CAPAM Growth Workshop

Focus Questions

Introduction

Growth has two main types of impacts on stock assessment models. The first is to use mean weight-at-age to convert estimated numbers of fish at age into catch, survey and population biomass, which are used in the stock assessment model and for fisheries management advice. The second is to estimate the length composition of the catch when fitting the model to catch at length data. In most applications the latter is probably most influential on the assessment results because small misfit to the observed length composition data can have a large impact on the estimates of fishing mortality and biomass. The focus questions are used to help promote discussion at the workshop and to structure the report from the workshop. If the question cannot be answered, then a clear research path should be outlined.

General

What should be done if the asymptotic length (L_∞) is uncertain and the model is fit to length composition data?

The average length of the oldest fish in the stock assessment model (related to L_∞) has a substantial impact on results in stock assessments fit to length composition data. If not many fish are observed at this length then the exploitation rate must be high (or natural mortality is high or selectivity is dome shape). On the other hand, if many fish are observed at this length the exploitation rate must be low. Several assessments have shown this sensitivity. L_∞ is often uncertain because some species are difficult to age at old ages. It is not clear which approach should be used to deal with uncertainty in L_∞. Using the largest fish seen may not be a good choice since there is variation in the length-at-age and therefore this fish does not represent L_∞ which is the average length of the oldest age. However, due to high fishing mortality, there may be no fish of size L_∞. These complications make it difficult to determine L_∞ without good ageing data.

Is the von Bertalanffy growth equation adequate or should other growth equations be considered?

There are a number of examples where the von Bertalanffy growth equation does not appear to be adequate. Some species show fairly linear growth for a range of ages before growth slows rapidly, perhaps when the fish become mature. This type of growth is not well described by the von Bertalanffy. Other species show a period of cessation in growth or other multi stanza growth curves. Other more flexible growth curves such as the Richards have been used. The problem with functional forms for growth curves is that data at any age can influence the estimated mean length-at-age for other ages. Often there is little data for young or old fish so that data on intermediate ages controls the mean length for young and old fish based on the von Bertalanffy curve and in some cases extrapolating outside the range of the data. This is particularly problematic when fitting to length composition data. This illustrates a problem with model selection, parsimony, and estimating the growth curve outside the stock assessment model. If the more parsimonious model (less parameters) is selected, it may not represent the mean length of old fish and cause a bias in management advice due to the fit to the length composition data. For example, a linear growth model may be selected, which has occurred in some applications, but it will cause the average length of the oldest fish to be too high making the population estimated to be highly depleted when fit to length composition data. Alternatively, if a more flexible model is chosen, the uncertainty in the parameter estimates are generally not propagated into the stock assessment model and management advice.

Should non-parametric methods be used for modeling growth?

Parametric functional forms used for growth curves may not be flexible enough to represent mean length-at-age for some species. They may also be influenced by the abundant data points at intermediate ages. Nonparametric methods may allow more flexibility in the growth curve. One issue with nonparametric growth curves is that it may need an appropriate approach to specifying the asymptotic property for older ages. Nonparametric approaches have a parameter, dimension, or similar concept to determine the amount of smoothness and this may be difficult to integrate into an assessment model.

Is there a growth form that performs well in most applications?

There has not been enough research to determine if there is a growth form that performs well in general. This is because most growth research has not focused on the effect that the functional form has on the stock assessment results (e.g. the effect on fits to length composition data).

When there are no sex-specific biological data, but growth is thought to differ among sexes, should a sex-structured model be used?

It is logical that if growth differs between males and females that a sex structured model should be used when there are reasonable estimates of growth for each sex. However, without sex specific size composition data it is not possible to model differences between male and female selectivity. Selectivity by either age or size has to be assumed to be the same for males and females and the choice may influence the results.

What methods can be used to diagnose growth misspecification and assist appropriate specification?

There are various methods available to diagnose model misspecification. These methods include residual analysis (ensuring the residuals have the same variance as the likelihood function and there are no trends in residuals), retrospective analysis, likelihood component profiling, age-structured production model diagnostic, and sensitivity analysis. However, none of these diagnostic methods are specifically designed to identify misspecified growth. The most promising approach is to look at patterns in residuals for length composition data or in the age-conditioned on length data, and determine if changing the growth parameters improves the residuals. There is likely to be confounding between growth and selectivity, so the residual patterns may be hard to interpret.

How important are growth uncertainties compared to other typical assessment uncertainties, such as the form of the stock-recruitment relationship, catchability estimation, choice of a Fmsy proxy, etc.?

The importance of growth uncertainties is dependent on the type of model. Models that do not fit to size compensation data (e.g. delay difference models, stock reduction analysis, and catch at age models) will be less sensitive to growth uncertainties than those that do. They only use growth to convert abundance (e.g. catch) in weight into numbers. In these models, the length (weight) of the most common aged fish is probably most important. Models that fit to size composition data can be highly sensitive to growth. The size of the fish caught relative to those predicted in the model influences the estimates of absolute abundance and fishing mortality rate. The results are particularly sensitive to the asymptotic length. They are also sensitive to the variation of length-at-age of the oldest fish. The influence of growth on fits to size composition data interacts with the selectivity parameters. The relative effect of growth compared to other population and fishing processes is probably application specific.

How do growth model assumptions interact with key management parameters?

The growth rate (K) can influence key management quantities. Yield per recruit reflects a tradeoff between growth and natural mortality. The quantities B_{MSY}/B_0 and MSY/B_{MSY} are a function of the biological (e.g. growth natural mortality and the stock recruitment relationship) and fishery (e.g. selectivity) processes. The sensitivity of the shape of the production function (B_{MSY}/B_0) to growth is about the same as natural mortality, but it is more sensitive to steepness of the stock-recruitment relationship (Maunder 2003). The productivity rate (MSY/B_{MSY}) is very sensitive to growth, natural mortality, and the steepness of the stock recruitment relationship (unpublished results). These management parameters are independent of the maximum length. However, due to the interaction with data used to fit the model (e.g. size composition) the estimates of management parameters can be sensitive to L_∞.

Should forecasts include trends in growth?

It is unusual for forecasts to include trends in growth. Any trends would need a rationale. For example, density dependent or genetic selection might be reasonable rationales to include trends in growth. Climate change is probably to speculative to use as a rationale. It might be more reasonable to assume that growth rates are due to current environmental conditions and current conditions are likely to continue into the future. Projections using stochastic growth based on historical variation and autocorrelation might provide a more accurate representation of uncertainty.

Is it inappropriate to rely on simplifying assumptions when modeling growth?
Growth is used for two main purposes in stock assessment models: 1) to convert from biomass to numbers and 2) to fit to size composition data. Simplifying assumptions are probably adequate for converting from biomass to numbers, but not for fitting to composition data. Functional forms are very rigid and allow all data to influence the length of all ages. Unfortunately, the size at the extreme ages (e.g. maximum age) can be influential but these sizes are controlled by the preponderance of data at intermediate ages. Therefore, model misspecification caused by simplifying assumptions can influence the results particularly when fitting to size composition data.

Is the influence of selectivity on growth estimates something to be concerned about?
The influence of selectivity on growth has been investigated in several studies. (Summarize results). In particular, size specific selectivity can bias the estimates of growth parameters. Integration of growth estimation into the stock assessment model will automatically account for selectivity on growth estimates.

How should growth curves be fit to data to avoid the abundant data points at intermediate aged fish influencing the mean size-at-age for old fish?
Some researchers have fit growth curves to age-length data giving equal weight to each age (e.g. fit to the mean length-at-age). However, this may overly emphasize data points for ages where there are very few data. In addition, this approach does not estimate the variability of length-at-age, which is also needed for stock assessment models that fit to size composition data. Using a more flexible growth curve may be a better alternative.

Can we integrate methods which allow for individual variation in growth into assessment models – is it worth it?
Modeling individual variation in growth might be important in stock assessment models where there is strong length based selectivity and the fishing influences the distribution of length-at-age. Most age-structured stock assessment models assume that length-at-age is normally distributed and instantaneously reverts back to a normal distribution after fishing at the start of each time period. This is not a realistic assumption. However, methods to include individual variation in growth are generally too computationally intensive to include in stock assessment models. Methods such as growth platoons, which model groups of individuals, are more practical. Unfortunately, the data required to estimate the parameters of these types of models are generally not available and there use has been limited.

Variation of length-at-age is important when fitting to size composition data. Variation of length-at-age can be due to a number of factors including individual variation, temporal variation, spatial variation, ageing error, and different times at birth or capture. Individual variation is only one component, so it may not be worth integrating methods which allow for individual variation in growth into assessment models unless the other sources of variation are also accounted for. Variation of length-at-age can be estimated inside the stock assessment model, but the relationship with age or size generally has to be assumed and the model estimates will be more uncertain. Information about the relationship between variation of length-at-age and age or length from information on individual variation might be useful in constructing stock assessment models.

Does the time step in the stock assessment model need to be shortened for fast growing species?

The faster a species grows the more likely the length of a fish at a given age will change over the time step of the model. This may cause problems when fitting to length composition data. For example, the variation of length-at-age from the length catch composition data in a single year from a fast growing species will be larger than from a slow growing species, but this may not be related to individual variation in growth. It may also be difficult to identify modes in the length composition data for fast growing species unless the composition data is separated into shorter time periods. However, splitting the data will reduce the sample size for each time period. Although, unless there are additional parameters as the time periods are increased, it does not reduce the effective sample size. There may be a cost of increased computation time if the number of time periods is increased, however with modern computers this should not be a major impediment. Therefore, it is recommended to reduce the time step for fast growing species. Some applications just run the same model on a time step shorter than a year (e.g. quarter), but this generally means that there is recruitment each time step and may be appropriate for some species (e.g. tunas). Other applications use a seasonal framework where recruitment only occurs once a year (or as many times as required) and this method is implemented in Stock Synthesis.

The timing of the model and the ageing data need to be consistent. For example, the birthdate used for the ageing data or growth model needs to be consistent with recruitment time periods in the model. Also, the time of the year used for the average length in the ageing data or growth model needs to make sense in the model (e.g. middle of the year).

Theory and experimental evidence

Can underlying processes be used to determine a growth form (e.g. linear, von Bertalanffy)?

How much of growth is genetically determined and how much is environmentally, and how does this influence how we model growth in movement models.

How prevalent is density dependent growth and do we need to include it in our stock assessment models?

What biological (e.g. natural mortality) and fishing processes (e.g. selectivity) are influenced by fish size and do they impact stock assessments?

Natural mortality due to factors such as predation is likely to vary with size and therefore variation in growth rates will influence natural mortality. However, this affect is likely to be for small fish that are not vulnerable to the fishery, except for species that are small in the adult phase (e.g. sardines and anchovies). Growth of adults may influence the number of eggs produced or the time it takes to become sexually mature. However, due to the weak (or lack of) relationship between stock and recruitment for many species this is unlikely to influence the dynamics of the population. However, it may influence management quantities and reference points that are based on spawning biomass. Substantial changes in size-at-age are probably needed for these affects to be important or to be detectable.

Fishery or survey selectivity may be a different story and changes in growth combined with sized based selectivity and size composition data may have a large influence on stock assessment results.

Is size-based genetic selection common in exploited species and do we need to consider it in stock assessments and management?

Specification and estimation: growth determination from direct ageing methods as used in age-structured models

What is the best model for variation of length-at-age?
Variation of length-at-age can have a substantial impact on assessment results when fitting to length composition data, particularly that for the maximum age in the model. Similar to L_∞, the variation of length-at-age determines the maximum sized fish in the population. If set to low so large fish are not expected the population will be estimated to be lightly depleted. If set too high the expected large fish will not be observed so the population will be estimated to highly depleted. Stock synthesis has several linear based formulations for the variation of length-at-age. Either the standard deviation or the coefficient of variation can be a linear function of age or mean length-at-age. The relationship is determined by a parameter for a young age and a parameter for an old age. The relationship is linear between these two ages and constant outside them. It is not clear which relationship is most appropriate. However, assuming a constant cv as a function of age appears to be inappropriate. This can produce relatively large standard deviations (sd) for the old fish or unrealistic small sds for the young fish. This is because growth rates decline with age and variation is not expected to increase much at old ages, given growth has slowed. It also might be reasonable to expect variation to increase over time as the fish ages and grows. Therefore, if there is insufficient information to estimate a linear relationship, constant cv as a function of mean length may be most appropriate. Research is needed to determine the most appropriate relationship. For example, a meta-analysis of well-aged random samples of age-length data from a number of stocks.

How should variation in length-at-age other than individual growth variation be dealt with?
Variation in length-at-age is important when fitting to length composition data. Ideally this represents individual variation in growth. However other factors can cause variation in length-at-age. These factors include ageing error and temporal or spatial variation in growth. If the variation of

length-at-age is fixed based on individual growth variation it will under estimate the variation in length-at-age seen in the data unless the other processes are modeled. It is not clear how this would influence the results.

How should age-length data be combined with tagging growth increment data to provide improved estimates of growth?
There are many stocks for which growth estimates are available from both age length data and tagging growth increment data. Typically these two types of data are analyzed sperately and the results compared. Combining the results is difficult because the error structures are different. Laslett et al. (2002) developed a method to combine the two types of data that treats the tagging data as age-length data by estimating the age-at-release of each tagged fish. Because the fish is measured twice, the tag data still contains some information after estimating its age. However information about absolute age is lacking and age-length data are needed to calibrate the absolute age. There are still some issues with the approach that need consideration. For example, how should correlation between the length-at-release and length-at-recovery be incorporated in the model? How should ageing error and reduction in growth rates due to tagging be dealt with.

How and when should ageing error be incorporated in the stock assessment model?
Between reader error estimates may not be adequate for some applications because there is correlation among readers. Ageing error can be estimated inside the stock assessment model in some applications. For example, ageing error is estimated inside the stock assessment model for pacific cod. This is because there are clear modes for young ages in the survey length composition data that differ from the age length data. However, the modes are not clear for older ages and linear extrapolation is used but it is not clear if it is appropriate.

Should age length data be used inside the stock assessment model to estimate growth?
Growth rates are generally estimated from age length data outside the stock assessment model. However with the development of integrated stock assessment models it is possible to include this data inside the stock assessment model. The advantages of this approach include 1) growth can get information from other data (e.g. modes in the length composition data) 2) uncertainty is automatically propagated throughout the analysis 3) the assumptions are consistence (e.g. selectivity is automatically taken into consideration) 4) the sampling design can me more explicitly included (e.g. using age conditioned on length and length composition). It is not clear if length and age conditioned on length data is adequate or if joint age-length data be used. In some cases the sampling within a length class for age is not random (e.g. otoliths from older fish are harder to age so some of them are discarded from the sample). Estimating growth inside the model with inadequate information may allow the growth parameters to be estimated in a way to compensate for model misspecification unrelated to growth.

Is the assumption that length-at-age is normally distributed adequate?
Most age structure models assume that length-at-age is normally distributed and the distribution resorts back to this form at each time step even if there is high length-based fishing mortality. A

length based model automatically adjusts the implicit length-at-age distribution. The change in the length-at-age distribution can be approximated using several growth groups (platoons or morphs in Stock Synthesis) modeled desperately, each with their own growth curve.

How does the choice of the plus group interact with growth specification and estimation?
There are two types of plus groups used in stock assessment models. The first is the plus group used to model the dynamics of the population. It is used to accumulate all fish of a certain age and older and fish in this plus group are assumed to have the same values for biological (e.g. mean length-at-age, natural mortality, fecundity) and fishing (e.g. selectivity) processes. If fish grow after they enter this plus group it will influence the average weight in the plus group. Typically, the mean length and weight-at-age of the plus group is assumed to be equal to the mean for the youngest age in the plus group and may under estimate the mean for the plus group. The actual mean will change with the exploitation rate: being lower as the exploitation rate increases. Stock Synthesis uses an adjustment to increase the mean length and weight of the plus group for growth within the plus group. It may be appropriate to set the plus group large enough so the fish are no longer growing or that in a virgin population (because it is used for reference points) there are very few fish in the plus group. However, the computational demands will increase with the number of age classes used in the model.

The second type of plus group is for the composition data. If the bin size is too large, then the model may not be able to pick up the cohorts in the length composition data. Smaller bin sizes will increase the computational demands. If the plus group is at too small size it will not allow the length composition data to provide information on the asymptotic length of the growth curve. Using a lower size for the plus group may eliminate bias caused by misspecifying the asymptotic length of the growth curve trading it off for more uncertainty. However, it may be better to use a flexible growth curve and estimate the asymptotic length inside the stock assessment model to better represent uncertainty.

When estimating growth inside a stock assessment model does one fishery need to have an asymptotic selectivity to stabilize estimation?
Assuming asymptotic selectivity for at least one fishery or survey generally helps stabilize estimation in stock assessment model. This is particularly true if growth or natural mortality is being estimated. It may be less of a problem for growth if the model includes age conditioned on length data. Length composition data is particularly problematic because the absence of large fish in the composition data could be explained by several factors including high fishing mortality, high natural mortality, dome-shape selectivity, or a low asymptotic length.

What is the asymptotic length confounded with: a) the specification of natural mortality (M); b) increased age-specific M for older fish; c) the selectivity of the oldest age class?
Length composition data is particularly problematic because the absence of large fish in the composition data could be explained by several factors including high fishing mortality, high

natural mortality, dome shape selectivity, or a low asymptotic length. Therefore, asymptotic length might be confounded with the right hand limb of the selectivity curve, the rate of natural mortality and how it changes with age, and fishing mortality. It may be less of a problem for growth if the model includes age conditioned on length data.

Are VPAs using cohort slicing more or less sensitive to growth assumptions than integrated stock assessment models that fit to length composition data?
Intuitively, misspecified growth should also bias VPAs because the catch-at-age will be incorrect. However, direct comparison of age-structured, catch-at-length models and VPAs using age data based on cohort slicing needs to be conducted to determine which approach is least biased.

Specification and estimation: growth determination from size increment data as used in size-structured models

How should one choose the number of size classes and their widths when conducting size-structured assessments – should this issue be considered in terms of the amount of growth-related tagging data?
The number of size classes will have an impact on the computational demands of the analysis. However, unless the model is being run a large number of times, it should be practical with modern computers to cope with the number of size classes need to extract the most information out of size composition data. Too wide size classes will prevent the model from extracting detailed information about the shape of the growth transition or the cohort strengths. Two small of a size class may cause the model to fit noise rather than signal due to the low sample size of the length composition data in each bin. However, this will probably not be the case unless there are additional parameters added to the model for each size class. Most models assume a functional form for processes that are size specific and this will prevent the model fitting to noise and will average over the fit similarly to if the data was condensed into fewer bins.

Tagging data are likely overdispersed – how can this be accounted for when tagging data are integrated into assessments?
There have been several methods used to account for over dispersion in tagging data in cases where the tagging data is used for estimating biomass, but it is not clear if the same approach can be used for tagging growth increment data. Random effects have been included in growth models to account for individual variation and a similar approach could be used for groups of fish tagged together to deal with overdispersion.

Spatial-temporal variation

When and how should temporal variation in growth be modeled?
There are a number of factors such as environmental conditions and density that could cause

growth rates to vary over time. The ability to model time varying growth will depend on the amount of information available in the data. For example, if there is mean weight-at-age available for all years, then modeling time varying growth using empirical weight-at-age might be the appropriate approach. If there is only one year of age-length data, then assuming constant growth might be appropriate. The choice will be a tradeoff between variance (time varying growth) and bias (constant growth). Theoretically, a state-space model with time varying growth should be used in all cases to most accurately represent the uncertainty, but practically, priors on the amount of variability are needed. Research based on stocks with good growth data that describes the amount of temporal expected in fish population should be conducted.

How should spatial variation in growth rates be dealt with in spatial models?

For many species it is clear that mean size-at-age differs spatially. If there is movement among the population the stock assessment model may need to deal with this variation. Spatial models are becoming more frequently used in stock assessments. If movement is low then separate stock assessments with different growth rates may be adequate. If movement is moderate to high then modelling movement and dealing with the growth differences may be needed. One main consideration is what happens to the size and growth rate of a fish when it moves from one area to another. If the difference in growth rates is environmental then the growth rate may change to that of the new area. If the difference is due to genetics then the growth rate may stay the same. The influence of the change in growth rate will depend on the type of stock assessment. If the model does not fit to length composition data, the growth is mainly used to convert catch in weight into numbers in the model. It is also used to turn model numbers of fish-at-age into estimates of stock biomass. In this case, the influence of growth variation among areas may not be that influential. However, if the model is fit to composition data, then spatial variation in growth may influence the fit to the length composition data and have more influence on the model results. In a simple spatially-structured/age-structured model without tracking the origin of a fish, the fish will automatically grow or shrink to the new size-at-age when it moves—this is unrealistic. In a length-structured model, it will move into the correct length bin, but will take on the new growth rate of the new area. An age- and length-structured model may be able to model growth as a function of both age and length to partially take this into consideration. Modeling genetic cohorts as well as length or age structure may allow more flexibility.

Time-invariant (constant) growth is a strong assertion. Is it justified and how does it influence model results?

Temporal variation in growth is expected, however it is not clear if the amount of variation is enough to bias the stock assessment results when growth is assumed to be constant. The influence will probably be application-specific and will depend on how much variation there is and what type of model is being used for the assessment. Stock assessment models that fit to composition data and assume constant growth might be the most sensitive to time varying growth.

When should empirical weight-at-age be used instead of explicitly modeling growth?
The choice between using empirical weight-at-age data and explicitly modeling growth will be a function of several factors, but primarily a tradeoff between sampling error (which may include random sampling error and ageing error) and process error. Using empirical weight-at-age data assumes all the error is temporal variation in growth, while explicitly modeling the growth general restricts the temporal variability. An ideal situation would include empirical weight-at-age data with low sampling and ageing error for all time periods and fisheries (this also implies age-composition data with low sampling error). In this case the obvious choice would be to use the empirical weight-at-age data. However, as the sampling or ageing error increases, or when there are time periods without data, explicitly modeling the growth becomes more appropriate. This is also the case when there are time periods or fisheries without age data and size composition data is used instead. The growth can be modeled as time invariant or temporal variation can be modeled explicitly. The growth model can be configured to closely match the empirical data, but the model may be computationally intensive with convergence issues, so using the empirical data might be more practical.

Tuna stock assessments

What is the evidence for the two stanza growth proposed for tuna?
For some species of tuna in some oceans there are unusual patterns in growth where at intermediate ages the growth slows down and then speeds up. In others the growth is linear and then slows down rapidly around the age at maturity. It is unclear why these growth patterns are not seen in all oceans. The patterns could be naturally occurring caused by physiological ontogenetic changes or environmental conditions or caused by the ageing method (i.e. tagging effects on growth). It is important to understand the cause of these changes in growth so that the growth can be modeled correctly.

Stock Synthesis modeling framework

What growth sub-model developments are needed in stock synthesis?
In a sex structured model it is not possible to estimate both the young and old variation of length-at-age parameters and make them both the same for males and females.