reserve density for both individuals shows that one individual first grows slightly faster than the other, then the other individual was more lucky, a length difference developed and social interaction then.
further amplifies the size difference beyond the capabilities of stochastic effects to turn the tables. Again after an erratic start, the scaled reserve densities settle at constant values, with the consequence that length-at-age is very close to von Bertalanffy growth curves. The mean scaled reserve density of the larger fish is slightly smaller than that of the single fish, which means that it experiences some competition of the smaller fish. The number of food particles was constant, so the mechanism must be that due to the feeding, the particles jump more frequently which elongates travelling time and reduces food intake. The smaller fish obviously experienced much more competition from the larger one.

We can conclude that this extension of the standard DEB model can indeed mimic the effect as seen in Fig. 1, and can result in very different growth curves despite the fact that the individuals were identical in all their parameters.

4. Discussion

The presented simple model for social interaction can be extended into many directions, but here I tried to keep the number of extra parameters down to the absolute minimum of one, while still including the key feature that the larger the size-difference the larger is the social interaction. I also stylised the movement of food particles in a way that is primarily motivated to reduce computational effort and requires just a single parameter. The waiting time when catching a food particle and the travelling speed directly follow from the standard DEB model, and are no new model elements. The fact that speed works out to be proportional to squared length, rather than length (Kooijman, 2000), is a consequence of the less realistic assumption that the fish observes all food-particles and travels in a straight line to the nearest one. The number of food particles has been kept constant in this study to facilitate the interpretation of the results. This extension of the DEB model is not meant to be realistic, but serves well for the point I wanted to make.

Even at intimidation length zero, the fish interact by increasing the jumping rate of food particles, which decreases the feeding rate. So feeding rate is no longer a function of food density only, and this mechanism has the potential of enhancing co-existence of more than one species on a single food source. Yet it is an open question how strong the effect actually is. This links up with the revived discussion that is initiated by the work of Arditi and Ginzburg about feeding being density dependent (Akcakaya et al., 1995; Harmand and Godon, 2006). Although density dependent effects might be frequent in nature, examples that are supposed to present solid evidence, such as the feeding of myxamoebes on bacteria (Bazin and Saunders, 1978), can be explained more convincingly with reserves, (Kooi and Kooijman, 1994), which have the effect of delaying the response of predators to changes in prey abundance and of reducing the yield of predator on high prey densities. A (rather general) phenomenon that complicates the discussion is the occurrence of organisation levels between that of individuals and populations, such as schools (of fish, for instance). The feeding rate of individuals in a school doubtless depends on the size of the school; the school acts as a super-individual. Population dynamics, however, requires rules for the birth and death of schools, and at this level the effect of density dependence is much less evident.

The photograph in Fig. 1 shows better than a long argumentation that the huge size difference between individuals of equal age makes that age-based growth models are bound to fail. This illustrates that age cannot serve as a satisfactory basis for the description of growth of different age-based models despite the fact that the individuals were identical in all their parameters.

References


Further reading

Information about the DEB research program and its results can be found at http://www.bio.vu.nl/thb/deb/.