

One approach utilizes general life history principles to solve for steady-state mortality rates over a broad range of environmental temperatures and copepod body sizes (Hirst and Kiørboe 2002). These authors observed a negative size-dependence of development rates of planktonic copepods, which is generally consistent with allometric scaling of other biological processes (e.g. Peters 1983). Combining this observation with average egg production rates, Hirst and Kiørboe (2002) solved for the average mortality over a generation. For broadcast-spawning species, they suggested that average mortality rates of copepods living in the epipelagic zone could be described by body size together with ambient temperature. For egg-sac-bearing copepods, average mortality rates were not related to body size but varied with environmental temperature. Another approach based on allometric principles is the use of plankton biomass size spectra to infer rates of growth and mortality (Edwardsen *et al.* 2002; Zhou *et al.* 2004). In the absence of immigration, emigration, and patchiness, the biomass spectrum is defined primarily by growth, which leads to propagation from smaller- to larger-size classes, and mortality, which reduces abundance within a size class. This approach assumes that all organisms of the same size grow and die at the same rate. Commonly, OPCs (see Section 6.3.1) have been used to assess the biovolume size spectrum, assuming that all particles sensed are living zooplankton, which is not the case in all ocean regions (e.g. Heath *et al.* 1999b; Checkley *et al.* 2008). Both steady-state and non-steady-state applications of biovolume spectra have been reported (e.g. Zhou 2006).

By definition, methods that assume equilibria, such as some allometric methods or the use of Production:Biomass ratios to approximate average lifespan mortality, cannot resolve the time-dependent variations that affect seasonal and interannual variations in populations. Averaged over a growing season or a year mortality may balance birth, but it is the variability in both that determines the timing of population variations and the temporal variability of abundance and secondary production. During the GLOBEC years, different inverse methods have been developed and refined to solve for time-dependent rates in stage-structured populations (Wood 1994; Aksnes and Ohman 1996; Caswell

2001; Li *et al.* 2006). Such inverse methods utilize the observed abundances and stage structure of a field population, usually together with independent estimates of development rates, to estimate mortality rates that would be consistent with the observed stage structure. These inverse methods are commonly described as either *horizontal* life table methods, referring to changes in demographic structure of a population followed sequentially over time, or *vertical* methods, referring to the static stage structure of a population measured at a single point in time. Although both horizontal and vertical methods were under development prior to GLOBEC, they advanced and were applied more extensively during the GLOBEC years. Some of the comprehensive GLOBEC field studies provided unusual opportunities where all essential measurements needed to make these estimates (including ocean circulation, egg production rates, stage-specific abundances and vertical distributions, measurements of food concentration and temperature) were available.

Of the inverse horizontal methods, the Population Surface Method (Wood 1994) was successfully applied to subpopulations of *Calanus* in two Norwegian fjords that were geographically close (ca. 20 km apart), but had markedly different predation regimes. One fjord (Sørfjorden) was dominated by zooplanktivorous fish, while the other (Lurefjorden) had few fish and high population densities of carnivorous zooplankton (Eiane *et al.* 2002). Eiane and co-authors found pronounced differences in the stage-specific patterns of mortality in the two fjords, apparently a consequence of different size/stage preferences of the two groups of predators. McCaffrey (2000) showed that even if the final abundances of adults were the same in the two fjords, the observed differences in stage-specific mortality significantly alter rates of secondary production. A delay-difference method was used to investigate the time-dependent mortality of *Calanus finmarchicus* at Weathership M in the central Norwegian Sea (Ohman and Hirche 2001). These authors suggested that the spring onset of population growth of *C. finmarchicus* may be affected as much by reductions in mortality rate as by increased birth rate. They uncovered a density-dependent mortality relationship for *C. finmarchicus* in the open