## *Comment*

# Comment on Mollet and Cailliet (2002): confronting models with data

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In a recent paper, Mollet and Cailliet (2002) developed demographic models for four species of elasmobranchs for which substantial amounts of data were available. In their work, they compared predictions from life history tables (LHT), age-based or Leslie matrix projection models and stage-based matrix projection models. Mollet and Cailliet conclude that LHT or Leslie matrix models provide the most reasonable estimates of demographic parameters and should form the basis of elasmobranch management. We suggest that the piecemeal comparison of the performance of structurally similar models for a few selected species does not provide a reliable foundation from which to understand elasmobranch life histories; nor does it provide a foundation from which to make recommendations for elasmobranch management. We recommend that three criteria be evaluated before deciding how best to examine the ecology and management of these fishes: the biology of the species, the nature of the available data and the objectives of the analysis (Hilborn and Mangel 1997).

The choice of model framework depends on decisions regarding the central factor regulating life histories and survival. Age-based and stage-based models differ fundamentally in this regard. Both age-based and stage-based population models represent the population as discrete components. In age-based projection models, each component represents a different age class. In stage-based projection models, the components of the population represent distinct stages that may be life history-based, size-based or even collections of age classes. Stage-based projection models can be analyzed with the same mathematical tools applied to age-based projection models. A key difference between age-based and stage-based projection models is that individuals are constrained to move from one age class to the next at each time step in age-based models, whereas individuals may spend multiple time steps in each stage in stage-based projection models.

Often stage-based models are appropriate frameworks in which to explore questions regarding the ecology and management of elasmobranchs because the demographics of many elasmobranchs are not age-based. For example, as noted by Mollet and Cailliet (2002), many elasmobranchs exhibit complex reproductive physiologies that may involve resting stages, extended gestation periods, and both ovipary and ovovivapary that are best described by discrete stages (e.g. Brewster-Geisz and Miller 2000). Moreover, for many elasmobranch species size is a better predictor of an organism's demographic contribution to the population than is age. Furthermore, stage-structured models can deal easily with biological characteristics (e.g. maturity, fecundity) and fishery-related factors (e.g. size limits) that are more closely related to size than age. Thus, when population demographics are not well predicted by age, stage-based models are an appropriate approach (Caswell 2001).

Mollet and Cailliet (2002) correctly note that age-structured models and stage-structured models formed by the collapsing of age classes into stages do differ with respect to predicted transitional dynamics, and in estimated elasticities of demographic parameters. But both models provide similar estimates of the intrinsic rate of natural increase. Mollet and Cailliet (2002) also recognise that stage-based projection models imply the potential for immortality because there is no terminal stage. In reality, however, when correctly parameterised, the fraction that survives beyond the assumed maximum age becomes extremely small. Importantly, however, key issues, such as determining the limiting level of fishing mortality that a population can sustain, are directly related to the intrinsic rate of increase and thus are not affected by the concerns over transient dynamics raised by Mollet and Cailliet (2002).

Mollet and Cailliet (2002) focus their analyses on populations for which age-structured data are available. Clearly, if age is believed to determine the likelihood of an

individual surviving, and if the available data are age-structured, then age-structured models should be employed. However, in contrast to teleosts and many other marine vertebrates, validated age analyses for elasmobranchs are comparatively rare (although this issue has recently received increased attention). The lack of validated age information can limit the application of age-structured models to elasmobranchs. Even in Mollet and Cailliet's (2002) analyses, only two of the four species considered have had ages validated using accepted methods. In contrast, stage-structured models require information on transition probabilities that can be derived from other sources of information including mark–recapture studies, a common source of our knowledge of elasmobranch dynamics, without knowing absolute age.

In cases where we are ignorant about fundamental aspects of elasmobranch biology, the application of age-structured models will suffer the same shortcomings as the application of stage-based models. For example, in the absence of data to the contrary, there is no basis for establishing a maturity ogive. Thus, fecundity in an age-based model would become a knife-edge transition, a fault Mollet and Cailliet find in stage-based projections. Yet, where a maturity ogive is available, the observed maturity schedule could be modeled using either age-based or stage-based projection models. In the former case, size-at-maturity data could be converted into age at maturity using a growth model and entered directly into the model. Indeed, all projection models are characterised by knife-edge selection inasmuch as an individual cannot be in two stages (life history, age or size classes) at the same time. For example, age-based models exhibit the ultimate knife-edge selection in that all individuals in the final age class die during the time step. However, neither approach necessarily captures the entire pattern observed because the age-based projection ignores variability in 'size at age', and the stage-based projection does not constrain a particular individual to a set period before maturity. The fundamental point we wish to emphasise is that it is the particular biological characteristics of the species and the availability of the data that determines the appropriateness of the model (e.g. Frisk *et al.* 2002).

Mollet and Cailliet (2002) further caution that the simplification of life history to calculate surrogates for the intrinsic rate of increase can be misleading. Jennings *et al.* (1998) recognised that demographic estimates from exploited populations that may be far from a stable age/stage structure due to selective exploitation of larger/older fish will be unreliable and, therefore, proposed an index of potential population growth. The Jennings *et al.* (1998) index, $r'$, is a surrogate for the intrinsic rate of population growth. It is given by the ratio of the log of the fecundity at the onset of maturity and age of maturity. Thus, contrary to Mollet and Cailliet (2002), no assumption of annual reproductive cycles is made. Jennings *et al.* (1998) note that $r'$ does not estimate the intrinsic rate of increase ($r$) and that it should not be used directly in management contexts. Rather, Jennings *et al.*'s (1998) approach should be used in comparative studies, furthering our understanding of life histories and species responses to exploitation. Frisk *et al.* (2001) calculated $r'$ values for elasmobranchs in a comparative study estimating a weak relationship between lower $r'$ values and species' maximum size.

In summary, we suggest that Mollet and Cailliet's focus on the performance of alternative models with regard to a fully age-structured model fails to recognise that such models are sometimes inappropriate, and that we are likely not to have such data for the majority of elasmobranch species currently under exploitation or threat. In data-poor species, application of stage-based and other less data intensive models can provide insights into elasmobranch population dynamics, thereby permitting management agencies to promote conservation of these important resources. Moreover, restricting analysis to age-based methods for elasmobranch species would preclude both development of population models for many elasmobranch species and the application of comparative life history analysis for understudied species that has been so informative in other fields (e.g. Charnov 1993).

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