Introduction
Dynamics of Size-Structured Populations: An Overview

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The size range of organisms is enormous, spanning over 21 orders of magnitude, with the blue whale and giant sequoia being $10^{21}$ heavier than the smallest microbe (McMahon and Bonner 1983). An organism is often identified as an individual in a given developmental stage, usually as a full-grown adult, which is, in many cases, a questionable point of view. As J. T. Bonner (1965) has argued, the ultimate description of an individual includes the whole life cycle. In many organisms the individuals pass through a wide spectrum of sizes, spanning more than four orders of magnitude, during the independent part of their life cycles; well-known examples are plants, fishes and reptiles. Thus, also within a species, individuals often vary greatly in size. Such large variation in size will have profound evolutionary and population dynamic consequences, which is the topic of this book.

In classical demography, mortality and fecundity have been considered as functions of age. However, in many organisms, size is more important than age in determining the fate of an individual and is, no doubt, one of the most important characteristics of any organism. Size will directly affect the type of prey an organism can eat, what predators will attack it, its physiology and energetics, and its reproductive success (Peters 1983; Calder 1984; Werner and Gilliam 1984; Sauer and Slade 1987; Sebens 1987; many contributions in this Volume). Size and morphology determine the ecological niche and hence influence competition within and between species. In some species, size even determines the sex of an individual (Policansky 1982; Charnov 1982).

The fact that fecundity and mortality are often directly connected with the size of an individual and only indirectly with its age suggests that it is more appropriate to discuss life histories in terms of size than in terms of age. Present life history theory is almost exclusively based on age-classified demographic models (e.g., Charlesworth 1980). In only a few cases has size itself been a component in life-history optimization models (Roff 1986; Kozlovski and Wiegert 1986, 1987; Pugliese 1987). Including size makes it possible to undertake a more mechanistic analysis of the constraints and trade-offs in life-history evolution that are caused by genetic correlations between traits expressed in different stages of a life cycle. For example, in traditional life history theory the concept of trade-off between current reproductive effort and residual reproductive value is applied to explain a negative correlation between early reproduction and later survival and/or reproduction. However, as pointed out by Kozlovski and Uchmanski (1987), it

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seems that taking growth into account and considering the relation between size and survival/birth rate allow a more straightforward and mechanistic explanation. Understanding the evolution of growth and size is, thus, critical to an understanding of the life history and population biology of many organisms (Kirkpatrick; Lynch; Lynch and Arnold; Werner this Vol.).

Natural selection can act either on size itself (Kirkpatrick this Vol.) or on the degree of plasticity by which organisms vary growth and size in response to the environment (Via and Lande 1985; Stearns and Koella 1986; Schlichting 1986). Kirkpatrick outlines a predictive theory for the evolution of growth trajectories based on quantitative genetics and argues that only a relatively restricted set of growth trajectories can be realized because patterns of genetic covariation between sizes at different ages constrain evolution. Genetic covariance between sizes/morphologies at different ages is thus an important constraining factor in the evolution of growth patterns, and it is therefore essential to develop methods to be able to measure such constraints. Path analysis is one method that can be used to gain insight into the genetic and environmental factors that are responsible for variation and constraints on a growth process (Lynch this Vol.). Lynch and Arnold (this Vol.) outline a method for reconstructing the phenotypic covariance matrix for components of growth and size before selection, and then use this reconstruction to estimate measures of directional, stabilizing and correlational selection.

The genetic covariance structure is itself subject to evolutionary modification (Clark 1987). One way of breaking up the genetic covariance structure may be the evolution of metamorphosis and complex life cycles (Werner this Vol.; Ebenman unpubl.). In a sense, complex life cycles represent an ultimate expression of the problems confronted when considering the ecology and evolution of size-structured populations. In species with complex life cycles, individuals of different ages differ not only in size, but usually also in form, function and in their ecological niche (Werner this Vol.). Development from newborn to adult for many groups that today exhibit sharp and abrupt metamorphic events (holometabolous insects, many marine invertebrates and amphibians) was, at the origin of their phylogeny, of a more continuous nature. The ancestors of frogs closely resembled the metamorphic stage, not the larvae or the adults, of present-day species (Szarski 1957; Wassersug and Hoff 1982; Alberch 1987); they passed through a long metamorphosis without undergoing any dramatic morphological changes. The same pattern was shown by the ancestors of the holometabolous insects (Sharov 1957; Kukalova-Peck 1978) as well as by the forerunners of many marine invertebrates living today (Strathmann 1985). Thus, there has been a general evolutionary trend towards a morphological diversification of the life cycle in several widely unrelated taxa.

Werner (this Vol.) advances the thesis that the increase in body size over the life cycle of an individual often necessitates a shift in the ecological niche, and that, to be effectively utilized, the different niches may require different body designs. Thus, the different ecological niches of the life stages result in different selection pressures on each stage. However, genetic correlations between traits expressed during a life cycle (e.g., body shape, structure of mouth parts as young and adult) constrain the evolutionary adaptation to the different ecological