

Chondrichthyan demographic modelling: an essay on its use, abuse and future

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The state of play

Increasing knowledge of the life history of numerous species of chondrichthyans has spawned a rather large body of literature on demographic models in the past two decades. These life tables or matrix population models typically aim at estimating the productivity of a given species or population and characterising its vulnerability to exploitation.

Use and abuse of demographic models

While population parameters such as the intrinsic rate of increase can be useful for intra- or inter-specific comparisons, interpretation of these quantities must be undertaken with caution. Use of demographic models—as typically done in chondrichthyan studies—implies tacitly making many assumptions, most notably, time invariance and density independence. This largely stems from treating the population in relative (in a horizontal life table or a transition matrix) rather than absolute (where a renewable, age-specific vector of abundance is also available) terms. While this crucial shortcoming is generally unavoidable owing to sampling limitations, ignoring the implicit assumptions is not (Cortés 2004). Conclusions derived from this approach can be misleading, especially when fishing mortality (F) is added to natural mortality (M) to determine what level of F will result in the population being stationary ($r = 0$), but no density-dependent compensation is incorporated into the model.

Contentious issues

While stochastic approaches used more recently have allowed us to capture uncertainty—rather than natural variability because it is seldom known—in estimates of vital rates used to parameterise demographic models, they still do not address the central issue of credibility of the estimates of vital rates, particularly natural mortality, the most important input into these models. Indeed, there is considerable debate about the best method to estimate M and the shape of the relationship between M and age. Owing to the lack of empirical studies, with the exception of work on the lemon (*Negaprion brevirostris*; Gruber *et al.* 2001) and blacktip (*Carcharhinus limbatus*; Heupel and Simpfendorfer 2002) sharks, estimates of M have had to rely on the use of indirect methods

based on life history invariants. From a life history theory perspective, it is sensible to assume that M initially decreases with age, but remains fairly stable once individuals attain a certain size or age and predation risk decreases. Some have also advocated U-shaped curves (Walker 1998), with M initially decreasing to a minimum, but increasing thereafter to the same initial maximum to reflect the fact that animals must die off in their terminal year of life. It is clear that knowledge of the biology of the species must be used to the greatest extent possible to rationalise, for example, why M would increase after individuals reach a certain size or age, especially given the lack of evidence for reproductive or other senescence in most chondrichthyan species. The ‘bathtub curve’ (Chen and Watanabe 1989; Siegfried 2006), which looks like the vertical section of a bathtub, is probably more appropriate for chondrichthyans because the initial decrease in M is followed by a flat profile, with M increasing exponentially only when animals approach their terminal age. It is also clear that methods providing age-specific estimates of M are more biologically sound than those providing a single value for all ages. Some fishery models applied to sharks have also predicted that natural mortality of pre-recruits must be higher than that of recruits (Walker 1998). However, it is impossible to gauge the accuracy of any of these estimates without comparison with empirically derived estimates, which rarely exist.

While M exerts the greatest influence on the output of demographic models, one should also question the credibility of the other biological inputs. Although growth rates (and the associated age at maturity/first reproduction and maximum lifespan estimates) and especially reproductive rates (the product of fecundity and the proportion of mature females reproducing) tend to be known with more certainty than estimates of M , one should question the validity of these estimates if counterintuitive results are obtained. For example, maximum age and/or the frequency of parturition may have been underestimated leading to negative population growth rates for species that are perceived to be relatively abundant, such as the blacknose (*Carcharhinus acronotus*) and blacktip sharks (Carlson *et al.* 1999; Cortés 2002). Another required check should be the proportion of the population remaining alive in the terminal year, with anything other than a small percentage (e.g. 1%; Hoenig 1983) being an indication that something is wrong in the model. One should

also be aware of the bias potential introduced when estimating age-length and length-maturity (or maternity) relationships from samples subjected to length-selective fishing mortality (Walker 1998, 2005, 2007). When possible, maternity—rather than maturity—ogives should be used for modelling purposes because the latter can lead to overestimation of reproductive output (Walker 2005; Braccini *et al.* 2006).

As noted earlier, a density-independent framework is often used to make projections that incorporate exploitation (F) but not the subsequent compensatory response one would expect. Again, this framework—a life table or transition matrix—is essentially inadequate as used because it portrays the population dynamics in relative rather than absolute terms and does not allow for proper inclusion of (time-lagged) compensatory responses. One partial solution to this problem is to assume that the demographic model *implicitly* incorporates the density-dependent compensatory response by exhibiting, for example, an increased age-0 survivorship (or even one equal to adult survivorship as in Gedamke *et al.* (in press)). This approach allows us to merge density-independent and density-dependent theory and is more appropriate to calculate population parameters that were conceived based on density-dependent theory, such as the steepness of the stock-recruitment curve, or that are intended to be used as input to traditional fisheries models, such as the surplus production term (also known as r) in a biomass dynamic model. An alternative approach is to use the modified demographic method developed by Au and Smith (1997), which assumes that the compensatory density-dependent response or ‘rebound potential’ is manifested solely as increased juvenile survival.

Interpretation of r

The interpretation of the intrinsic rate of increase is thus framework-dependent. In a density-independent framework it is the result of projecting infinitely into the future the present vital rates, which should correspond to those of an unexploited or virgin population. In contrast, in the density-dependent paradigm assumed in traditional fisheries modelling, positive r values can only be achieved after exploitation, reaching a maximum at low population levels.

Applications of demographic model results to conservation, stock assessment and management

Ultimately demographic models should provide practical management advice or further input for quantitative stock assessment models. Management measures generated from demographic models should be qualitative (e.g. protection of juvenile stages through imposition of minimum size limits) rather than quantitative (a given level of F) because of the caveats listed above. Elasticity (proportional matrix sensitivity) analyses of sharks have typically found that juvenile (age 1–age at maturity) survival is the vital rate exerting the greatest influence on population growth rate, followed by adult survival and fertility (or age-0 survival), owing to the late attainment of maturity in most species. That the greatest opportunity for compensation occurs during the juvenile stages was also implicitly recognised in the modified demographic model of Au and Smith (1997) and subsequent work by these authors (Smith *et al.* 1998, in press). Further

support for protection of juveniles and the associated preservation of reproductive potential (the sum of the reproductive values of all individuals in a population) as a preferred management strategy comes from recent work based on matrix and yield-per-recruit analyses by Gallucci *et al.* (2006). Results of elasticity analyses of batoids are more limited and equivocal to draw strong conclusions about their elasticity patterns, whereas no work has been published on other chondrichthyans.

Other approaches, however, have resulted in different conclusions. For example, simple sensitivity analyses of life tables or correlation analyses of life history traits and the population growth rate have found that other vital rates, such as age at maturity and reproduction, can have a great effect on r (e.g. Cortés 1995, 2002). Protection of the first mature ages (young adults) has been recently advocated based on results from modified demographic models linking stock-recruitment and abundance-per-recruit relationships (Au *et al.* in press). There is also the view that harvesting juveniles might be advantageous because natural mortality at young ages is high and one would only be substituting M with F, whereas protecting older sharks that have been through the ‘gauntlet’ and only experience low levels of M might be preferable since they can immediately contribute to the population through breeding (Walker 1998). These opposing views are not easy to reconcile and clearly need empirical testing.

An attempt should also be made to link the results of demographic analyses to quantitative stock assessments. In addition to values of r obtained with density-dependent considerations, quantities such as the lifetime reproductive rate (the product of the net reproductive rate and first-year survivorship; Myers *et al.* 1999), the steepness of the stock-recruitment curve (a function of the lifetime reproductive rate; Hilborn and Walters 1992), and the position of the inflection point of population growth curves (Cortés in press) can easily be generated to use as inputs to stock assessment models, especially when formulating prior probability functions in Bayesian approaches.

Future research

While much progress has been achieved, more work is clearly needed, especially pertaining to life history traits. Empirical estimates of M (or alternatively, Z) are the most urgently needed because all models and approaches require them, and other biological parameters, such as age and growth and reproductive rates are known with more certainty. Estimates of M at different population sizes would be especially valuable, but in reality they will be very difficult to obtain even for the commonest and most easily studied species. Simultaneous determination of age and reproductive parameters (age at maturity, reproductive rates) should also be undertaken when possible to eliminate the error caused by back-transforming length into age through a growth curve.

From a methodological standpoint, more systematic comparative work is needed to evaluate the relative advantages and potential pitfalls of using age- v. stage-based matrix models for characterising the demography of a given species and generating management advice. One of the topics that needs further scrutiny is the influence of the number of stages considered in stage-based models on the ensuing elasticity patterns (Mollet

and Cailliet 2002, 2003; Miller *et al.* 2003). Until the adequateness of these alternative approaches has been fully explored, the choice of the model should be dictated by the data available (Miller *et al.* 2003) or the feasibility of obtaining the data (e.g. empirical estimates of mortality of juveniles of a certain size range are likely to be easier to generate than the corresponding mortality of those juveniles across multiple age classes). Further, any comparative studies of derived quantities, such as elasticities, obtained with these different approaches should be avoided and management advice interpreted very cautiously.

More generally, demographic models should be used in concert with more complex age-structured population dynamics models. Demographic models can continue to be useful, especially in the absence of fishery data, because they provide a relatively easy and rapid assessment of the exploitation potential of a given population and of the vital rates that most affect population growth rates when used in conjunction with sensitivity or elasticity analyses. Expanding demographic models to estimate quantities such as the steepness of the stock-recruitment curve, lifetime reproductive rate, and the inflection point of population growth curves can be of direct practical use in age-structured stock assessment models, particularly when density-dependent considerations are taken into account.

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