

# ESTIMATION OF NATURAL MORTALITY IN ECOLOGICAL MODELS

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"The true mark of intelligence is an unwillingness to fill in the many gaps in our understanding with a set of irrational beliefs." John Keats 1795-1821.

It was traditionally believed in natural history and early ecology that natural systems were orderly and stable. This stemmed partly from order and coherence being characteristic of Divine Providence in the Christian tradition, and partly from the Greek metaphysical worldview, which proposes that nature must ultimately express an orderly reality (Wiens 1984). The formal mathematical population theory that was developed during the 1920s by Raymond Pearl, A.J. Lotka, and Vito Volterra was based on the assumption of a well mixed population of identical individuals in a constant environment; in these earliest models parameters did not vary as a function of time or space. Lotka developed his models of biological systems from an analogy with chemical systems where concepts of uniformity are more applicable.

The science of ecology has taken a long time to evolve from the equilibrium concept but has begun to embrace the concept of variability. The many sources of variability now being considered have all served to extend ecological analysis beyond consideration of a uniform population to consideration of populations or metapopulations influenced by abiotic factors and complex interactions between the populations and species.

The presumption of equilibrium in ecology has affected the methodology employed to analyse patterns in natural populations (Wiens 1984). This is especially evident in the population dynamics used in applied disciplines such as fisheries, where emphasis has been on the mathematically rigorous treatment of fuzzy data rather than on the realistic portrayal of events in the natural environment. However, there has been an increasing number of studies where equilibrium concepts have been relaxed to varying degrees by incorporating additional population structure into analyses of fished populations. In effect, realisation of the complex and variable nature of fisheries has caused redefinition of parameters held constant in earlier mathematical models. The constant parameters of earlier models are the variables of more recent models incorporating spatial structure, environmental change, changes in fishing gear and fishing effort, and trophodynamics.

A straightforward example is catch at age analysis where temporal changes in age structure of the recruited component of a commercially exploited population were traditionally considered to be solely a function of fishing mortality, while all other sources of mortality (or natural mortality) are assumed constant. Recent extensions of catch at age analysis have included populations structured through space (Quinn *et al.* 1990), trophodynamics (Gislason and Helgason 1985) and gear type (Deriso *et al.* 1985).

Inclusion of population structure into catch at age analyses is necessary because in these analyses fishing mortality is inseparable from other mortality (or even migration); any trend in natural mortality with time or age will be interpreted as a trend in fishing mortality (Ulltang 1977). If density dependent factors operating through, for example, competition for resources or vulnerability to predation, exist in fish stocks then natural mortality will not be constant through time and the relative strengths of strong or weak year classes will be wrongly estimated by catch at age analyses.

It would be reasonable to assume that natural mortality in fish populations remained relatively constant over the time period for which a catch at age analysis is performed if the major sources of natural mortality (usually predation) remained constant, or were relatively minor compared to catch. This might be the case if the major predators of fish populations were longer lived animals like marine mammals or if predation mortality were a minor component of the total mortality.

An analysis of the sources of fish mortality in six diverse exploited marine ecosystems (Bax 1991), showed first that the major predators of fish in these ecosystems are the fish themselves and second that predation mortality is the major component of the total mortality experienced by the fish in these six ecosystems (Figure 1). Therefore, the major component of mortality affecting fish populations, in these systems at least, is predation by animals with comparable lifespans (i.e. other fish), and it becomes an untenable assumption that variability in catch mortality alone would cause any detected interannual changes in age class composition of the recruited stock.

Because fish predators are almost invariably larger than their prey (especially when the prey is other fish) and there are generally fewer large fish than small fish, there remains the possibility that mortality of the recruited component of populations will not be severely im-

acted by predation. In this instance, variability due to fishing would form a more significant fraction of the total mortality and analysis of changes in age class strength would provide an unbiased view of changes in fishing mortality. The degree to which this argument applies depends greatly on the species being considered. For example, larger fish will have relatively few fish predators once they have reached the size at which they recruit to the adult population, whereas small pelagics may never attain a size at which they become immune to predation. There are several published examples which demonstrate this.

The most comprehensive studies of impacts of fish predation on fisheries assessment has been the ICES multispecies VPA (virtual population analysis) (e.g. Gislason and Helgason 1985; ICES Multispecies Assessment Working Group 1993; unpublished data). Comparing the predation on cod and herring with the fishing mortality on the same two species indicates that interpreting a likely change in predation mortality as a change in fishing mortality is a more serious problem for herring, a smaller prey fish, than for cod, a larger predator (Figure 2a). Similar results are seen for a comparison of whiting and sandeel (Figure 2b). Predation mortality will be underestimated in these scenarios because mortality due to predators not among the five fish predators in the model is only included in residual (constant) natural mortality (not shown).

Sometimes the significant predator on the smaller fish can be the adults of the same species. Leonart *et al.* (1985) presented an expanded catch at age analysis of Cape hake off the coast of Namibia that included cannibalism. Cannibalism can constitute over 50 percent of the diet for Cape hake over 60 cm. In their analysis, total natural mortality ( $M$ ) was maintained at the same average level used for standard catch at age analysis ( $M=0.3$ ), but cannibalism mortality ( $Q$ ) was computed to provide almost half ( $Q=0.143$ ) of that natural mortality. Because the effects of cannibalism

are not the same for all age classes this results in a variable natural mortality with age (Figure 3). A variable natural mortality with age results in changed estimates of numbers at age and would require marked changes in management advice especially with regard to choice of mesh size in the fishery (Lleonart *et al.* 1985). The same conclusion was reached after assessing results from the North Sea multispecies VPA: "A changed exploitation pattern and a higher natural mortality for the younger age groups will change both the yield per recruit and the mesh-size assessments. It thus seems likely that much of the current advice, which is based on calculations where the same natural mortality has been applied to all ages, is wrong." (Gislason and Helgason 1985)

Changes in natural mortality as a result of changing predation affect not only results from catch at age analysis, but also the measurement of other biological variables. Sparholt and Jensen (1992) studied the impacts of cod predation on herring in the Baltic Sea. Because cod prey mostly on small food items, the smaller herring suffer greater mortality from predation than the larger herring. This results in differential predation even within an age group; fluctuating predation pressure from cod between 1982 and 1988 was estimated to have resulted in a 20 percent variation in the weight-at-age of herring over the same period.

The above cases indicate the variability in natural mortality between age groups, and size classes within age groups. Although not demonstrated, it is evident that there will be variability in natural mortality over time, especially following rapid changes in abundance of fish i.e. those events that are likely to be of most interest to managers of fishery resources. It may seem intuitive that natural mortality would be highest on the younger, smaller fish where predation pressure is the highest, and perhaps again for older fish where spawning stress or senescent mortality might operate (Beverton and Holt 1959), but unfortunately this is not well represented in fisheries population models, where it

is still often assumed that the rate of natural mortality remains constant over all ages and over all time (though see Walker 1992). Changes in natural mortality will have been attributed to changes in fishing mortality where this assumption has been made.

The difficulty in moving forward to include more population structure in fisheries assessments lies in the increased number of parameters required of the resulting models. For example, a point estimate of natural mortality is usually hard enough to obtain and rarely is fisheries assessment provided the luxury of sufficient data to enable a multispecies analysis that could provide a more realistic estimate. It is here that new approaches to fisheries assessment are required based on our understanding of the ecological properties of the fish stock being assessed and the surrounding environment that sustains and limits it. This is especially evident in many of Australian fisheries that are too small with too little economic value to sustain even the routine monitoring required for traditional fisheries assessments. It is not sufficient to defend simplistic models of an abstract population because they make analysis simpler, because the simplicity may be dearly bought when the price is measured in departure from reality (Andrewartha and Birch 1984). The debt undertaken for the simplicity must be repaid before a realistic knowledge of the natural population can be claimed.

It has been thirty five years since Beverton and Holt (1959) noted the relationship between estimates of natural mortality and growth parameters for 39 fish stocks (Figure 4). Twenty years later, Pauly (1980) extended this analysis to 175 fish stocks and provided a linear regression of growth and environmental parameters that explained 85 percent of the variability in natural mortality (although since natural mortality estimates may have often been derived from the same data set as growth parameters, the figure of 85 percent is undoubtedly high). These approaches begin to incorporate a fraction of our ecological knowledge into the population

models used in fisheries assessment, but it is likely that a new approach is required if we are to make significant advances in the provision of assessment advice to managers of fisheries. To quote Albert Einstein: "We're not going to solve the problems we've created with the same thinking that created the problems ..... we need to start thinking differently."

The way forward is not clear. Perhaps Winemiler and Rose (1992) provide an approach in their study of 216 North American fish species representing 57 families, where they elected to study and then observed correlations between life history traits and demographic variables that could be used to characterise periodic, opportunistic, and equilibrium strategists. Their approach provides an indication of population processes that would directly impact their management, yet are not provided by current fish stock assessments derived from equilibrium mythology. At the other end of the spectrum is the work by Rice *et al.* (1993) that suggests the importance of individuals in populations (as against age classes or cohorts) in determining year class strength.

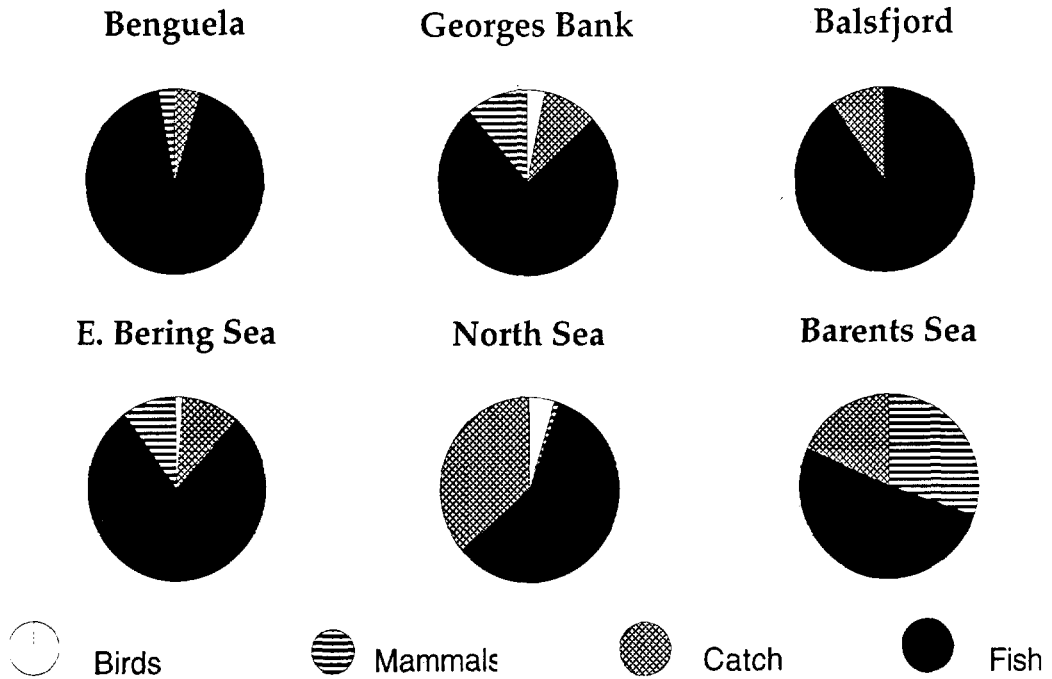
Knowledge of ecological processes has increased vastly in the last seventy years, yet, hiding behind the shield of mathematical simplicity, we still use the same models of population dynamics that we now know to be wrong. Yet "patterns" that are detected by application of an equilibrium-based methodology to a non-equilibrium community have a strong likelihood of being more myth than reality (Wiens 1984). Thus not only are we not using our increased ecological knowledge, we may well be gaining a distorted view of population processes through our demand for simplicity. It is time to integrate the accumulated ecological wisdom of the last seventy years and to move forward to provide to managers of fisheries resources, conceptual models and mathematical assessments that come closer to reality.

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**Figure 1.** Relative loss of biomass of fish to birds, marine mammals, human catch and fish. Redrawn from Bax (1991).

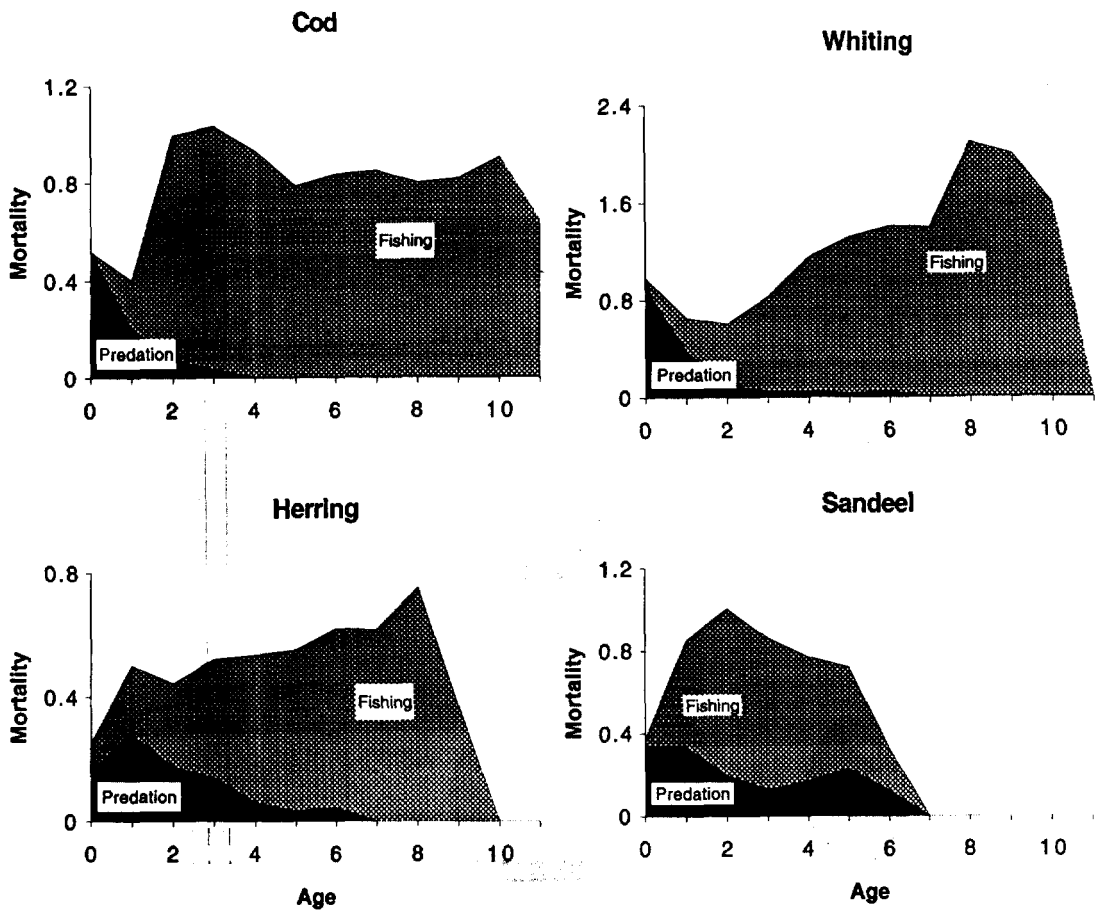


Figure 2. Comparison of mortality due to predation with that due to fishing as estimated from MSVPA. Values are average values for 1986-1991. Data are unpublished data presented at the ICES 1993 Multispecies Assessment Working Group.

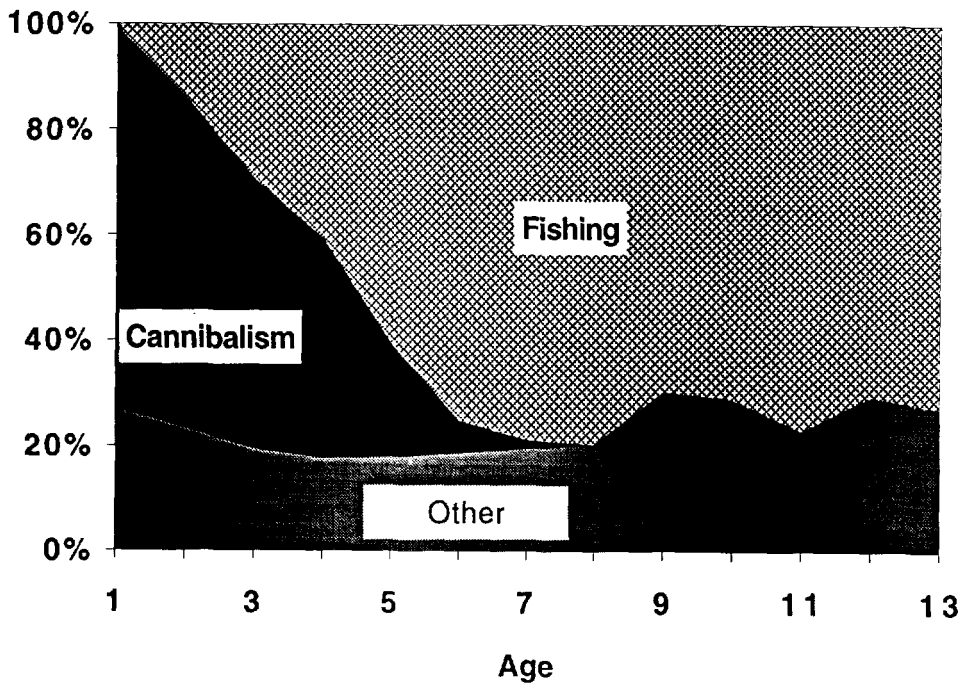
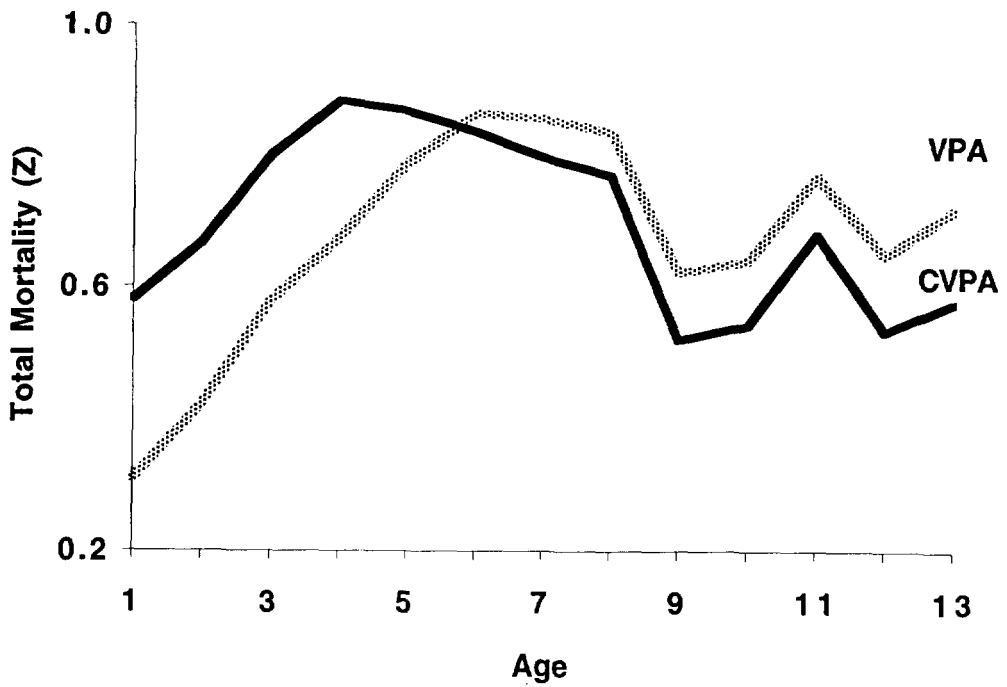


Figure 3. Average values of  $Z$  by age for standard VPA on Cape hake, and a VPA incorporating cannibalism (upper graph), and composition of mortality as a function of age for Cape hake estimated from a VPA incorporating cannibalism (lower graph). Figures redrawn from Leonart *et al.* (1985).

## Relationship between M and K

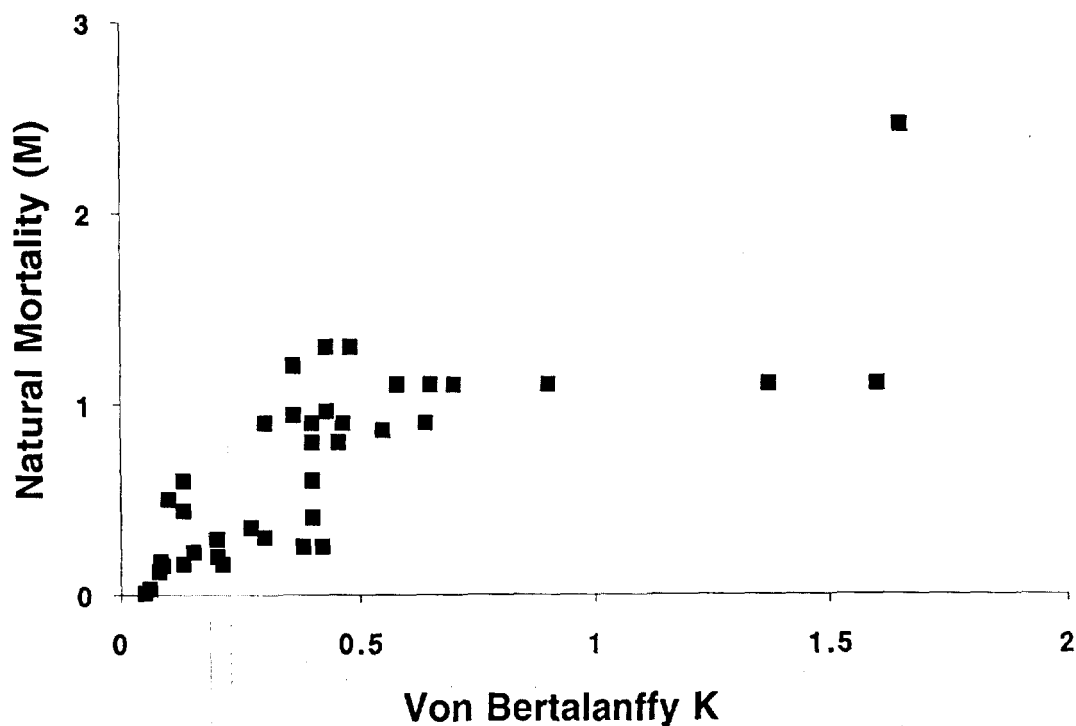


Figure 4. Relationship between estimated natural mortality and the growth coefficient, K, from the von Bertalanffy growth equation for 39 fish populations. Figure redrawn from Beverton and Holt (1959).