Same terms, different meanings: the impact of semantic aspects on biology students' reasoning in mathematical modelling tasks

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In response to a continuously growing need for quantitative literacy of biology graduates, more attention is being paid to their mathematics education. Mathematical modelling and simulations are viewed as the most efficient approaches impacting students' learning of mathematics. Subject induced peculiarities in the training of future biologists influence students' approaches to the solution of modelling tasks and mathematical modelling in general. This paper addresses semantic aspects which may hinder students' understanding of tasks and affect their reasoning.

Keywords: Interdisciplinary education, mathematical modelling, biology undergraduates, science terminology, semantic differences, conceptual understanding

To the memory of Professor Simon Goodchild,
a respected educator and a wise friend

> "Whereas the limits of human understanding are strictly confined, there are no limits to human misunderstanding" (Nicolson, 1947, p. 113).

For many decades, "biology education is burdened by habits from a past where biology was seen as a safe harbor for math-averse science students" (Steen, 2005, p. 14). A cultural gap between biology and mathematics students is often established by high school: "what attracts students to mathematics, physics, and engineering tends to repel students who are interested in biology" (Chiel et al., 2010, p. 250). This division remains a fundamental obstacle that must be overcome because today "mathematics has become pervasive in biology" (May, p. 790). The attitude of biologists towards the use of mathematics in research and teaching has been

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rapidly changing: they acknowledge that understanding of mathematics enriches and improves biological understanding and that "mathematics is a forgotten tool that we should use" (Ortiz, 2006, p. 461).

A continuously growing need for quantitatively literate biology graduates requires reform in the mathematics education of future biologists. Although Ortiz (2006) suggested that mathematics can be integrated into the explanation of the most basic biological concepts, Karsai and Kampis (2010) warned that introducing more mathematics to biology students would not, by itself, solve the problem of quantitative literacy and conceptual understanding. They stressed that students should understand science before they start learning applications of mathematics in science suggesting that "the strongest effect of math on biology education will be the extensive use of models and simulations" (p. 636). In fact, "in some ways mathematical modelling could serve as a prototype for interdisciplinary mathematics education" (Ferri & Mousoulides, 2018, p. 905). However, for biology students the learning of mathematical modelling can be hindered by epistemological differences between the two disciplines, succinctly described in Lior Pachter's blog (2014): "biologists draw figures and write papers about them. Mathematicians write papers and draw figures to explain them. [...] The extent to which the two cultures have drifted apart is astonishing".

Pointing to cultural and epistemological differences between biology and more quantitatively oriented sciences, Chiel et al. (2010, p. 249) stressed that "in general biology students and faculty have a 'different way of knowing' than students and faculty in mathematics, physics, and engineering", which is directly related to the ways they are trained. Biologists (i) emphasise the importance of biological terminology in communication; (ii) tend to know all the details of a complex biological system and use them for as long as possible; and (iii) face difficulties with the quantitative articulation of qualitative models of complex biological systems. In contrast, the training of mathematics, physics, and engineering students focuses on the design of simplified descriptions for complex real-life systems, followed by their analytical analysis and numerical simulations. Methodological approaches differ: in mathematics, assumptions are made and theories are laid out explicitly; results are established analytically, mainly by proof, whereas biologists search for "evidence to present the claim of a hypothesis beyond reasonable doubt" (Karsai & Kampis, 2010, p. 636). Distinctions are also observed in the perspectives of the two communities on mathematical modelling (Rogovchenko & Rogovchenko, 2024).

Although mathematical modelling is viewed as one of the most efficient formats for teaching biology students mathematical ideas that can be directly applied to exploring complex biological systems, many conceptual and technical difficulties may be encountered. Chiel et al. (2010) emphasised students' struggle with understanding "how the specific components of the actual biological system are mapped into the mathematical descriptions", which includes "initial conditions, state variables, and parameters" and "the significance of the terms within the model equations." Other obstacles are related to "the actual implementation of the model" and "conceptual difficulties with nonlinear dynamical systems theory, which is often used for analyzing biological models" (p. 260).

In addition to traditional difficulties with mathematical subjects faced by biology students, even more confusion may arise when mathematics lecturers include applied, biologically meaningful tasks in lectures and seminars without considering all subject-related particularities. It is common for mathematicians to omit non-essential details, promptly proceeding to an abstract model or starting with it. As a result, students "may easily survive in mathematics without the effort of careful reading and understanding given mathematical tasks cast in an extra-mathematical context" (Niss & Blum, 2020, p. 116). Empirical research has demonstrated that the mathematisation part of a modelling cycle is particularly difficult for students (Blum, 2011; Jankvist & Niss, 2020; Niss, 2017; Niss & Blum, 2020; Stillman et al., 2010; Viirman & Nardi, 2019). Niss and Blum (2020) stress that students should possess both sufficient mathematical knowledge and "a fair amount of extra-mathematical knowledge, ... especially when undertaking pre-mathematisation, de-mathematisation, validation and evaluation" (p. 92). They emphasised that understanding and correct interpretation of a given modelling task requires, in addition to general language proficiency, mathematical communication competency, which is crucial for "translating specific extra-mathematical concepts and relations into mathematical entities, or interpreting mathematical objects in extra-mathematical contexts" (p. 92).

If a modelling problem is set in a science context and uses terminology that has multiple, context-dependent interpretations in different STEM disciplines, students' difficulties may substantially increase. Our interest in this important aspect of mathematics education for future biologists grew during an extra-curricular teaching experiment with a group of biology undergraduates at a large Norwegian university (Rogovchenko, 2021). We noticed that significant differences in the interpretation of the notion of population density in biology and mathematics affected students' reasoning (Rogovchenko & Rogovchenko, 2023). In this paper, we address the problem of semantic differences between the ways mathematicians and biologists interpret basic terminology in standard mathematical modelling tasks. We examine several widely used biology and mathematics texts, focusing on differences in the comprehension of the terms *population density* and *carrying capacity* across the two disciplines and the possible influence of distinct perceived meanings on students' work on modelling tasks. The research question we address in this paper is: *How do semantic differences between biology and mathematics impact students' reasoning in modelling tasks?*

Scientific communication and terminology

Research in biology and other empirical sciences is often accompanied by ambiguity and guided by intuition; scientific discoveries frequently require the recognition and characterisation of phenomena that are yet unknown. Communicating half-formed, unsettled ideas demands particular attention to vocabulary because "for scientific discussions it is necessary to clearly define the terms used. Otherwise, scientific statements are open to interpretation and remain unclear which hampers scientific progress" (Langer, 2018, p. 230). Although it is widely accepted that conceptual understanding and the use of correct scientific language are intimately linked (Ausubel et al., 1978; Novak, 1977; Wandersee, 1988), the importance of language in scientific education is often overlooked (Wellington & Osborne, 2001). Wandersee (1988) argued that "scientists use terminology to precisely communicate their findings to other scientists. Students are taught such terms in order to understand important scientific concepts and principles, to become scientifically literate, or to lay a foundation for further learning in the sciences" (p. 97).

Vygotsky (1986) emphasised the close connection between thinking and language, communication and understanding, positing that

> [W]e all have reasons to consider a word meaning not only as a union of thought and speech, but also as a union of generalization and communication, thought and communication. The conception of word meaning as a unit of both generalizing thought and social interchange is of incalculable value for the study of thought and language (p. 9).

He stressed that word meanings change, and concept formation is a creative intellectual process that evolves through engagement in communication, understanding, and problem-solving (p. 55). With the rapid advancement of science and new research discoveries, definitions of concepts may be revised to reflect new knowledge. Both researchers and students should keep their scientific vocabularies updated to ensure meaningful communication and mutual understanding. This may not be easy across different STEM disciplines, and "conceptual understanding may accordingly suffer when language learning is not supported" (Zuckswert et al., 2019, p. 2).

Historically, interdisciplinary research between biologists and chemists or physicists has been facilitated by the use of similar methods and language. Biology shares 39% of its vocabulary with chemistry, 25% with physics, and 16% with psychology (Benjafield, 2020). Bartholomew (1986) argued that due to the rapid fragmentation of biological research and the development of niche expertise

> their vocabularies, their techniques, and the questions they consider important differ so much that it is difficult for biologists in widely separated fields to remember that they are all trying to understand the same thing – the nature of living systems (p. 325).

This narrowing specialisation impacts undergraduate biology education, making the correct use of discipline-specific vocabulary challenging for students (Wandersee, 1988; Zuckswert et al., 2019). Biology programmes are notorious for their vast vocabulary, much of which "is technical, unintuitive, ambiguous, or abstract, and so it may be considered 'jargon', especially by a novice in the field" (Zuckswert et al., 2019, p. 2). Technical vocabulary typically used in biology classes includes both specialised terms that would not be used outside the field and terms used in everyday language. Difficulties in understanding an unintuitive scientific vocabulary are amplified by frequent misinterpretation of common terms that have different context-dependent meanings across STEM disciplines. Marshall et al. (1991) noticed that students struggle with frequently used non-technical terms that do not represent complex notions but have multiple interpretations in everyday and scientific communication; this results in "the high number of mismatches in actual understanding versus perceived understanding" (Zuckswert et al., 2019, p. 8).

Given that "the interaction of mathematics with science has never been smooth [...] because mathematics and science have significantly different roots and approaches" (Karsai & Kampis, 2010, p. 635), mediation between the disciplines should be based on correct interpretation and unambiguous use of basic scientific terminology by mathematicians. Semantics, known as the "science of meaning, or the study of significance" (Lady Welby, as cited in Iacobelli, 1948, p. 16), examines how an appropriate symbol (word or phrase) is associated with a referent (an actual object or thing). This mapping is achieved through the reflective thought process that occurs in our brains because "there is no direct relation between referent and symbol, between thing and word" (Iacobelli, 1948, p. 16). Consequently, a productive academic discussion can only be carried out by acknowledging that "the understanding of the significance of words, and a realization of the flexibility of words, are the fundamental factors which govern the attainment of good communication" (Iacobelli, 1948, p. 16).

The need to correctly interpret multivalent terms that have several, often conflicting, contextualised meanings complicates the learning of mathematical modelling by science students. For instance, the term *cell* has different meanings in biology, meteorology, chemistry, mathematics, and nucleonics (Wandersee, 1988). In biology, a cell designates the fundamental unit of life. In mathematics, it may refer to a three-dimensional object that is part of a higher-dimensional object or a fundamental spatial unit in a cellular automaton. In mobile communication, a cell is a geographical area covered by the frequency emitted by a base station in a cellular network, but it also stands for a small room in a prison in everyday language. For evolutionary biologists, the term *function* mainly relates to selection; most molecular geneticists and biochemists associate it with a molecule's activity; mathematicians use it to relate elements in two sets, and in everyday language, it is associated with a number of concepts ranging from professional occupation to a purpose for which a device has been designed (Keeling et al., 2019). The term *limits* arises in the evolution of the form of different animal groups to describe functional and developmental constraints on possible evolutionary trajectories in a morphospace of hypothetical forms (McGhee, 2015). In mathematics, it designates values approached by functions when the independent variable tends to certain finite or infinite values. The list of terms with multiple meanings includes scores of words like *accumulation*, *complement*, *consistent*, etc., interpreted differently in biology, mathematics, and everyday life. Sometimes the context helps to understand the meaning of a term unambiguously, but this is not always the case.

Semantic difficulties may also lead to the misinterpretation of important mathematical concepts that biologists and other empirical scientists use in their experimental work. The concepts of correlation, necessity, and sufficiency are important for designing experiments in biochemistry and cellular biology (Coleman et al., 2015). Insufficient training and lack of relevant reasoning skills could hinder students' ability both to understand and correctly interpret experiments reported in the literature and to design their own experiments. Yoshihara and Yoshihara (2018) warned about the danger of "an incorrect use of logic which involves the careless application of the 'necessary and sufficient' condition originally used in formal logic. This logical fallacy is causing frequent confusion in current biology, especially in neuroscience" (p. 53). Last but not least, some fundamental concepts like *carrying capacity* have multiple, not fully compatible interpretations even within the field of biology (Hixon, 2008).

Carrying capacity and population density: biologist's views

Carrying capacity is an important biological concept used to understand interactions between the biotic potential of a population and environmental resistance (Wisniewski, 1980). It is often defined as the maximum population size that a given environment can support indefinitely. However, "the simplicity of this definition belies the complexity of the concept and its application. There are at least four closely related but nonetheless different uses of the term in basic ecology, and at least half a dozen additional definitions in applied ecology" (Hixon, 2008, p. 528). The term carrying capacity is often attributed to the variable K in the logistic equation introduced by Verhulst (1838), even though he never employed it (Sayre, 2008). Prior to its adoption in biology in the 1870s, the term was introduced in mechanical engineering for calculating the load that a steamship could carry (Sayre, 2008); it initially retained its literal application, referring to the mass of meat that pack animals could physically transport (Chapman & Byron, 2018, p. 2).

In his influential treatise on ecology, Odum (1953), contrary to contemporary views on carrying capacity as 'an upper limit of population growth' or 'a maximum population size possible', assigned the term to the asymptote of the logistic curve (Sayre, 2008). According to Wisniewski (1980), "the implications of this subtle but profound difference in conceptualization of carrying capacity for unwary human ecologists cannot be overstated" (p. 56). This new interpretation aligned well with mathematicians' views on the asymptotic behaviour of solutions to the logistic differential equation but, lacking empirical support, created confusion in biological literature (Wisniewski, 1980) and undoubtedly influenced a generation of biologists (Chapman & Byron, 2018). In the third edition of his textbook, Odum (1971) acknowledged that in reality "almost always the population overshoots the upper asymptote and undergoes oscillations before settling down at the carrying capacity level" (p. 185). Sayre (2008) commented on the complicated nature of this issue, arguing that "if carrying capacity is conceived as static, it is theoretically elegant but empirically vacuous; but if it is conceived as variable, it is theoretically incoherent or at best question begging" (p. 131). Despite these weaknesses, carrying capacity remains an important construct for many ecological studies, including basic fisheries and wildlife yield models (Chapman & Byron, 2018; Hixon, 2008; Sayre, 2008; Wisniewski, 1980).

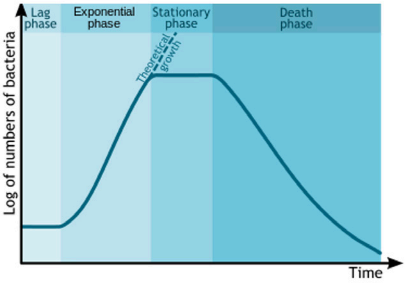

Figure 1. *Four phases of bacterial growth over time.*
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Let us now explore how the concepts of carrying capacity and population density are presented in three popular textbooks for biology undergraduates. Tortora et al. (2021) explain the process of binary fission, a form of asexual reproduction in which a single parent cell divides to produce two daughter cells, each inheriting one copy of the genetic material from the parent cell. Bacterial growth over time has four basic phases: lag, log, stationary, and death (see figure 1). During the lag phase, intensive metabolic activity occurs, but no increase in population is observed. During the logarithmic (exponential) phase, cells are most metabolically active, and binary fission in bacteria or mitosis in yeasts takes place. If binary fission continued unchecked, an enormous number of cells would be produced. However, during the stationary phase, bacterial growth slows due to environmental constraints; production of new cells is balanced by microbial deaths. "Exponential growth stops because the bacteria approach the **carrying capacity**, the number of organisms that an environment can support" (Tortora et al., 2021, p. 194, emphasis in original). Factors influencing carrying capacity include the availability of nutrients, space, and the accumulation of waste. When the number of deaths exceeds the number of new cells produced, "the population enters the **death phase**, or **logarithmic decline phase**" (Tortora et al., 2021, p. 194, emphasis in original). For understandable reasons, the concept of population density is not discussed in the microbiology textbook.

Miller and Harley (2001) characterise animal population changes over time either in terms of survivorship curves (plots of the number of survivors versus age) or in terms of population growth (plots of the number of organisms versus time). They argue that exponential growth cannot continue indefinitely due to environmental resistance factors (climate, food, space), and population growth is referred to as logistic: "the population size that a particular environment can support is the environment's carrying capacity and is symbolized by K" (pp. 77–78). Logistic growth curves have a sigmoid, or flattened S-shape, reflecting the effect of limited resources placing an upper limit on population size. The number of organisms approaches the limiting value K asymptotically, but "during its exponential growth phase, a population may overshoot carrying capacity because demand on resources may lag behind population growth" (Miller & Harley, 2001, p. 78). The number of organisms may cycle on either side of K, or form a J-shaped curve, overshooting the carrying capacity and approaching it asymptotically from above (Campbell et al., 2021, figure 53.10, p. 1257; cf. Odum, 1971). Density-independent factors (climate, human activities, natural disasters) affect populations regardless of the number of individuals per unit space, whereas density-dependent factors (competition for space and food resources, disease, predation) have a more pronounced impact at higher population densities (Miller & Harley, 2001).

Population density is often used in biology as a measure of an organism's response to local conditions. It is low if conditions are unfavourable and organisms die or emigrate, but if conditions are favourable, density is high and organisms reproduce and immigrate into the area (McArdle, 2013). Density can serve as a substitute for population size, an important variable for ecologists, but the link between population density and population size is not always direct. If the area to be sampled includes the entire population, density multiplied by the area gives total population size, as in mathematics. Biologists regard density as a reliable proxy for population size in scenarios of constrained range (e.g., on islands), but in most cases it merely reflects the number of organisms within a defined study area (McArdle, 2013).

Campbell and Reece (2005) discuss the relationship between population dynamics and density, defined as the number of individuals per unit area or volume (p. 1137; cf. Campbell et al., 2021). Sampling techniques are employed to estimate population densities and total population sizes, the most popular being the use of several randomly located plots and extrapolation to the entire area, and the mark–recapture method. Campbell and Reece (2005) emphasise that density is not a static property of a population and is influenced by birth, death, immigration, and emigration. Dispersion (the pattern of spacing among individuals) accounts for substantial variation in local densities within population boundaries. The most common dispersion pattern is clumped (individuals aggregated in patches); less common uniform and random dispersion result from direct interactions between individuals.

Campbell and Reece (2005) define carrying capacity K as the maximum population size that a particular environment can support, emphasising that it is not fixed but "varies over space and time with the abundance of limiting resources" (p. 1145). Growth patterns of some laboratory populations of small animals (crustaceans, beetles) and microorganisms (bacteria, yeast) in a constant environment without predators and competition for resources fit a sigmoid curve quite well. However, one of the basic assumptions built into the logistic model (that populations instantaneously adjust growth rate and smoothly approach carrying capacity) does not apply to all populations; in most natural populations, the impact of negative changes causing population decline is delayed. A population may overshoot its carrying capacity before settling down to a relatively stable density (e.g., *Daphnia*) or fluctuate markedly in response to drastic seasonal climate changes (e.g., song sparrow). Thus, "although the logistic model fits few, if any, real populations closely, it is a useful starting point for thinking about how populations grow and for constructing more complex models" (Campbell & Reece, 2005, p. 1146). The model is particularly useful for estimating environmental impact in conservation biology and aligns well with the presentation of carrying capacity in mathematics texts.

Carrying capacity and population density: mathematician's views

Autonomous differential equations represent an important class of equations in which the independent variable does not appear explicitly. They are often used for modelling population dynamics because the rate of change of a population usually depends only on its current size, thus making the equations time independent. Two widely used textbooks on calculus (Adams & Essex, 2018) and differential equations (Boyce & DiPrima, 2013) introduce logistic growth to illustrate applications. Boyce and DiPrima (2013) discuss an autonomous differential equation

$$\frac{dy}{dt} = f(y) \qquad (1)$$

in the context of population growth. Under the simplest assumption that the rate of change of the population $y = \varphi(t)$ at each instant t is proportional to the current value of $y = y(t)$, i.e., $f(y) = ry$, $r > 0$, the differential equation describing exponential growth is obtained:

$$\frac{dy}{dt} = ry\,, \qquad (2)$$

also known as the Malthusian growth model in population dynamics. If the rate of change depends on the population size, equation (2) is modified to the form:

$$\frac{dy}{dt} = h(y)y\,, \qquad (3)$$

where the function $h(y)$ is selected to behave like r for small values of y, and decrease and take on negative values for large values of y. The choice of the simplest such function, $h(y) = r - ay$, where a is also a positive constant, leads to a differential equation:

$$\frac{dy}{dt} = r\left(1 - \frac{y}{K}\right)y\,, \qquad (4)$$

known as the Verhulst equation or the logistic equation (Boyce & DiPrima, 2013, pp. 58–60). Analysing the phase line for equation (4) and plotting its solutions, the authors conclude that "K is the upper bound that is approached, but not exceeded, by growing populations starting below this value. Thus, it is natural to refer to K as the **saturation level**, or the **environmental carrying capacity**, for the given species" (Boyce & DiPrima, 2013, p. 61, emphasis in original; cf. Odum, 1953). Although solutions with initial values larger than K approach asymptotically the horizontal line $y = K$ from above, this mathematically correct but biologically unrealistic argument remains unsettled.

Adams and Essex (2018) introduce equation (4) as a possible model for describing the growth of a rabbit population, mentioning that such models are thought to apply to several species of fish and trees, and revisit it later to illustrate applications of integration in business, finance, and ecology. Their concise description of (4) refers to the constant K as "the natural limiting size of the population – the carrying capacity of its environment" (Adams & Essex, p. 434).

Given that both texts refer to the notion of carrying capacity primarily to illustrate mathematical techniques and do not attend to biological details, it is not surprising that the concept of population density is not discussed. However, from a mathematical point of view, computation of population density in simpler cases requires merely dividing the number of individuals by the area they inhabit. More sophisticated mathematical approaches to the concept of density are based on an implicit assumption of homogeneous mixing (uniform dispersion), which is generally not feasible for most populations. Calculus textbooks also explain how one can find the total population using a definite integral if a radial density function ρ(r) is known (Rogawski & Adams, 2018, p. 385) or by calculating a double integral if a multivariable density function ρ(x,y) is given (Buono, pp. 198–199). However, these approaches are too distant from the realm of biology because populations are usually aggregated in patches (Campbell & Reece, 2005) and, to our knowledge, neither biologists nor mathematicians can efficiently compute a radial density function ρ(r) or a multivariable density function ρ(x,y) for finding population density via integration.

Analysis of students' work on mathematical modelling tasks

We analyse students' work on two modelling tasks offered to a group of twelve biology undergraduates (nine female and three male) at a large Norwegian university, focusing primarily on discipline-dependent semantic aspects in small-group discussions. At the time of the teaching experiment, eleven students were enrolled in a large first-year mathematics course for natural science students, and one second-year student had already completed it. All students had no previous modelling experience and volunteered to take part in four three-hour extra-curricular modelling sessions led by the second author, signing a consent form prior to participation. The main goal of the teaching experiment was to introduce students to simple modelling techniques relevant to their profession and motivate them to take further mathematics courses beyond the compulsory one.

In each session, fundamental ideas and techniques (such as a seven-step modelling cycle, compartmental models, choice of variables and parameters, assumption-making, and modelling using geometric similarity) were explained and illustrated with examples. Similar problems were suggested for independent work in small groups of three to five students. For more details on the organisation of the experiment, see Rogovchenko (2021). Since students were offered only minimal support, their discussions "represent students' unscaffolded, decontextualized ideas about models and do not reflect what students can do with models in more supportive or appropriately contextualized settings" (Svoboda & Passmore, 2011, pp. 18–19).

Problem A: Rabbits on the road

The task "Rabbits on the road" (Harte, 1998, pp. 211–213) was given in the first session after students were introduced to the modelling cycle and some simple models. Our goal was to explore how they might approach an open-ended modelling problem and relate it to their previous experience in biology and mathematics.

> Problem A. Driving across Nevada, you count 97 dead but still easily recognisable jackrabbits on a 200-km stretch of Highway 50. Along the same stretch of highway, 28 vehicles passed you going the opposite way. What is the approximate density of the rabbit population to which the killed ones belonged?

Problem A turned out to be challenging for students since it was the first time they encountered an open-ended problem requiring multiple assumptions. This aspect caused difficulties: on the one hand, students often focused on biological arguments that would not typically be considered by a mathematician; on the other hand, they did not attempt to make other biologically meaningful assumptions. For instance, one student recalled the mark–recapture method used in fisheries (catching, tagging, releasing, and recapturing fish to estimate population size) and asked whether this method could be applied to Problem A.

The solution to the problem suggested by the author, an ecology professor, combined mathematical and biological reasoning (Harte, 1998, pp. 211–213). He assumed that:

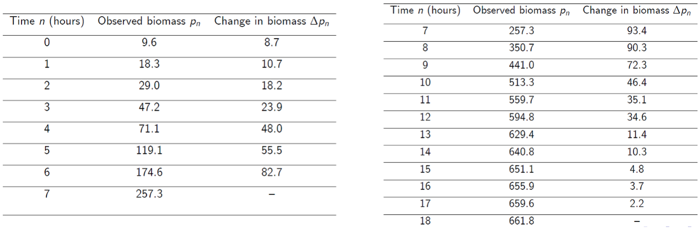
> (A1) The rabbit population inhabits land of area $A = 200\,w\,(km)^2$, with width w on both sides of the highway along the entire 200-km stretch, so that the density of this population is:
>
> $$d = \frac{R}{A} = \frac{K}{200wnr} \text{ rabbits per } (\text{km})^2,$$
>
> where K is the highway kill rate (number of rabbits per day), R is the size of the rabbit population, n is the average number of road crossings per unit time attempted by each rabbit, and r is the likelihood of a rabbit being run over during an attempt to cross the road.
>
> (A2) Rabbits hop randomly about their habitat for 1 hour per day at a speed of s km/day. Thus, they cover about $0.04\,s$ km/day and, very roughly, cross the road $n = 0.04\,s\,/\,w$ times per day.

Problem B: Growth of a yeast culture

The second task, "Growth of a yeast culture", was adapted from a modelling textbook (Giordano et al., 2014, pp. 10–13) and suggested in the second session. Unlike the open-ended Problem A, this task was partly mathematicised and split into several steps. The goal was to explore how, with some guidance embedded in the problem, students could relate experimental data and a simple mathematical model, assess its efficiency and predictive power, and recognise the need for model adjustment.

> Problem B. The data in table 1 describe the growth of a yeast culture versus time in hours and come from Pearl (1927).
>
> (a) Analyse the numerical data in table 1 (left panel). Plot the data and analyse the graph. Suggest a simple model based on a difference equation of the form:
>
> $$\Delta p_n = p_{n+1} - p_n = k_1 p_n$$
>
> where p_n is the size of the yeast biomass after n hours, Δp_n is the change in biomass between two measurements, and k_1 is a positive constant. What would be your expectations regarding the predictive power of the model you constructed? Explain.
>
> (b) Analysing the data in table 1 (right panel), note that the change in population per hour decays as resources become limited. Plot the population against time and explore the shape of the graph. What would you expect in the long run? Based on the graph, observe that the population approaches a limiting value, known in biology as carrying capacity. What would be your expected value for carrying capacity in this case?
>
> (c) Estimating carrying capacity to be 665 (this value is approximate; your estimate may differ slightly), adjust your simple linear model by replacing it with a nonlinear model:
>
> $$\Delta p_n = p_{n+1} - p_n = k_2(665 - p_n)p_n$$
>
> Test the new model by plotting Δp_n against $(665 - p_n)p_n$ to check whether a reasonable proportionality is observed and estimate the proportionality constant k_2.

Table 1. *Growth of a yeast culture versus time in hours (Pearl, 1927).*



Time n (hours)	Observed biomass p_n	Change in biomass Δp_n
0	9.6	8.7
1	18.3	10.7
2	29.0	18.2
3	47.2	23.9
4	71.1	48.0
5	119.1	55.5
6	174.6	82.7
7	257.3	–

Time n (hours)	Observed biomass p_n	Change in biomass Δp_n
7	257.3	93.4
8	350.7	90.3
9	441.0	72.3
10	513.3	46.4
11	559.7	35.1
12	594.8	34.6
13	629.4	11.4
14	640.8	10.3
15	651.1	4.8
16	655.9	3.7
17	659.6	2.2
18	661.8	–

The authors' solution (Giordano et al., 2014, pp. 11–13) focused on plotting Δp_n versus p_n and $(665 - p_n)p$, followed by fitting straight lines to the data to determine the proportionality constants k_1 and k_2. Plotting the *change of biomass* versus *biomass* rather than *biomass versus time* was the most difficult part for students, as they had no prior experience with such tasks. On the other hand, they had been taught at school how to use linear regression to fit a straight line to a data set, but they did not relate this knowledge to the task at hand.

We illustrate students' reasoning with six excerpts from small-group discussions, paying particular attention to the interpretation of the concepts of population density and carrying capacity, which are crucial for the correct understanding and solution of the problems.

Episode 1 (Group 1: meaning of population density)

1 S1: Now we answer the wrong question; they ask about "What is the approximate density." They ask about density here. Density per square mile then, right?

2 S2: On the stretch. [...]

3 S3: Yes, but we first have to sort of find the population and then we have to find, take an area and take the density...

4 S2: If it is 20,000 per 200 km, if we only make it into the area. [...]

5 S3: No, but let us just assume, as she says, that we have 20 miles that way and 20 miles that way, then we have 20 miles on the stretch.

6 S1: Yes.

7 S3: But then there is still a very large area, for only 20,000 rabbits.

8 S1: Yes, I think, I do not know if this is what they mean by density. There is no point in calculating density per hypothetical square kilometre.

9 S2: You never know how big it is as well...

10 S1: So, I do not know if that is what they mean by density, or if it's just a part of the population they're looking for. It's like "What is the approximate density of the rabbit population?"

11 S3: To obtain density, we have to have the whole area; we cannot use just a stretch. You must have something like a square.

12 S5: Can't we just divide the number of individuals in the area and find out how many are there in each square metre?

13 S1: But we don't know what the area is; we only know the stretch. We don't know how wide it is.

S1, S2, and S3 discussed the meaning of population density (turns 1-3, 10), and S1 deemed the calculation of "density per hypothetical square kilometre" (turn 8) meaningless. S5 suggested a straightforward mathematical approach (turn 12), but S1 was convinced that the "whole area" is needed (turns 11, 13). Note that assumption (A1) was introduced by the author (Harte, 1998, p. 212) to conveniently resolve the issue of the area inhabited by rabbits. S3 attempted a similar step, mentioning several times the area along the stretch of the highway (turns 2, 5, 11). Students in Group 1 actively discussed what the total population and percentage of killed rabbits could be but did not consider making a simplifying assumption for the area.

Episode 2 (Group 2: recalling a sampling method and desperation)

14 S4: ... but didn't we have such a bad population, population growth thing in biology then? So, to find out the population, you had to first take one area, then another, then another, then another...

15 S2: Yes, and then you took the average.

16 S3: I'll try to find it on Google, what is the rabbit population in Nevada. [...]

17 S2: Hmmm, this was a frustrating task. You think it's a math problem, but then you know nothing. So, you can't solve it.

18 S4: Yes, we have to, we have to [solve it] somehow. Find our own numbers.

S4 and S2 recalled a sampling technique (turns 14, 15) but were unable to apply it to solve the task. S4 also referred to a "bad population" (turn 14), presumably associating population density with habitat conditions. We believe that students were oriented towards finding the total size of the population rather than its density (turns 14–16). Lack of progress eventually frustrated S2 (turn 17).

Episode 3 (Group 2: likelihood of rabbits being run over)

19 S4: Yes, you have to say how many make it out alive, that's something.

20 S2: Yes, not everyone who jumps over there [on a highway] dies.

21 S3: I imagine a whole herd of rabbits jumping for all those who are hit, but...

22 S1: So ... if there had been a hundred rabbits jumping out into the road at the same time, the twenty-eight cars have also run over ninety-seven rabbits, it seems ridiculous. (inaudible) [...]

23 S1: Well, but it only assumes that the cars are driving towards you, and not the cars ahead. So, it's only [cars driving] on one side then.

24 S4: Yes, not the ones driving ahead of you or behind you.

25 S1: Yes, that's true. But I think that then the rabbits must jump only from one side. [...]
26 S4: But should we also assume that all the rabbits that jump across the road are hit?
27 S2: Not when there are only twenty-eight cars in two hundred kilometres.
28 S1: No.
29 S4: No, but how many possibly?
30 S3: One third.
31 S4: A third of the rabbits that jump across the road get hit?

In Group 2, students actively discussed the likelihood of a rabbit being run over by a car—an important part of the problem's solution addressed by its author in assumption (A2) (Harte, 1998, p. 212). They debated whether all rabbits crossed the road at the same time (turn 22), whether the killed rabbits were jumping from only one side of the road because the number of cars driving in one direction was given (turn 25), and whether all rabbits that cross the road are hit (tuns 26, 27). Failing to formulate an acceptable approach to the solution, the students resorted to guessing what proportion of rabbits might be run over on a highway (turns 29–31).

Episode 4 (Group 1: plotting exponential growth and using logarithmic scale)

32 S3: (plotting the graph) It is going to be beautiful, you know. And then there is, um... Shall we put it on there? But then we take in equal (inaudible) spaces. It will be easiest to see where (inaudible). Then we sort of take 10, 20, 30.
33 S2: Yes, yes, yes!
34 S3: Mhm. Then we get one that is... (pointing at a graph).
35 S1: But then, uh, you have to bring, yes, you have to have exponential, yes.
36 S3: Or if we are going to somehow take 10, 100, 1000.
37 S1: Yes. But, not really, you know either, because that's not true. And then we are going to make a line, or make a linear function then. [...]
38 S1: What else are we going to play around with now then?
39 S3: The change in... (inaudible).
40 S1: A constant... So, there must be something... logarithm case is here.
41 S3: Or exponential...

S3 plotted the graphs while discussing exponential (turn 35) and logarithmic functions (turns 36, 40) with S1, before realising that a biomass increment should be plotted (turn 39). Students referred to changes in population size over time, drawing on their experience of plotting exponential growth and using logarithmic scales in biology classes (Campbell & Reece, 2005; Campbell et al., 2021; Miller & Harley, 2001). They did not use linear regression to find the proportionality coefficient, although S1 mentioned using a linear function (turn 37) and a constant (turn 40).

Episode 5 (Group 2: plotting the logistic curve)

42 S3: Oh, we are going to analyse the graph. It grows quite nicely, even when it is soon exponential, no, not like that, what is it called?

43 S1: When it stops growing?

44 S3: Yes, please. Yes. You can see it flattening out.

45 S2: Yes, it is very (inaudible), and then it flattens out.

Students discussed the sigmoid (logistic) curve (turns 42–44), paying attention to the characteristic flattening of the graph (turns 44, 45).

Episode 6 (Group 2: making sense of bacterial growth and carrying capacity)

46 S3: He wants us to find the carrying capacity, sort of. I do not think it will crash, because you often have population crashes, but does it happen in yeast? Maybe it does?

47 S2: Yes, it does.

48 S3: I guess that is it.

49 S2: But I do not understand that; the yeast will flatten out, but the food will run out some time. Do they eat each other then? Are they cannibals somehow?

50 S3: It is a population crash then, but we don't have that here.

51 S3: They don't want to grow, but they can stay constant somehow. It would not grow because there is no more room for it. But they can stay constant.

52 S2: Mhm, so, say, you have ten people in a room then. If you feed them every day, they still will be living.

53 S3: We need to sterilise them all, so there are no more people added, because there is no room for that.

Students discussed restricted population growth (turns 51, 53), limited food availability (turns 49, 52), the stationary phase (turn 51), and possibilities for population crash (turns 46, 50), cf. the phases in the yeast growth model in figure 1. Carrying capacity was not mentioned explicitly, even though all but the first fast phase of bacterial growth in figure 1 were touched upon in the discussion.

Discussion and conclusions

In this paper, we explored the impact of semantic differences between biology and mathematics on students' reasoning in mathematical modelling tasks. We analysed how two important interrelated concepts – carrying capacity and population density – are perceived by the biology and mathematics communities. The key distinctions that may influence students' thinking can be summarised as follows.

For mathematicians, population density in simple cases implicitly assumes homogeneous mixing and is calculated by straightforward division of the total population by the area it inhabits. If a radial density is known, the total population in two- and three-dimensional cases can be computed by integration. These views do not match the perspective of biologists, who often use population density as a proxy for population size or environmental fitness. The mathematical assumption of homogeneity corresponds to uniform dispersion, which is not feasible for most populations. Since biologists pay attention to dispersion and density-dependent (and density-independent) population properties, they prefer sampling techniques to integration.

Mathematicians usually introduce carrying capacity with reference to the logistic differential equation (4), whose right-hand side satisfies the conditions of the Existence and Uniqueness Theorem (Boyce & DiPrima, 2013, p. 82). This is why the consideration by biologists of solutions that oscillate around carrying capacity before approaching it at infinity (Miller & Harley, 2001, p. 78) contradicts the uniqueness of solutions and makes little sense to mathematicians. The death phase of bacterial growth (see figure 1), supported by numerous laboratory experiments, does not agree with the logistic model (4). Finally, the multiple interpretations of carrying capacity in contemporary ecology (Hixon, 2008, p. 528) require particular attention from both communities.

Our analysis of students' reasoning confirms its strong connection with professional training (Chiel et al., 2010). Working on Problem A, designed by an ecology professor (Harte, 1998), students struggled with mathematisation, but their reasoning resembled some of his arguments. Students also experienced difficulties with Problem B, based on real data from a biological experiment (Pearl, 1927). Although linear regression is studied in Norwegian high schools, students did not recognise its relevance for finding proportionality constants and were confused by the request to plot biomass increment versus biomass. Previous experience with plotting functions against time negatively influenced their perception of Problem B and hindered progress.

The teaching experiment provides empirical evidence supporting the claim that, in teaching mathematics to biology undergraduates, science should come first (Karsai & Kampis, 2010). The prevalence of biologically motivated interpretations of concepts emphasised in the biology curriculum can overshadow students' understanding of mathematics and its potential applications in biology. For instance, the process of binary fission in bacteria is well understood by biology undergraduates. Although they encountered the exponential function in high school, biological ideas of cell fission and exponential growth may dominate their views on the dynamics of more complex biological populations. Students' interpretations of carrying capacity and population density reflect semantic differences between the two disciplines, and their approach to solutions often relies more on biological arguments than on mathematical reasoning. Such trends can affect students' ability to effectively use mathematical modelling to address biological problems. To support students' learning, "teachers must have at least the same mathematical and extra-mathematical knowledge needed to manage these tasks as expected from the students" (Niss & Blum, 2020, p. 94). Teachers should carefully select applied tasks, paying attention to the correct interpretation and use of multivalent terms across the two disciplines.

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