Size-dependent mortality rate profiles

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HIGHLIGHTS

- A conservation law theory of the shape of size distributions in populations is extended.
- Size-specific mortality rate equations of populations for realistic cases are derived.
- Two applications of contrasting characteristics are presented as case studies.
- The extended theory is useful in the stock assessment of small-scale and invertebrate fisheries.

ARTICLE INFO

ABSTRACT

Knowledge of mortality rates is crucial to the understanding of population dynamics in populations of free-living fish and invertebrates in marine and freshwater environments, and consequently to sustainable resource management. There is a well developed theory of population dynamics based on age distributions that allow direct estimation of mortality rates. However, for most cases the aging of individuals is difficult or age distributions are not available for other reasons. The body size distribution is a widely available alternative although the theory underlying the formation of its shape is more complicated than in the case of age distributions. A solid theory of the time evolution of a population structured by any physiological variable has been developed in 1960s and 1970s by adapting the Hamilton–Jacobi formulation of classical mechanics, and equations to estimate the body size-distributed mortality profile have been derived for simple cases. Here I extend those results with regards to the size-distributed mortality profile to complex cases of non-stationary populations, individuals growing according to a generalised growth model and seasonally patterned recruitment pulses. I apply resulting methods to two cases in the marine environment, a benthic crustacean population that was growing during the period of observation and whose individuals grow with negative acceleration, and a sea urchin coastal population that is undergoing a stable cycle of two equilibrium points in population size whose individuals grow with varying acceleration that switches sign along the size range. The extension is very general and substantially widens the applicability of the theory.

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1. Introduction

The shape of the cross-sectional size distribution of large populations contains information about several interesting processes affecting it since the time the oldest individual was born, such as mortality, growth, and possibly reproduction when the time dimension is considered (Kristensen et al., 2014). Sinko and Streifer (1967) developed a general theory for the flow of organisms through size and age using a formulation similar to the Hamilton–Jacobi equation of motion in classical mechanics. Their theory contained as special cases previous models of age-structured populations and allowed to formulate new models for the dynamics of age-, size-, and general physiological age-structured populations, as well as to introduce vaying environments and interacting species (Streifer, 1974; Van Sickle, 1977a; DeAngelis and Huston, 1987). Here I present the theory to solve for one of the processes affecting size distributions, namely mortality rates, under realistic situations typically occurring with marine populations of fish and invertebrates, extending previous work by Van Sickle (1977b).

Knowledge of mortality rates is crucial to understanding population dynamics and to management of free-living natural resources. When cross-sectional -and optionally- time series data of the distributions of ages in the population are available, the shape of these cross-sections directly reflect mortality and recruitment patterns. Solid theories for age-dependent mortality (Suematsu and Kohno, 1999) as well as age-dependent recruitment (Quinn

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and Deriso, 1999) can then be used to understand population dynamics. These theories however are not useful for the analysis of populations composed of individuals that cannot routinely be aged by analysts in the laboratory or that are not economically important enough to establish protocols and laboratories in the first place. This is the case of the vast majority of small scale fisheries for invertebrates and finfish. For those populations more useful theories can be built from size rather than age distributions. Moreover, some demographic processes are more directly connected to the size rather than the age of the individuals.

With these motivations and based on Sinko and Streifer (1967) theory, Van Sickle (1977b) derived several equations to estimate mortality rate from size distributions. However, Van Sickle (1977b) derivations are of limited scope because they are valid for (i) stationary, steady-state populations that do not change in total abundance, (ii) whose new individuals enter at a constant rate, and (iii) that grow according to a constant acceleration of growth model. Conditions of stationarity or steady-state are seldom achieved in marine populations of fish and invertebrates due to the combination of life history strategies and environmental variability. On the contrary, in the marine environment both fish and invertebrate populations are characterised by strong fluctuations because of intense recruitment variability (Pritt et al., 2014). Moreover, it is common for fish and invertebrate populations to exhibit non-constant entry of individuals because of marked seasonality in recruitment, as a consequence of both, seasonality in spawning and environmental forces acting during the larval phase (Munro et al., 1990; Hufnagl et al., 2013). Finally, large groups of marine organisms do not grow according to the constant acceleration model considered by Van Sickle (1977b), instead growing at varying growth rates over their lifetime, particularly invertebrates which precisely are the groups that most often are not regularly aged in the laboratory (Arkhipkin and Roa-Ureta, 2005; Roa-Ureta, 2010).

These characteristics of free-living marine populations could be the reason why Van Sickle (1977b) formulas have not been used by applied marine biologists in spite of the conceptual appeal of their underlying theory and that they allow to evaluate mortality rates that are size-specific. In a recent methodological paper (Hufnagl et al., 2013) analysing the shortcomings of eight widely used methods to estimate mortality and growth rates from size distributions of aquatic populations, Van Sickle (1977b) formulas were ignored, even though the methods that were included in Hufnagl et al. (2013) are not as solidly grounded in biological theory as Van Sickle (1977b) formulas and that they produce aggregate mortality rate estimates instead of size-dependent profiles. This latter aspect is most remarkable when considering that it is widely acknowledged that mortality rates vary over the lifetime of marine organisms (Quinn and Deriso, 1999) and that there is in fact substantial variation in mortality rates along the life history of taxa across both the plant and animal kingdoms (see Fig. 1 in Jones et al., 2014).

Therefore, in this paper I extend Van Sickle (1977b) treatment of the problem by deriving new solutions for mortality rate that are valid for non-stationary populations composed of individuals that exhibit variable growth rates along their lifetimes and that enter the population at seasonally varying rates, while preserving the size-specific formulation. As illustration of the potential of the extended theory I apply it to two contrasting cases of benthic marine invertebrate populations.

2. Theory

In this section I show an equation of balance for all the processes shaping the size distribution of populations, explain the conceptual grounds of each of the processes, illustrate the result with specific cases that have been presented by previous authors, and finally lay out specific models for each of the processes. This is aimed at deriving equations that can be used to estimate the size-dependent mortality rate profiles. Essentially I extend Van Sickle (1977b) approach to non-stationary populations, general individual growth models, and pulse, seasonal recruitment. Let t be time and y be individual size, and define the number density function as the number of individuals at a specific point in time in a given size interval, that is

$$\eta(t, y_0, y_1) = \int_{y_0}^{y_1} \eta(t, y) \, dy \tag{1}$$

In this definition two more variables that are relevant in population dynamics, age and space, are ignored in order to find theoretically sound expressions that are useful for a spatially aggregated view of a population whose individuals cannot be aged routinely in the laboratory, so they are observed from the size distribution only. A simplified version of the proof in the appendix of Sinko and Streifer (1967) shows that the processes shaping the size distribution obey a balance equation

$$\frac{\partial \eta}{\partial t} + \frac{\partial (\eta g)}{\partial y} + \eta D = 0 \tag{2}$$

where $g = dy/dt$ is the rate of growth in size of individuals and D is the mortality rate (the proof is provided in Appendix 1 of the Supplementary Material). With the focus on solving for $D(y)$ at a moment in time, apply first the product rule, then divide all resulting term by the density function, and finally solve for $D(y)$, which yields

$$D(y) = -\frac{1}{\eta(y)} \frac{\partial \eta(y)}{\partial t} - \frac{\partial g(y)}{\partial y} - \frac{g(y)}{\eta(y)} \frac{\partial \eta(y)}{\partial y} \tag{3}$$

In the reasoning above it has been assumed that both the individual growth rate and the mortality rate are time-invariant. The resulting equation tells that the size-specific mortality rate profile is a balance between total population growth spread over the size distribution (first summand), the acceleration of individual growth (Schnute, 1981, second summand), and the g-corrected size-dependent change in population density (third summand). Since Eq. (2) is a conservation law (Van Sickle, 1977b), in any specific application the processes acting in opposite directions in the flux of individuals through small size intervals must have opposite signs. Specifically, when the mortality rate is on the left-hand side as in Eq. (3), those processes on the right-hand side that add individuals into size intervals or that delay the exiting from size intervals must have positive signs while those facilitating the exit of individuals from size intervals must have negative signs (see Fig. A1.1, Appendix 1 in the Supplementary Material). The resulting mortality rate profile must be positive throughout the size range.

The first two summands and the coefficient of the third summand are clearly recognised as the contributions of population growth and individual growth to the shaping of the size distribution. The nature of the third summand is less clear. Van Sickle (1977b) simply called it the slope of the $\ln(\eta(y))$ over the size range, which lacks conceptual substance. In discussing his formulas he recognised that it is related to recruitment and that in his proposed form only applies to the older segments of a population, leading to discarding the part of the size distribution corresponding to smaller individuals that are increasing in density (see Fig. 1 in Van Sickle (1977b)). Here I complete Van Sickle (1977b) formulation by giving this derivative its proper theoretical grounding. The third derivative in the general theory of Eq. (3) corresponds to the effect of the recruitment pattern, meaning whether the new individuals enter the population in a smooth,