Growth: theory, estimation, and application in fishery stock assessment models

CAPAM Workshop Series Report 2 March 2015

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Preface

The Center for the Advancement of Population Assessment Methodology (CAPAM) is a collaborative effort, jointly supported by the Southwest Fisheries Science Center (SWFSC, NOAA Fisheries), the Inter-American Tropical Tuna Commission (IATTC), and Scripps Institution of Oceanography (SIO, University of California, San Diego). This Report is the second in a Workshop Series published by CAPAM, with CAPAM staff serving as editors, i.e., Workshop Series Report 1 addressed the topic of selectivity (Crone et al. 2013). The CAPAM advisory panel, keynote speakers, and various workshop participants provided useful reviews for improving the Report. Workshop presentations and recordings are available online from the CAPAM website (visit www.CAPAMresearch.org). Formal papers produced from proceedings of the workshop and other contributions will be included in a special issue publication of the journal Fisheries Research (Maunder et al. In preparation); see Maunder et al. (2014) and related papers for special issue on selectivity. This Report summarizes presentations and discussions from the week-long meeting, which represents general views expressed by participants, rather than any achieved consensus regarding definitive conclusions or recommendations. In the Summary below, statements presented at the workshop by particular researchers are cited accordingly (readers should consult the respective abstracts, presentations, recordings for further details). Finally, important areas of future research are identified throughout the Report, including work needed to further develop good practices for modeling growth in integrated assessment models.

Background

The Center for the Advancement of Population Assessment Methodology (CAPAM) hosted a workshop on Growth: theory, estimation, and application in fishery stock assessment models from November 3-7, 2014 at the Southwest Fisheries Science Center (SWFSC) in La Jolla, CA, USA. The five-day meeting was part of a broader program under CAPAM that focuses on developing guidance for Good Practices in Stock Assessment Modeling. The workshop was sponsored by NOAA/NMFS and the International Seafood Sustainability Foundation (ISSF). Mark Maunder (IATTC) served as chairperson for the technical forum. A diverse body participated in the workshop, including 100 scientists from federal, state, and international fishery institutions, 30 researchers who contributed recent analysis and case studies pertaining to growth, and 5 invited speakers who provided reviews on major topics associated with growth parameterization and considerations in fishery assessment models. Keynote speakers included: biological processes/ontogeny (Kai Lorenzen, University of Florida); specification and estimation: age-structured models (Chris Francis) and length-structured models (André Punt, University of Washington); spatial/temporal variation (Steve Martell, International Pacific Halibut Commission); and modeling growth in tuna assessments (Dale Kolody, CSIRO Marine and Atmospheric Research).

The workshop was structured in a manner that allowed both novice practitioners and experienced analysts to gain insight into growth properties and parameterizations involved in developing robust stock assessment models. Each topic above comprised a review and several research presentations, followed by group discussion that addressed focus questions and outlined priorities for future research. Additionally, two special sessions related to modeling growth in integrated assessment models were held as part of the overall workshop. The first session was based on the widely-used stock statistical modeling framework Stock Synthesis (SS, Methot and Wetzel 2013), with Ian Taylor (Northwest Fisheries Science Center, NWFSC) presenting an overview and tutorial for addressing growth parameter options available in SS. The second session was led by Jim Thorson (NWFSC), who provided an introduction to Template Model Builder, an AD Model Builder inspired R-package for fitting flexible state-space and hierarchical models.

Summary

Individual growth is a fundamental biological process exhibited by animal populations and an integral part of fisheries stock assessment models. In contemporary age-structured stock assessment models, which are founded on the number of fish-at-age, a mathematical model of growth is used to: 1) convert input catch estimates from biomass to numbers; 2) convert output numbers into biomass; 3) convert length-based selectivity to selectivity-at-age; and 4) calculate expected length compositions (Francis). In length-structured models, growth models are used to determine the transition between length bins and calculate expected length compositions (Punt). In most applications, the calculation of expected length compositions is likely to be most influential in terms of derived quantities useful to management generated from the assessment, given small misfits to the observed length composition data can have a large impact on the estimates of fishing mortality and abundance (Lee et al. 2014). Unfortunately, "biologists do not always understand how their data will be used in an assessment or the assessment analysts do not appreciate the limitations of the data that they are working with" (Kolody), making modeling growth much more problematic than it should be. Major findings and areas of future research generated from presentations and discussions during the workshop are presented below. See Appendix C for focus questions that were used to guide group discussions and assist developing the following major topics.

Biological processes

The majority of fish species show continuous growth that slows down at older ages, with variability among years (Stawitz; Thorson), seasons (e.g., krill stop growth in summer, Kinzey), cohorts (Stawitz), and individuals (Ortiz de Zárate). Some species, such as crustaceans, have more complex growth patterns that require molting to grow further, resulting in discrete growth and in some cases, may have terminal molts, whereby growth ceases (Punt; Siddeek). Variation

in growth is likely related to the variation in excess energy available after essential functions, such as maintenance, have been satisfied. The energy available may change temporally and spatially, depending on the environmental conditions and prey availability or quality. Growth may also vary due to ontogenetic changes in the species' niche (e.g., gape limitation for ingesting prey). Individual variation in energy use efficiency may be substantial for some species due to underlying genetic disposition or environmental factors (e.g., temperature). Energy is used for metabolism, growth in weight and length, and reproduction; processes that should all be considered when developing a growth model. However, such underlying processes are often complicated and would be necessarily difficult to parameterize in a comprehensive physiological model that accurately describes growth for a particular stock and thus, a simpler model (e.g., the von Bertalanffy, VB) will need to be considered for fitting to age-length data. In addition, most energetic models are based on individual weight, whereas stock assessment models that fit to length composition data are more sensitive to the length-at-age relationship. Growth rates may be determined internally via genetics, externally via environmental conditions, or both. Given that the plasticity of growth observed in wild and cultured populations is relatively high, genetics may not be the most important driver of growth for many populations in respect to fisheries management.

Ontogenetic changes in growth rates not represented by the standard VB growth curve are commonly observed for many species. Many species show a sharp decline in growth rate around the age-at-maturity. Others show multi-stanza growth, such as a growth cessation or increase (e.g., some tuna stocks exhibit slowing of growth at intermediate ages, Kolody). These changes may be caused by factors, such as a change in prey species, development of a functional swim bladder, and growing beyond predatory concerns. Migrations likely coincide with environmental changes that can impact growth rates and the maximum size that can be attained. However, apparent ontogenetic changes in growth may be simply an artifact of sampling (e.g., time varying selectivity, Kolody).

Most common growth curves, such as the VB, do not take into consideration the energetic cost of reproduction and the consequent reduction in growth rates. In some cases, growth slows so quickly that the VB growth curve is unable to accurately represent the mean length-at-age and other growth curves will need to be considered. It has been hypothesized that reduction in growth rate is due to energy costs related to reproductive activities, leaving less energy available for growth (McGarvey; e.g., American lobster, Chen). On average, about 15% of energy goes into reproduction, which is unaccounted for in the derivation of the VB growth curve (Lorenzen). For some species, the cost of reproduction is evident, including spawning migrations (e.g., most salmon species that lose considerable body weight and subsequently, die), high reproductive investment (e.g., shark species that give birth to fully-developed pups), and continuous spawning (e.g., tropical tuna species). For many species of crustaceans, slowing down of growth following maturity is more pronounced for females than males, presumably because of their larger

investment in reproduction (McGarvey). Growth rates of wild tilapia are slower and they reach a larger size than cultured tilapia, possibly related to reared tilapia typically reaching sexual maturity at a smaller size (Lorenzen).

Research generally indicates that there is substantial individual variation in growth rates (Chen; Ortiz de Zárate) and that growth can differ between males and females (Chen). Terminal molts in some crustacean species can result in large differences in asymptotic length. Similar to temporal variation (see below), individual variation is attributed to variation in asymptotic length (Ortiz de Zárate).

Changes in growth rates may also influence other processes. For example, survival, fecundity, and movement may be related to size. Further, the process that most likely interacts with growth rates is selectivity to the fishery. Growth may be negatively or positively correlated with recruitment due to density dependence (trade-offs between recruitment and growth due to a limited energy supply) or environmental conditions that are favorable for both recruitment and growth (Lorenzen). Growth parameters (e.g., K of VB relationship) are correlated with other life history attributes that are more difficult to estimate (e.g., natural mortality, recruitment compensation), with such relationships commonly used to determine reasonable estimates for the related life history parameters (Lorenzen).

Growth specification

There are several examples where growth is not well described by the classic von Bertalanffy (VB) relationship. Other parametric growth forms, such as the Richards growth curve, provide more flexibility for estimating length-at-age for a wide variety of species than possible using the VB equation. However, a major problem with functional forms for describing growth curves is that data for any particular age can influence the estimated mean length-at-age for other ages. Often there are few observations available for modeling growth of very young or old fish and thus, information for intermediate ages strongly influences estimate mean length for young and old fish based on the parametric growth curve, including in some cases, extrapolating outside the range of the sample data. This is often the case when fitting to length composition data and illustrates an inherent problem with model selection, parsimony, and estimating the growth curve outside the stock assessment model. If the more parsimonious model (fewer parameters) is selected, it may not represent the mean length of old fish and ultimately, resulting in potentially biased estimates useful to management due primarily to fitting the length composition data (Aires da Silva 2015). Alternatively, if a more flexible model is chosen, there is increased uncertainty in the parameter estimates and the uncertainty is typically not propagated into the stock assessment model and associated management advice.

Growth curves based on parametric functional forms are likely not flexible enough to estimate mean length-at-age for some species. On first principles, nonparametric methods should allow

more flexibility, to some degree, for estimating growth in an integrated stock assessment. However, a potential limitation of nonparametric growth forms is determination of objective approaches for specifying asymptotic properties of the older ages. Nonparametric methods in general require parameterization regarding the amount of smoothness underlying the curve, which may be difficult to formally integrate within the statistical framework of an assessment model.

Francis outlined several guidelines when choosing the best growth model: 1) there are no fixed rules; 2) be guided by your data (quantitative and qualitative); 3) try alternative models and see what works; 4) start simple and use Occam's razor to limit the complexity; 5) the more complex model should produce a visible improvement in the model fit and a non-trivial change in the stock status; and 6) make sure the model is plausible. These are a good set of guidelines to follow while additional research is carried out, so a more definitive guide to good practices can be developed. In data limited situations, using models with biologically meaningful parameters and priors based on well-studied systems or theory may be a useful way forward (Márquez-Farías). However, more research is needed across a broad range of stock assessment applications to evaluate the robustness of alternative growth forms, i.e., most growth research to date has not addressed the effect of different functional forms fitted to length composition data on derived management quantities generated from the stock assessment.

Variation of length-at-age is an important component of growth modeled in stock assessments that fit to length composition data, but typically, is not as influential as the mean length-at-age curve (Zhu). Despite its importance, variation of length-at-age has generally not been an area of concern in biological studies involving growth. In fact, age data are often collected by length bins, which can result in biased estimates of variation of length-at-age when analyzed using traditional methods (Lee). Age conditioned on length methods produce more robust estimates of variation of length-at-age in these cases (Lee).

There are a variety of factors that influence variation of length-at-age, including environmental conditions, density, individual variation, spatial distribution, variability in birth dates, and ageing error, with no straightforward methods for apportioning the variance accordingly. For this reason, it may not be appropriate to use individual variation in growth rates to represent variation of length-at-age in assessment models but rather, such variation should be addressed inside the stock assessment model or by using some other alternative approach.

There are a variety of methods to relate variation of length-at-age to age or mean length to reduce the number of parameters used to represent variation of length-at-age. It is generally recommended that the relationship be based on mean length to ensure that the variation does not become too high for older ages when growth rate has declined (Francis). The standard deviation of length-at-age typically increases with age and a constant coefficient of variation (CV) may be the most appropriate assumption in the absence of information, with a value around 10% being

commonly observed. However, the relationship may be complicated by a number of factors. For example, variability in birth dates may lead to higher variation at younger ages. If individual variation is a function of growth rate (K) rather than asymptotic length (L_{∞}), then the variation of length-at-age may decrease with age as all fish approach the same asymptotic length. Data for hoki suggest that the CV versus mean length is not linear and the relationship used in MULTIFAN-CL, sd(L) = $a \cdot \exp(b\overline{L})$, may be a better alternative (Francis). Mesocosm studies have indicated a constant CV with mean length, but some wild populations are characterized by decreasing CV with mean length (Minte-Vera), which may be a consequence of length-specific mortality. Halibut show a much larger variation of length-at-age (e.g., 35-40%) than other species, as well as exhibit substantial variation in growth spatially (Martell). The variation of length-at-age is also dependent on the assumed distribution. Normal, log-normal, and gamma distributions are often used (Quinn), but with typically low CVs for length-at-age associated with most species, there is not likely to be notable differences between the shapes of these distributions.

Temporal variation

There is considerable evidence for temporal variation in growth parameters (Stawitz; Thorson). The variation can be manifested seasonally (Kinzey; Chen; Fukuda), annually (Stawitz; Thorson), or by long-term trends (Isely; Martell). Causal mechanisms for variation over time include environmental conditions (Matthias), selectivity-induced genetic selection, and density dependence (McGarvey; Matthias). Environmental variability may mediate density dependence through changes in habitat availability (Matthias). Annual variation that is correlated among all ages appears to be more common than cohort-specific variation caused by intra-cohort density dependence (Stawitz). Research indicates that the variation is most pronounced in the asymptotic length, rather than the growth rate (Lorenzen; Matthias). However, this effect is potentially misleading due to the common parameterization of the VB equation, which was not formulated in the context of time-varying processes. It is more informative to use the formula for the expected annual growth increment, $\Delta L = \alpha - \beta L$, where $\alpha = L_{\infty}(1 - \exp(-K))$ is related to the total energy available and $\beta L = (1 - \exp(-K))L$ is related to the energy used for maintenance, with the difference being related to the energy available for growth. It makes sense that variations in the total energy available due to environmental factors (e.g., prey availability or nutrient content) would result in temporal changes in estimated L_{∞} of the VB equation, since L_{∞} is only accounted for in the calculation of α . The β may be genetically determined or affected by factors that influence metabolism, such as temperature. One problem is that allowing for variation in L_{∞} may indicate that some fish actually decrease in size as they approach their maximum size (in reality, such fish would be expected to lose condition and likely die). In most cases, growth should be expected to vary more than natural mortality or proportion mature at age, but less than recruitment and perhaps selectivity and fecundity.

Simulation analysis shows that estimating time-varying parameters in the absence of temporal variation does not substantially degrade model performance (similar to that found for other processes, such as selectivity), but ignoring temporal variation when it is relevant can lead to biased estimates (Chang). Simulations have also indicated that modeling annual-varying parameters works well for both annual variations in growth parameters and cohort-specific growth, but modeling cohort-specific growth does not inherently address annual variations in growth (Chang). Therefore, it is recommended that when there is an adequate amount of growth information available, estimation of annual variation in L_{∞} should be the default assumption. The growth increment approach in which the growth increment changes over time should be used to model growth over time, rather than using different growth curves for each year, to ensure that mean length-at-age builds on growth rates in previous years. This approach will also allow a basis for relating growth in the model to environmental conditions. In general, appropriate approaches are needed to ensure fish do not decrease in size as they grow over time. The level of the temporal variation can be fixed at a value based on well-supported meta-analysis of data-rich stock assessments until more appropriate estimation techniques are developed. Alternatively, changes in growth might be addressed by modeling time-varying selectivity. More research is needed to determine the best methods to address potential variability in growth over time.

Finally, temporal variability in growth rates may be due to density dependence. Traditionally, density dependence has had an important role in management advice. Typically, density dependence is considered solely in recruitment or in terms of an aggregated population concept (e.g., surplus production methods) and not specifically related to growth processes. Density dependence is an influential phenomenon in equilibrium models, but of less concern in dynamic applications associated with underlying environmental variability. However, in some cases, it should be noted that environmental variability can often mask density-dependent effects (Matthias).

Spatial variation

There is substantial evidence that growth rates vary spatially. For example, there is large variation in: asymptotic length of scallops by depth (Hart); depth-specific growth rates of southern lobster (McGarvey), and growth rates of bigeye tuna between the western and eastern Pacific Ocean (Harley). However, even in cases where growth in each region is known, there is no straightforward methods to model growth within meta-population models that contain movement. For example, in an integrated assessment model, should a fish of a given age automatically be assigned the mean length-at-age of the new area as it moves or does it maintain the same mean size and take on the new area's length-based growth rate (the latter situation requiring more complicated modeling efforts, but more likely to be correct). Also, a related problem for considering spatial variation in growth is determination of appropriate geographic strata in the model.

Harley outlined modeling approaches to deal with movement and evaluated them under different levels of movement (Figure 1). When movement is low, independent assessments in each area is most appropriate. However, a single assessment based on spatial strata without movement might be appropriate if it is desirable to share information (e.g., growth, larval dispersal). Growth is unlikely to vary spatially with a stock that moves substantially, so a single assessment that incorporates the stock's entire range might be most appropriate. The most difficulty in modeling growth generally occurs at intermediate levels of movement.



Movement Low Moderate High

Figure 1. Appropriate levels of population structure in a stock assessment model under different assumptions for levels of movement and spatial variation in growth rates (Harley).

Growth estimation

Information about growth comes from a variety of sources, including age-length data from hard parts, tagging growth increments, and length compositions. Obviously, age-length data are most informative if ageing error is low and data cover the entire range of ages. Length composition data are typically least informative because modes in the length composition data attributable to cohorts overlap at older ages and are difficult to identify definitively. In addition, for some species, notable length modes often appear and disappear or change position and it is unclear if this is due to growth variation, sampling error, changes in selectivity, or spatial distribution. Limited analyses have shown that only a few years of conditional age-at-length data may be adequate to represent growth (He). However, stocks with large temporal variation in growth are likely to require more years of data to adequately model time-varying processes.

For many species, there can be different estimates of growth rates, given studies included different data types (e.g., age-length, length composition, mark-recapture). Confounding issues are generally associated with each data type used in growth estimation, including impacts from selectivity, tagging, ageing error, pseudo replication, and length bin sampling of age data (Lee; Xu). At this time, it is unclear how to determine the most reliable data sets and consequently, the quality of the growth estimates from different studies. For example, should growth curves for each data set (or the data) be combined to create a single growth curve or should the assessment be conducted separately for each growth estimate and the results combined using some form of model averaging. Methods have been developed to integrate multiple sources of data to improve growth estimation (Carvalho; Fay). These methods appear promising for species for which older individuals are difficult to age accurately and growth increment data from tagging of older individuals can be used to supplement the available age data. Some of the statistical issues of combining the different data sets have been resolved, but issues still remain (Francis).

A choice needs to be made regarding whether growth should be estimated outside or inside the stock assessment model or alternatively, if empirical weight-at-age data should be used (Kuriyama; Taylor). The appropriate decision will depend on the quality of the data that are available. If reliable catch-at-age data are available for all years and fisheries, using empirical weight-at-age data and essentially bypassing growth estimation should be strongly considered. In such applications, length-at-age and the variation of length-at-age considerations are irrelevant because the models are not fit to any length composition data. Also, time-varying growth is implicitly assumed in applications based on empirical weight-at-age data. Further, different weight-at-age data for particular fisheries and for the population can be used to account for potential issues surrounding length-based selectivity. However, it is important to note that reliance on empirical weight-at-age data requires reliable age and weight composition data for all fisheries, time periods, and ages. That is, for many cases, there exist only length data and thus, age composition information must be extracted from the available length data. Fisheries, time periods, and ages with little information may need to be supplemented (e.g. information borrowed from other years or fisheries) to avoid including spurious values resulting from low sample size. For example, missing or imprecise mean length or mean age data might be improved by some form of smoothing, such as two (or three) dimensional splines over time, age, and/or cohort. Alternatively, the age-length data can be integrated into the stock assessment model and time-varying growth parameters estimated simultaneously with the other model parameters. The advantages of internally estimating growth using these data include: 1) allows both age-length data (in an age-structured model) or growth increment data from tagging (in a size-structured model) and length composition data to provide information on growth (growth increment data from tagging has yet to be appropriately integrated into an age-structured model); 2) uncertainty is automatically propagated throughout the analysis; 3) assumptions are consistent (e.g., selectivity is inherently taken into consideration); 4) sampling design is more explicitly

considered (e.g., using age conditioned on length and length composition data). However, growth is typically a well-estimated quantity and integrating growth estimation in the stock assessment model may result in model misspecification (e.g., incorrect value of natural mortality) causing biased estimates of growth, which lead to erroneous estimates of management quantities. The statistical fit to the data can be about the same for different hypotheses (growth rate, natural mortality, fishing mortality, selectivity), but the policy implications differ. Some management policies may be more (effort limits) or less (minimum legal size) robust to variability in growth rates.

Fitting to length composition data

Specification of growth is particularly important for stock assessment models that fit to length composition data because growth interacts with recruitment, natural mortality, fishing mortality and selectivity to determine the frequency of large fish expected in the catch. The larger the mean length-at-maximum age and to some extent the variation of length-at-age, more large fish will be expected in the catch and a small difference in growth rates can result in a large difference in the predicted length composition of the population. In the stock assessment model, fishing mortality may be adjusted higher or lower to match the observed number of large fish and thus, it is important to obtain an accurate estimate of the asymptotic length. Unfortunately, for many stocks, data are scarce for older fish, with no straightforward methods for addressing this lack of critical information for estimating growth. Growth parameters can be estimated inside the stock assessment model (Zhu), which often results in better fits to the data than growth parameters specified from analyses conducted outside the model (Kinzey). However, internally estimating growth may be confounded with other estimated or fixed parameters, since the frequency of large fish is also related to selectivity, exploitation rates, and natural mortality (Valero). Growth parameters may be less sensitive to misspecified natural mortality than selectivity or recruitment (Szuwalski). A prior could be used for the asymptotic length, allowing the model to update L_{∞} based on information in the data (Márquez-Farías). At a minimum, sensitivity analysis should be conducted based on a range of assumed values of the asymptotic length and robustness of results contrasted.

Hypothesized sex-specific growth is not easily addressed, given sex data are not typically collected as part of many fishery sampling programs, particularly those sampling lengths only (Courtney). Differences in growth are often related to behavior and distribution, which inherently would be associated with differences in selectivity between males and females. In the absence of information, selectivity is typically assumed to be the similar for males and females, recognizing that the same length-based selectivity implies different age-based selectivity and vice versa. It is unclear whether length- or age-based selectivity is more robust to sex-specific assumptions. As research accumulates, it is likely that sex-specific population dynamics are exhibited to varying degrees by many marine populations and thus, additional efforts to collect sex-specific

composition data in the field would provide a basis for improving stock assessments in the future.

Length-based models

Length-based models are primarily advocated when ageing is not possible or problematic. However, a potentially more important reason for using size-structured models is when lengthbased processes (e.g., high fishing mortality and knife-edged selectivity) modify the distribution assumptions associated with length-at-age. Age-length models and age-based models with platoons (groups of fish with different growth parameters) can be used to model changes in the distribution of length-at-age, but they generally are more computationally intensive and require more information to estimate the additional growth parameters.

Weight-at-age data

For many fish species, weight is roughly proportional to length cubed, making it hypersensitive to variation in length. In addition, body mass can be increased and decreased readily, while bone structure formation related to length is a more permanent process. Therefore, for most species, variation in size-at-age is more pronounced in weight than length and temporal variation in weight-at-age is common (Thorson). Large variation in weight-at-age may influence management results, since weight estimates are used to convert catch in weight into numbers of fish and, conversely, back into biomass for deriving reference points useful to management. Some assessment models (e.g., MULTIFAN-CL and Stock Synthesis) are capable of fitting to weight (vs. length) composition data. However, the additional variability associated with weight-at-age will typically result in weight compositions that are less reliable than fitting to length compositions. Finally, if age composition data are available and considered reliable, along with associated weight-at-age data, analysts should consider and evaluate via sensitivity analysis the utility of using empirical weight-at-age data and essentially bypassing growth estimation in the integrated assessment model.

Management considerations

Growth is an important determinant of quantities used for management advice. Yield-per-recruit analysis is founded on a tradeoff between growth and natural mortality and is combined with the stock-recruitment relationship to provide sustainable yields and related reference points (MSY, B_{MSY} , F_{MSY}). The optimal size of a fish caught and the fishing mortality rate that maximizes yield is a function of the growth rate. For example, due to changes in growth rate estimates for Pacific swordfish, interpretation of current fishing mortality changed from one-half to above F_{MSY} (Kolody).

Variation in growth rates among areas and over time implies that management will also need to change to ensure sustainable and optimal fishery operations (Thorson). Further research is needed to determine appropriate methods for distributing fishing effort among areas when

growth rates vary spatially. Temporal changes in the asymptotic length may have different consequences to time-varying growth rates. Management actions can also impact assumptions surrounding growth rate changes. Further, differences in growth rates among areas due to ontogenetic factors can complicate management using minimum legal sizes because under a common size limit, few individuals will be large enough to be kept in some areas, while in other areas, they will be caught at too young of an age (e.g., before they mature). Changes over time similarly complicate management. Reductions in growth rates may result in a large amount of discarding, which can be problematic if discard mortality rates are high (e.g., Pacific halibut, Martell). Differences in growth rates between males and females can complicate the use of minimum size regulations. For example, female flatfish are often associated with faster growth than males and coupled with minimum size restrictions, could translate to elevated fishing mortality rates for females (e.g., Pacific halibut, Martell).

Projections of stock status, such as those used to evaluate rebuilding plans, require a definition of the weight-at-age and in cases when growth changes over time, results may differ depending on what time period is relied on for the weight-at-age estimates. An extreme example would be the possibility that the population can never recover to the rebuilding target because average growth rates are used to define the target biomass, but in fact, growth rates have declined. Similar issues arise when calculating reference points and the choice of average weight-at-age used for the reference points (e.g., B_{MSY} and B_0). Dynamic reference points that take into consideration the change in growth rates, similar to those used for temporal variation in recruitment, may be appropriate.

Management Strategy Evaluations (MSE) should be used to collectively address assessment methods and harvest control rules to ensure model results are robust to spatial-temporal changes in growth rates. At a minimum, variability in growth rates should be included in MSE operating models, even if not included in the assessment model. Meta-analysis could be conducted using available data for a variety of stocks to determine the extent of growth variation due to the environment and density dependence, and this variation then included in the operating model used for the MSE. Alternatively, well studied systems could be used to understand biological processes, with heuristic models developed to provide plausible ranges for operating models (Lorenzen). Finally, good practices for growth estimation in integrated stock assessments should focus primarily on model performance in terms of derived estimates useful to management and not strictly the growth parameter estimates.

Current thinking

The following list is based on information highlighted and emphasized in the Summary above. It reflects frequently discussed points and general consensus from the workshop. The information should be considered current thinking on modeling growth in integrated stock assessments that are used for advising resource management. However, as noted above, further research and

simulation analysis is needed presently on several areas related to growth parameterization and related parameter trade-offs and considerations discussed throughout the workshop.

- Specification of growth is particularly important for stock assessment models that fit to length (vs. age) composition data, given uncertainty associated with the mean and s.d. of length-at-maximum age and the estimated number of large/old fish in the catch can substantially impact estimates of fishing mortality-at-age and total abundance.
- Variation is most pronounced in asymptotic length (L_∞) of a growth relationship. Therefore, it is recommended that when there is an adequate amount of growth information available, estimation of annual variation in L_∞ should be the default assumption. The growth increment approach should be used to model growth over time, rather than using different growth curves for each year to ensure that mean length-at-age reflects growth rates in previous years and will also allow a basis for relating growth parameters in the model to environmental conditions. In general, appropriate approaches are needed to ensure fish do not decrease in size as they grow over time. The level of the temporal variation can be fixed at a value based on well-supported meta-analysis of data-rich stock assessments until more appropriate estimation techniques are developed.
- It is generally recommended that the relationship for variation of length-at-age be a function of mean length, rather than age, to ensure that the variation does not become too high for older ages when growth rate has declined. The standard deviation of length at age typically increases with mean length and a constant CV may be the most appropriate assumption in the absence of information, with a value around 10% being commonly observed.
- Growth estimation should be conducted inside the stock assessment when possible to ensure that selectivity, length-bin sampling, and additional information from length composition data are accounted for. Attention should be given to biased growth estimates due to misspecification of other fixed (e.g., natural mortality) and estimated (e.g., selectivity) model parameters.
- If sufficient age composition data are available and considered reliable, along with associated weight-at-age data, analysts should consider and evaluate, through sensitivity analysis, the utility of using empirical weight-at-age data which avoids the need to model the relationship between length and age.
- Sex-specific growth, to some degree, is likely more common in species than not and differences may be of magnitude to substantially impact population estimates from the assessment model. Current sampling programs should consider including sex determination along with obtaining size and associated hard parts from individual fish, given additional efforts to collect such information in the field and laboratory are practical.
- Growth estimation in integrated stock assessments models should focus primarily on model performance in terms of derived estimates useful to management and not strictly the growth parameter estimates.

• Growth models that more accurately account for broadly applicable ontogenetic changes exhibited in growth warrant further attention. For example, reduction in growth rate at the onset of maturity is a common physiological phenomenon that could be accounted for explicitly in a growth model. Other areas in need of further research include model dimension considerations, e.g., length of time steps, number and size of length bins, and plus group definitions.

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Appendix A: Agenda

Date and Time	<u>Topic</u>	Presenter
3 November (Mondav)		
1:00 pm – 4:00 pm	Stock Synthesis session	Taylor (IS)
4 November (Tuesday)		
8:30 am – 9:00 am	Welcome/Overview	Semmens/Crone
9:00 am – 10:00 am	A1	Lorenzen (IS)
10:00 am – 10:30 am	A2	Matthias
10:30 am – 11:00 am	Break	
11:00 am – 11:30 am	A3	Ortiz de Zárate
11:30 am – 12:30 pm	Group discussion – A	
12:30 pm – 2:00 pm	Lunch	
2:00 pm – 3:00 pm	B1	Francis (IS)
3:00 pm – 3:30 pm	B2	Lee
3:30 pm – 4:00 pm	Break	
4:00 pm – 4:30 pm	B3	Xu
4:30 pm – 5:00 pm	B4	Carvalho
5:00 pm – 5:30 pm	B5	Márquez-Farías
6:00 pm – 8:30 pm	Template Model Builder session	Thorson (IS)
5 November (Wednesday)		
8:00 am – 8:30 am	B6	Francis
8:30 am – 9:00 am	B7	Fay
9:00 am – 9:30 am	B8	Minte-Vera
9:30 am – 10:00 am	B9	Valero
10:00 am – 10:30 am	Break	
10:30 am – 11:00 am	B10	Maunder
11:00 am – 11:30 am	B11	Kinzey
11:30 am – 12:00 pm	B12	Не
12:00 pm – 1:30 pm	Lunch	
1:30 pm – 2:00 pm	B13	Monnahan
2:00 pm – 2:30 pm	B14	Crone
2:30 am - 3:00 pm	B15	Courtney
3:00 pm – 3:30 pm	Break	J
3:30 pm - 4:30 pm	Group discussion – B	
4:30 pm – 5:30 pm	C1	Punt (IS)
6:00 pm – 9:00 pm	Party	
6 November (Thursdav)		
8:00 am – 8:30 am	C2	Chen
8:30 am – 9:00 am	C3	Siddeek
9:00 am – 9:30 am	C4	Quinn
9:30 am – 10:00 am	C5	McGarvev
10:00 am – 10:30 am	Break	5

Date and Time	Topic	Presenter
10:30 am – 11:00 am	C6	Szuwalski
11:00 am – 12:00 pm	Group discussion – C	
12:00 pm – 1:30 pm	Lunch	
1:30 pm – 2:30 pm	D1	Martell (IS)
2:30 pm – 3:00 pm	D2	Thorson
3:00 pm – 3:30 pm	Break	
3:30 pm – 4:00 pm	D3	Stawitz
4:00 pm – 4:30 pm	D4	Isely
4:30 pm – 5:00 pm	D5	Chang
5:00 pm – 5:30 pm	D6	Hart
7 November (Friday)		
8:00 am – 8:30 am	D7	Taylor
8:30 am – 9:00 am	D8	Kuriyama
9:00 am – 9:30 am	D9	Harley
9:30 am – 10:30 am	Group discussion – D	
10:30 am – 11:00 am	Break	
11:00 am – 12:00 pm	E1	Kolody (IS)
12:00 pm – 12:30 pm	E2	Fukuda
12:30 pm – 1:30 pm	Group discussion – E	
1:30 pm	Closing	Maunder

Growth workshop – Major topics, special sessions, and invited speakers (IS)

- A. Biological processes/ontogeny (K. Lorenzen)
- B. Specification and estimation: age-structured models (C. Francis)
- C. Specification and estimation: length-structured models (A. Punt)
- D. Spatial/temporal variation (S. Martell)
- E. Modeling growth in tuna assessments (D. Kolody)
- Stock Synthesis session (I. Taylor)
- *Template Model Builder* session (J. Thorson)

Appendix B: Presentation abstracts

A. Biological processes / ontogeny

- A1. Title: Modeling body growth in fisheries assessment and management: why and how
- **Presenter**: K. Lorenzen (Invited speaker)
- Authors: K. Lorenzen
- **Abstract**: Body growth is a central but underappreciated process in the dynamics of exploited fish, crustacean and mollusk stocks. In addition to biomass production, body growth affects lifetime patterns of natural and fishing mortality, maturation and reproductive output. Phenotypic plasticity in the growth of fishes, crustaceans and mollusks is extraordinarily high and can play an important role in mediating population responses to exploitation and environmental variation. Growth is also subject to evolutionary effects of harvesting and environmental change. Finally, growth patterns correlate with other life history traits and such correlations are frequently used to estimate parameters such as the natural mortality rate or recruitment compensation which are difficult to estimate directly. The keynote reviews approaches to modeling body growth in the light of requirements arising from the above patterns, management implications and theoretical considerations of growth processes.

A2. Title: Decoupling the effects of density and environmental variability on fish growth

Presenter: B. G. Matthias

Authors: B. G. Matthias, R. N. M. Ahrens, M. S. Allen, T. Tuten, Z. A. Siders, K. L. Wilson

Abstract: Per capita productivity changes in fish populations resulting from competition for limited resources are likely expressed along a spectrum of density dependent mortality to density dependent growth. Simulations and pond/tank-based experiments have shown both increased mortality and decreased growth at high densities. However, detecting the effects of density in wild populations can be challenging due to tradeoffs between growth and mortality at high densities. Further, in highly variable systems that experience both droughts and hurricanes, environmental variability can often mask density dependent effects and make them even more difficult to detect. Our objectives were to determine the impacts of 1) cohort strength and 2) environmental variability on fish growth. We constructed a Bayesian mixed effects model to quantify changes in the mean length at age via $L\infty$, the variation around mean length via the coefficient of variation cv, and the lengthweight relationship allometric growth parameter β . Akin to previous studies, cohort density had negative impacts on mean length and weight and positive effects on growth variation. However, the biggest impacts of growth arose from changes in water level. Water level during the first year of life positively influenced growth in length and weight while negatively affecting growth variation. During subsequent

years of life, increases in water level decreased growth in length and weight and increased growth variation. We suspect that increased growth during years of higher water decreased juvenile competition by increasing the amount of habitat available for juvenile fish. For older fish, concentrated prey likely caused increased adult growth during periods of lower water levels. Decoupling the effects of density and environmental variability on growth can lead to a better understanding of plasticity in naturally fluctuating populations and better management of exploited stocks.

- **A3. Title**: Estimating individual growth variability in albacore (*Thunnus alaunga*) from the North Atlantic stock; aging for assessment purposes
- Presenter: V. Ortiz de Zárate
- Authors: V. Ortiz de Zárate, E. Babcock
- Abstract: Length-frequency data and catch at age matrices are used in north Atlantic albacore (Thunnus alalunga) stock assessment conducted within ICCAT. Growth is assumed to follow the von Bertalanffy model with the assumption that growth parameters are constant over time and the same for all fish. However individual growth variability is an important factor not considered and affecting the input into the modelling of the population. A Bayesian hierarchical model was used to estimate individual variability in growth parameters asymptotic length (Linf), growth rate (K), and age at length zero (t0) of the von Bertalanffy model. The method assumes that the Linf, K and t0 values for each individual fish are drawn from a random distribution centered on the population mean values, with estimated variances. Multiple observations of length at age for individual fish were obtained using backcalculation from spine section diameter. Then measurements of annual annuli of individual aged were used to estimate the back-calculated length and rebuild the individual growth of all fish being aged. Models with and without individual growth were compared using the deviance information criterion (DIC) to find the best model. Growth was found to vary significantly between individual fish.

B. Specification and estimation: age-structured models

- B1. Title: Growth in age-structured stock assessment models
- Presenter: R. I. C. C. Francis (Invited speaker)
- Authors: R. I. C. C. Francis
- Abstract: Growth, an important component in age-structured assessment models, has been dealt with in a variety of ways by different modellers. I will describe and discuss this variety under three headings: how growth is specified; what functions it serves in the model; and how it may be estimated. The pros and cons of different approaches will be evaluated, as will the assumption central to the currently popular approach of integrated modelling that analyses should be carried out within, rather than outside, the stock assessment model.

B2. Title: Comparison of traditional versus conditional fitting of von Bertalanffy growth functions

Presenter: H-H. Lee

- Authors: H-H. Lee, K. R. Piner, M. N. Maunder
- **Abstract**: Population level estimates of fish growth are a key component of population dynamic models, especially when age composition data are unavailable. Multiple types of information can be used to estimate the age-length relationship including tagging, length and age compositions, mean size, and conditional age-at-length data. When age-length samples are collected from fishery data, two estimation approaches are commonly used to estimate the growth form. A traditional methodology assumes that each length observation used in the fitting is a random sample of fish for a given age. The conditional methodology uses age conditioned on length and assumes that each age observation is a random sample of fish of a given length. The conditional method makes use of the underlying population age structure and therefore has only been used inside stock assessment models. We use an equilibrium approximation to the age structure to estimate growth using the conditional method outside the assessment model. We evaluated the performance of the traditional and approximated conditional method to estimating the von Bertalanffy growth curve using simulated data. Sampling of the fishery catch data is conducted randomly or systematically. We evaluated the importance of the correct age structure on estimates of the conditional approach. We evaluated the effectiveness of both estimation methods for the different sampling methods over a broad range of fish life-histories, population dynamics and sample sizes.
- B3. Title: Maximum likelihood estimates of North Pacific albacore (*Thunnus alalunga*) von Bertalanffy growth parameters using conditional-age-at-length data

Presenter: Y. Xu

Authors: Y. Xu, S. L. H. Teo, K. R. Piner, H-H. Lee, K-S. Chen, R. J. D. Wells

Abstract: Stock assessment results of North Pacific albacore tuna (*Thunnus alalunga*) have been strongly influenced by two recently published age and growth studies (Chen et al., 2012 and Wells et al., 2013). However, the most recent stock assessment in 2014 also highlighted the drawbacks of using traditional growth model estimation methods. The underlying assumption is that each datum is a random observation of size and age, and therefore contributes equally to the growth curve estimation. Sampling programs for age and growth studies (including the two most recent studies for North Pacific albacore) typically do not randomly sample the population, and most of these observations have associated sampling bias. For example, in Wells et al. (2013), samples from the entire size range of albacore were collected, and preferentially selected to obtain the largest fish available in the Honolulu fish market in some years, which is common practice in many age and growth studies. However, by doing so, and then assuming that these were random samples likely resulted in biased results. In this study, we obtained the otolith aging data from these two recent studies and treat them as conditional-age-at-length data in order to limit the sampling bias by weighting samples. We developed a simplified length-based and agestructured model for North Pacific albacore population, assuming von Bertalanffy growth, constant recruitment and mortality. Maximum likelihood estimates of the von Bertalanffy growth parameters were obtained by fitting the observed proportion of each age class for each size bin to the expected proportions from the simplified age-structured model, using a multinomial distribution. Conditional age-at-length data are typically used within an integrated stock assessment model. In contrast, this study is a novel use of these data with a simplified population model, without the complexity of an integrated stock assessment model, but treating the aging data appropriately as conditional age-at-length data. Preliminary results show that this method is able to reduce sampling bias by giving less weight to samples near the tail of the distribution (i.e., size classes that were oversampled). Simulation studies of this method will be presented by another study in this symposium.

B4. Title: The effects of length-biased sampling in growth models: a simulation approach $\mathbf{P} = \mathbf{P} \cdot \mathbf{P}$

Presenter: F. Carvalho

Authors: F. Carvalho, M. Maunder, A. Aires-da-Silva, Y. Chang

- Abstract: Growth parameters are key components in fisheries stock assessment and are commonly estimated using three approaches: 1) modal progression in length composition data, 2) age-length data, and 3) tagging growth increment data. In the real world, sampling biases may be inevitable, including a situation where only young fish or old fish are sampled. However, it is unclear how these biased samples affect growth estimates. We used the swordfish in the western North Pacific Ocean as a case study, and evaluated whether ageing only part of the population has strong effects on mean growth and variation of length-at-age estimates. An Individual Based Model (IBM) was developed as the operating model to generate age-atlength, length composition, and tagging data. These data were used to fit two different growth models: a simple growth model using age-at-length data, and an integrated growth model using age-at-length, length composition, and tagging data. Both models were run under two scenarios. In scenario I, only young fish were aged, while in scenario II, fish from all sizes were aged. In addition, we evaluated the performance of the integrated approach under different data availability situations (e.g. absence of length composition data).
- **B5. Title**: Suitability of the use of the Bayesian approach for the estimation of growth parameters for viviparous Chondrichthyans

Presenter: J. F. Márquez-Farías

Authors: J. F. Márquez-Farías, R. E. Lara-Mendoza

- **Abstract**: Age and growth estimates are essential in the study population dynamics and demographic analysis, and along with reproductive and survival rates represent a key element in formal fish stock assessment. In sharks, the age is estimated by counting growth marks of the vertebrae. The growth parameters are estimated by fitting a model (i.e., von Bertalanffy, Gompertz) to age-length data. It is now conventional to test other growth functions by using multi-model approaches. There is no general rule for the use of any growth model, and the selection of one over another is frequently assessed by a statistical criterion (AIC). However, biases caused by sizeselective fishing gears and migration can influence not only the representativeness (quality and contrast) of observed data but also could induce to distortions of the model's performance. This source of bias should be present for model selection and interpretation. Once the best observed data are acquired, competing models should be selected to satisfy both fit and biological pertinence avoiding nuisance parameters such as "to" in the BVGM. In this context, the Bayesian approach requires specification of the prior probability distribution of the model's parameters. While dealing with correlated parameters is inevitable, at some point, the judgment of experts to dimension parameters may represent a gain in model fit. In the present study, we review the benefits of building priors for the estimation of growth parameters for viviparous sharks taking advantage of available information on size of the first year of life and historical maximum length. We consider that competing growth models should be selected on the basis of not only statistical quantities, but also on biological meaningful parameters.
- **B6. Title**: Can we combine age-length and tagging-increment data?

Presenter: R. I. C. C. Francis

- Authors: R. I. C. C. Francis, A. M. Aires-da-Silva, M. N. Maunder, K. M. Schaefer, D. W. Fuller
- **Abstract**: In age-structured assessments it would be useful to be able to include all available information on growth, including age-length observations and length increments from tagging experiments. However, it was suggested in 1988 that combing the growth information from these two sources was problematic because the age- and length-based growth information they contain are not directly comparable. We evaluate some approaches that have since been made to this problem and conclude that though there has been some progress, no method has yet been found that combines logical consistency and biological plausibility, and also lies on the right side of Occam's razor.
- **B7. Title**: Using size increment data in age-structured stock assessment models

Presenter: G. Fay

Authors: G. Fay

- **Abstract**: Size increment data, often available from tagging studies, provide useful information for growth estimation. Such data are frequently used in size structured stock assessment models. Traditionally, this has involved estimating the size transition matrix though applications of integrated analysis can also fit to these data directly in the stock assessment model. Use of growth increment data from tagging for age structured assessment models has been less extensive. Estimation of growth curve parameters using these data is typically conducted outside of the stock assessment model, to either provide inputs or to corroborate model-based estimates of growth resulting from fits to more typical data (e.g. age-at-length). However, because of differences in model structural assumptions and that growth increment data from tag recaptures are conditioned by selectivity, the two modeling approaches (separate tagging analysis and assessment models) may be inconsistent. Age-structured assessment models that integrate tagging data in the estimation procedure (tagintegrated assessment models) have generally focused on including likelihood components for the distribution of tag-recaptures and not fitted to the size increment data (though analyses that model tag recaptures as a length-based process do alleviate this somewhat). I will discuss challenges associated with accounting for these longitudinal data in model frameworks such as Stock Synthesis, and review methods for including size increment data from tagging studies in age structured assessment models. I will outline an example of including a likelihood component for size increment data within a simple statistical catch at age model that accounts for the effects of selectivity on the expected distribution for growth increments, and present results of a simulation study aimed to evaluate the benefits of using these data to estimate growth when compared with alternative approaches. Finally, I will discuss modifications that might be made to Stock Synthesis to better make use of different types of tagging information for estimation of both growth and stock status.
- **B8. Title**: Guidance for modelling the variability of length-at-age: lessons from datasets with no aging error

Presenter: C. V. Minte-Vera

- Authors: C. V. Minte-Vera, S. Campana, M. Maunder
- **Abstract**: The variability of length-at-age can highly influence the interpretation of the lengthfrequency information in the context of integrated analysis for stock assessment. For example, the highly used Stock Synthesis 3.0 (SS) is an age-structured model that can be fit to length-frequency data, as well as age frequencies, tagging data, and abundance indices. Several stock assessments, such as those for tropical tunas, are done with no (or very limited) amount of age-frequency data and rely mainly on length frequencies. In some cases, those data so strongly affect model fit that they

may drive the absolute scale of the estimated biomass. Ideally, one parameter expressing the variability of length-at-age for each age should be estimated in an integrated model. This strategy will introduce extra parameters in the model for which there is limited information in the available data. To minimize this problem, assumptions about how the variability of length-at-age changes with age are adopted. As an illustration, five options are implemented in SS, four consider that the lengthat-age varies normally around the mean length-at-age and one considers that the length-at-age distribution is log-normal. When a normal distribution is assumed, the variability can be either modeled with the coefficient of variation (CV) as a function of either length-at-age or age, or with the standard deviation (SD) also as either a function of length-at-age or age. In this presentation, we will explore two rarely available data sets that provided length-at-age and age with no (or very minimal) ageing error. The first dataset consists of four groups of cod (Gadus morua) from Faroe, two of which were subject to fishing, and the other two were unexploited. The fish were hatched in captivity then tagged and released as young-of-year either into mesocosms, where no fishing took place, or into the wild, in two locations: Faroe Plateau and Faroe Bank. The fish released into the wild were recovered by fishers. The second dataset for Arctic trout (Salvelinus namaycush) from Zeta Lake. This population was never fished. The ageing was validated with bomb-radiocarbon methods and ageing precision was excellent, thus minimal ageing error is expected. We asked the following questions: (1) what probability density function best describes the variability of length-at-age for fished and unfished populations?, (2) what is the best summary statistics of the variability of length-at-age: CV or SD?, and (3) what functional form (e.g. constant with age, increasing with length-at-age) best summarized the changes of the variability of length-at-age over ages for fished and unfished populations? We finalize by discussing a set of lessons learned from this exercise that may help to guide decisions taken by stock assessment modelers when modeling variability of length-at-age in the context of integrated analysis.

B9. Title: Evaluating the impacts of fixing or estimating growth parameters, across life histories and data availability

Presenter: J. L. Valero

Authors: J. L. Valero, K. F. Johnson, C. Stawitz, R. Licandeo, S. C. Anderson, A. Hicks, F. Hurtado-Ferro, P. Kuriyama, C. C. Monnahan, K. Ono, I. Taylor, M. Rudd

Abstract: In statistical integrated age structured population models, there are two common practices used to incorporate somatic growth into the population dynamics. First, a parametric somatic growth model is fit externally to length-at-age data and the estimates are input to the model as fixed parameters. Second, the model simultaneously estimates growth parameters with other population dynamics and fishery processes. When growth is estimated externally to the stock assessment

model, the effects of population dynamics and the cumulative effects of fishing on size-at-age on growth estimates are typically not accounted for. In addition, ignoring gear selectivity when estimating growth (internally or externally) is problematic because fisheries tend to select faster-growing fish. Therefore, growth estimated from unrepresentative data may not reflect the true population growth curve, which can lead to biased stock assessment results, biological reference points and management quantities. Furthermore, the quality and quantity of length- and agecomposition data can affect the accuracy of parameter estimates and thus management reference points. Growth may be estimated internally when there is length composition data, or tag-recapture data. However, incorporating agecomposition data in addition to length-composition data may or may not improve stock assessment estimates. For instance, even if length- and age-composition data are both available, the quality and quantity of this information can affect the accuracy of stock assessment outputs, with larger repercussions on some life-history types than others. Thus, estimation of growth parameters within a stock assessment model is not possible for all life-history types. Therefore, it is important to quantify the importance of different data types and quantity to stock assessment estimates across life-history types. Here we used ss3sim, a simulation framework based on Stock Synthesis, to evaluate the types and quantity of data that are needed to estimate somatic growth within an assessment model and the tradeoffs between estimating growth internally versus externally. The focus of this research is not only on the ability to estimate growth but also on the impact of potential model misspecification related to growth estimation on assessment-derived quantities of interest to management across contrasting life-history types. We used measurements of bias and precision with respect to spawning stock biomass, fishing mortality level, and management reference points to quantify the performance of stock assessment models that internally estimated somatic growth parameters compared with stock assessment models that had somatic growth fixed at externally estimated values.

B10. Title: Estimation of growth within stock assessment models: implications when using length composition data

Presenter: M. N. Maunder

- Authors: J. Zhu, M. N. Maunder, A. M. Aires-da-Silva, Y. Chen
- Abstract: In contemporary fisheries stock assessment, growth modeling is an important component and typically conducted outside assessment models (i.e., fixed before running the assessment model). However, direct growth estimates may be difficult for some species because of difficulty in aging old individuals using otoliths. The objectives of this study are to evaluate the influence of mean length-at-age (mean length) and variation in length-at-age (variation) in relation to length composition on management advice and to determine if mean length and variation can be estimated

reliably inside stock assessment models. We conduct a sensitivity analysis regarding the parameters of mean length and variation using a full stock assessment model of bigeye tuna (BET; with Stock Synthesis (SS)) in the eastern Pacific Ocean. We then use a simplified SS model, as the simulator and estimator in the simulation analysis, to estimate mean length and variation of the von Bertalanffy growth model. Mean length is parameterized using L1 (length at minimum age), L2 (length at maximum age), and K (growth coefficient), and variation is parameterized using CVs for young and adult tunas (CVs for the young females are assumed to be equal to that for the young males). Twenty scenarios regarding L1, L2, K, CV, and selectivity assumption for the longline fishery (LL, asymptotic or dome-shaped) were considered. Median bias and CV are used to define the reliability of estimates of these parameters. Estimates of L2 are found reliable with the maximum median bias less than 7% (CV < 0.05), and robust to misspecification of LL selectivity. L1 can be estimated with maximum median bias being around 10.7% (CV < 0.11). K is not considered to be estimable because of the high median biases ($-20.2\% \sim -16.6\%$). CVs for young tunas are estimated with moderate median biases (maximum =10.5%) except for one scenario, but with high cv. CVs for both female and male adults can also be reliably estimated (minimum CV =16% and 14%, respectively). Influences of misspecification for parameters that could not be reliably estimated are also evaluated with respect to key management reference points.

- **B11. Title**: Estimating growth of Antarctic krill (*Euphausia superba*) in an age-based assessment model
- Presenter: D. Kinzey
- Authors: D. Kinzey, G. Watters, C. Reiss
- **Abstract**: An age-based assessment model for Antarctic krill has been extended to estimate von Bertalanffy growth. Estimating growth inside the model improved the fit to the length-compositions substantially over earlier models that used pre-specified growth parameters from previous studies. Model parameters that included growth were estimated in multiple trials using randomized phase sequences until a positive definite Hessian matrix was obtained. The reproducibility of model estimates for growth and other derived quantities was tested using simulated data. Multiple configurations of the models and data produced similar, robust estimates of growth. Growth estimated by the models was somewhat slower than growth rates used currently in managing the krill fishery. The two-stage approach of first randomizing the phase order and secondly verifying the reproducibility of the estimates of derived quantities through simulation-testing is recommended for the estimation of potentially confounded parameters using complex assessment models and data.

B12. Title: How many conditional age-at-length data are needed to estimate growth in stock assessment models?

Presenter: X. He

Authors: X. He, J. C. Field, D. E. Pearson, L. Lefebvre

Abstract: One of main usages of age information in stock assessments is as conditional age-atlength (CAAL) data to internally estimate growth and cohort strength(as well as inform natural mortality). Obtaining sufficient age data is not a trivial task, not only because it requires considerable sampling effort to cut fish and extract otoliths (and as such is often resisted by processors seeking to market whole fish) but also requires substantial effort to develop ageing criteria and subsequently age sufficient numbers of fish. The difficulties associated with developing reliable aging criteria (as well as validating estimated ages) vary from species to species, but can be substantial. For example, Bocaccio (Sebastes paucispinis) are a highly important commercial and recreational target in California, have been under a rebuilding plan since the early 2000s, and as such have been subjected to over 12 stock assessments since 1984. However, due to the difficulties with developing reliable aging criteria, as well as the rapid growth and variable recruitment that allowed resolution of growth and cohort strength in the absence of ages. In 2014, the Fisheries Ecology Division successfully developed ageing criteria for Bocaccio, and since then over four thousand fish have been aged for an upcoming assessment. In this study, we tested utilities of CAAL data in the 2013 Bocaccio assessment model, mainly on how many CAAL data are needed to get reasonable estimates of growth of the species. The same test was also conducted on the 2013 assessment model for Pacific Sanddab (Citharichthys sordidus), which has much shorter life span, and less variable recruitment, than Bocaccio. The tests were done by intermittently removing annual age data at various intervals (i.e. removing data every other year, etc.). Preliminary results showed that, for the Bocaccio assessment model, the results were very comparable among the model runs with different levels of input data, and that even with only one out five years of CAAL being used, the assessment outputs and estimated growth were similar to those with all available data included. For the Pacific sanddab assessment model, however, the assessment outputs and estimated growth rates were somewhat different, particularly with respect to estimating virgin recruitment levels. These could mainly be due to lack of CAAL data from early years of the fishery, and high variability in ageing data. Ongoing efforts are also underway to evaluate the influence of age data for a longer lived rockfish with slower growth (blackgill rockfish) as well as to simulate the effects of different levels of CAAL data availability on assessment outputs. Results will be presented at the workshop as they became available.

B13. Title: An evaluation of alternative binning approaches for composition data in integrated stock assessments

Presenter: C. Monnahan

- Authors: C. Monnahan, S. Anderson, F. Hurtado-Ferro, K. Ono, M. Rudd, J. Valero, K. Johnson, R. Licandeo, C. Stawitz, A. Hicks, M. Muradian, I. Taylor
- Abstract: Age and length composition data provide important information needed to estimate biological growth in integrated stock assessments. There is an extensive literature on estimating effective sample sizes and appropriately weighting compositional likelihoods relative to indices of abundance. However, there are other subjective decisions facing analysts with regard to how to incorporate length composition data in an assessment: the number and spacing of composition bins, whether to compress the tails of the distribution, and whether to add a constant to observed and expected proportions to make the likelihood calculations more robust. There has been little formal investigation of how these decisions impact the ability to estimate growth, leaving analysts to use personal preference. In this study, we investigate the implication of these options on the estimation of growth and management quantities using ss3sim, a simulation framework utilizing Stock Synthesis, a generalized, integrated stock assessment model. We performed simulations across life histories, fishery exploitation patterns, and a wide range of type, quantity, and quality of compositional and index data. We also explored model selection-based approaches to guide these decisions. Results from this study can be used to help guide analysts in the treatment of length composition data to optimize growth estimation and performance of stock assessments for management purposes.
- **B14. Title**: Model time step and species biology considerations for growth estimation in integrated stock assessments
- Presenter: P. R. Crone
- Authors: P. R. Crone, J. L. Valero
- **Abstract**: Modeling growth in modern statistical stock assessments typically requires fitting respective models to seasonal- or annual-based time series of growth-related data, often size- and age-composition time series developed from fishery and/or survey samples collected in the field. The underlying time step (quarter, semester, annual, etc.) is an important model dimension, serving as the basis for growth estimation and accurately identifying potential changes in growth over time. The objective of the study is to evaluate the influence of intra-annual variability in composition data on estimating growth parameters and dynamics in the model. In this evaluation, stock assessments are conducted based on alternative time-step dimensions and results are compared using simulation methods. Quantitative comparisons are presented for derived growth parameter estimates (e.g., *K*, length-at-age_{min} and -age_{max}, L_{∞}) and management quantities (e.g., SSB_{current}, depletion, MSY). Other practical

considerations related to model development, such as model complexity (total number of estimated parameters) and speed (run time), are qualitatively contrasted. Stock assessments and associated simulations are evaluated in terms of two broad life history strategies: shorter-lived, more productive species (e.g., small pelagic spp.); and longer-lived, less productive species (e.g., groundfish spp.). Finally, inherent sample size consequences associated with finer-scale time step considerations are generally discussed.

B15. Title: Sensitivity to sexually dimorphic growth of a length-based age-structured stock assessment model (Stock Synthesis) developed for North Pacific swordfish (*Xiphias gladius*)

Presenter: D. Courtney

Authors: D. Courtney, K. Piner

Abstract: Sensitivity to sexually dimorphic growth was evaluated for a North Pacific swordfish (*Xiphias gladius*) length-based age-structured Stock Synthesis model. The swordfish model was developed for the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC). The North Pacific swordfish model included options to implement sexual dimorphism and to estimate sexual dimorphic growth within the model, but neither of these options was included in the final model. Sensitivity analysis was conducted here to evaluate the effects of implementing sexual dimorphism and then estimating sexual dimorphic growth within the North Pacific swordfish model. Model sensitivity was evaluated based on relative changes in likelihood component fits for relative abundance indices and available length composition data. Model sensitivity was also discussed relative to input and output likelihood component variances (variance adjustments) obtained from Stock Synthesis for indices of relative abundance, available length composition data, and process error in recruitment variability.

C. Specification and estimation: length-structured models

- **C1. Title**: Estimating growth within size-structured fishery stock assessments: What is the state of the art and what does the future look like?
- **Presenter**: A. Punt (Invited speaker)
- Authors: A. Punt, M. Haddon, R. McGarvey
- Abstract: Most growth studies have considered the relationship between age and growth. Such relationships are essential to age-structured fishery stock assessments. In contrast, assessments based on stage-structured population dynamics models require information on the probability of animals moving from one stage to each of the other stages at each time step. Size-structured population dynamics models are a special case of stage-structured population dynamics models in which each class represents a unique set of sizes. These models form the basis of assessments for many valuable,

hard to age, marine species, including crabs, abalone, lobsters and prawns. Growth within these models is governed by a size-transition matrix. The values for the parameters of a size-transition matrix can either be estimated externally to the assessment, generally utilizing data from tag-recapture experiments, or the estimation of growth can be integrated within the assessment model. This paper reviews the approaches used to construct size-transition matrices, including the underlying structural formulation, statistical estimation framework, and the consequences of error when specifying these matrices on the ability to estimate population size and manage populations sustainably.

C2. Title: Modeling growth for American lobster Homarus americanus

Presenter: Y. Chen

- Authors: Y. Chen, J-H. Chang
- Abstract: Growth plays a critical role in regulating fish population dynamics, and modeling growth is one of the key components in stock assessment that provides vital information for fisheries management. For crustacean species like the American lobster, Homarus americanus, modeling growth tends to be complicated. Growth of the American lobster is not continuous, and molting is seasonal, mainly occurring in summer and fall. Molting frequency is size-dependent and influenced by the individual's reproductive status with the maturation being likely to significantly slow down the growth of female lobster. An egg-bearing female does not molt. There are also large thermal differences in lobster habitats, which may result in large differences in growth among individuals. As a result, there are large variations among individuals and between sexes in growth. In this study, we develop an individual-based lobster simulator (IBLS) to develop growth transition matrix required for a length-structured stock assessment model. The IBLS expresses various components of lobster life history and fishery processes as random Bernoulli trials and simulates the complex biological and fishery processes including size- and maturation-dependent seasonal molting and management regulations used in the fishery, such as minimum and maximum legal sizes, prohibition against the taking of egg-bearing lobsters, and protection of previously ovigerous females through Vnotching. For each time step, a certain number of lobster of a defined size, are added to the population in the IBLS as new recruits. Each lobster has a probability of being caught in the fishery, dying of natural mortality, growing and maturing, and, for females, becoming egg-bearing, V-notched, and/or losing V-notching due to a molt. When a lobster is caught in the fishery, it is examined to see if it needs to be protected according to existing requirements. If it is legal to be kept, its sex and size are recorded to generate catch and size-frequency data. V-notched lobsters are protected from fishing for two molts. Egg-bearing lobsters are protected from harvesting and need to be V-notched. The molt frequency of mature female lobster is

affected by maturation. Lobster undertake a major molting event in summer, and a small proportion of small lobster also experience a second molt in fall. Each individual lobster entering into the IBLS goes through all the processes again and again until it dies due to natural mortality or is caught in the fishery. We run the simulation for 50 years with constant recruitment. Once the simulation is completed, we calculate the average probability of a lobster of a given size staying in the same size class or growing into the other size classes, which yields growth transition matrix. Because the IBLS tracks the detailed life history and fishery processes of individual lobster and likely captures large differences among individuals in biology and fishery, the growth transition matrix derived from the IBLS can capture biological variability among individuals in the quantification of the lobster population dynamics. We also evaluate factors that may influence the estimation of the growth transition matrix. The approach developed can also be useful for other crustacean species.

C3. Title: Estimation of size-transition matrices with and without molt probability for Alaska golden king crab using tag–recapture data

Presenter: M. S. M. Siddeek

Authors: M.S.M. Siddeek, J. Zheng, D. Pengilly

- **Abstract:** Size-structured models are used for stock assessment of hard to age invertebrate populations, such as crabs, and size transition matrices play an important role in modeling growth in those models. Crabs grow by molting and then incrementing in size. Therefore, the size transition matrix estimator should contain the molt and the growth increment sub-models. Size transition matrices are estimated using tagrecapture data in an integrated model setting. Unless tag-recaptures are delineated by molt and non-molt stages, it will be difficult to estimate the molt probability unequivocally. We have that situation with the Aleutian Islands golden king crab (*Lithodes aequispinus*) tag-recapture data from the Dutch Harbor region. We considered a logistic molt probability and a normal growth increment models for the size transition matrix estimator. We used a number of diagnostic statistics (e.g., covariance matrix, length frequency fit, chi-square statistics) to investigate the estimator without the molt probability (scenario 1) and with the molt probability (scenario 2) sub models. Although molt probability and growth increment parameters are highly correlated, there is a very few differences in the diagnostic statistics.
- **C4. Title**: Combining the Cohen-Fishman growth increment model with a Box-Cox transformation: flexibility and uncertainty
- Presenter: T. J. Quinn II
- Authors: T. Quinn II, R. B. Deriso

- **Abstract**: Many choices are available for modeling the growth transition process. For lengthbased-only models, common choices include the normal, lognormal, and gamma distributions for uncertainty combined with a von Bertalanffy growth model. For length-and-age-based models, the Cohen-Fishman model has been used, which models growth increments with a von Bertalanffy growth model and two normal distributions for the initial size-at-age distribution and for the growth increments themselves. The combination of the Cohen-Fishman model and alternative error structures is a generalization of previous usages of the Cohen-Fishman model, including the von Bertalanffy model for size, the Gompertz model with logarithm of size, as well as all intermediate distributions with power function of size. The combined model can be used to estimate growth parameters with mark-recapture data and to develop a growth transition matrix for use in length-and-age-based models.
- **C5. Title**: A flexible approach to estimating length transition matrices: growth increment and variance as polynomial functions of body length

Presenter: R. McGarvey

- Authors: R. McGarvey, J. E. Feenstra
- Abstract: Increasing the flexibility of growth descriptions, within a growth transition matrix framework, is important for crustacean and other length-based fishery stock assessments, because these models are sensitive to growth assumptions. We present a relatively flexible growth transition estimation model, fitting to ordinary fishery single tag-recoveries, which reduces to von Bertalanffy mean growth as a default. As in most growth transition matrix estimation methods, the growth-transition probabilities are computed as integrals under a pdf curve over fixed body size intervals. We use normal or gamma pdf's specified by two parameters. Model flexibility is achieved by writing both pdf parameters as polynomial functions of the mid-point length of the (pre-growth) length bin. For the normal pdf model, the two pdf parameters quantify the mean and variance of model-predicted growth increment. A default von Bertalanffy growth submodel is achieved by setting the normal pdf mean parameter equal to a linear polynomial function of pre-growth body length. Adding higher polynomial terms permits more complex dependence of mean growth increment, and of variation in growth increment, on animal body length. We tested models of successively increasing polynomial parameter number, using likelihood ratios, from constant up to 4th order polynomials for both pdf parameters. Female crustacean growth is known to slow at the onset of sexual maturity. This relatively abrupt change in steepness of the curve of growth rate versus body length has been observed and analysed in many studies of crustacean growth, first modelled using a broken-stick approach. The flexibility achieved by adding higher polynomial terms permitted a more accurate growth model of female Jasus edwardsii lobster stocks in

South Australia. In particular, we found that the model using higher polynomials better fitted the relatively faster growth of smaller females, and the decelerated growth of larger ones. The range of body lengths at which female growth slows was also inferred. For male lobsters, the fit was not substantially improved with polynomials higher than linear, consistent with von Bertalanffy growth.

C6. Title: Uncertainty in growth, reference points, and selecting bin size

- Presenter: C. Szuwalski
- Authors: C. Szuwalski
- **Abstract**: Fitting growth data inside an assessment method, rather than fitting outside and specifying growth parameters within an assessment method, allows uncertainty in growth parameters to be propagated to reference points. Here, posterior distributions of reference points sampled via MCMC for Pribilof Island red king crab and Galapagos Island spiny lobster are compared for scenarios in which growth is estimated within the assessment method and specified based on models fit outside of the assessment method. The specified bin size (i.e. the range of sizes that are grouped within the population dynamics model) can bias derived quantities in assessment (like mature male biomass) that influence the posterior distribution of reference points. Methods for evaluating the tradeoffs between bin sizes are presented and the impacts of different bin sizes are presented for red king crab.

D. Spatial and temporal variation

- **D1. Title**: Spatial and temporal variation in Pacific halibut size-at-age and the harvest policy implications
- Presenter: S. Martell (Invited speaker)
- Authors: S. Martell
- Abstract: Since 1888, the Pacific halibut fishery has landed nearly 6 billion pounds net weight, or on average 47 million pounds per year. During this 126 year period there have been dramatic changes in halibut size-at-age. For example, in the early 1990's the average weight of an 18-year old female halibut was roughly 100 pounds net weight. Twenty years later the average weight has declined to less than 40 pounds net weight. There are a number of hypotheses regarding changes in size-at-age for Pacific halibut including, density-dependent growth, intra-specific competition, climatology and temperature effects, cumulative effects of size-selective fishing, bycatch, and potential biases in aging methods. The current harvest policy for Pacific halibut apportions estimates of coast-wide biomass into 8 regulatory areas and a fixed fraction of the biomass is harvested within each area. This paper examines the spatial and temporal variation in Pacific halibut size-at-age among regulatory areas and the harvest policy implications associated with spatial variation and continued changes in size-at-age.

- **D2. Title**: How much does growth vary over time, space, and among individuals? Three case studies and their implications on biological reference points
- **Presenter**: J. Thorson
- Authors: J. Thorson, C. Minte-Vera, D. Webber
- **Abstract:** Aquatic populations exhibit variation in growth over time, space, and among individuals. Variation in growth affects the values of fishing mortality and spawning biomass that will maximize sustainable yield. We summarize results from three ongoing projects, which estimate (1) temporal variation in von Bertalanffy growth parameters for 89 species worldwide, (2) spatial variation in relative condition factor for 28 species of groundfishes off the U.S. West Coast, and (3) individual variation in anabolism and catabolism parameters for Antarctic toothfish. Then we use elasticity analysis to illustrate the potential impact of temporal variation in growth on the biological reference points (BRPs) commonly used in fisheries management. We conclude by discussing a few practical steps for improving estimation and forecasting of growth and condition in stock assessment models and fisheries management strategies.
- **D3. Title**: A state-space approach for measuring size-at-age variation and application to North Pacific groundfish
- **Presenter**: C. C. Stawitz
- Authors: C. C. Stawitz, T. E. Essington, T. A. Branch, M. A. Haltuch, A. B. Hollowed, N. J. Mantua, P. D. Spencer
- Abstract: Understanding drivers and impacts of variation in demographic processes such as recruitment and somatic growth is key to improving fisheries population dynamics models. However, trends and the magnitude of growth rate variation are not quantified on broad scales for many commercially harvested fish species. This is likely related to the difficulty inherent in modeling growth from fisheries size-at-age data, which may contain multiple patterns of growth variation (i.e. cohort- or annualscale) in addition to measurement error. Here we develop a state-space approach to modeling size-at-age patterns in marine fish to make inferences about the underlying growth dynamics. Using Bayesian estimation methods, we then apply this technique to thirty-one Pacific groundfish species across the California Current, Gulf of Alaska, and Bering Sea/Aleutian Islands marine ecosystems. We find most stocks (35/41 stocks) experience size-at-age variation consistent with annual changes in growth expressed across all age classes. This variability was expressed either as interannual fluctuation or as sustained trends over longer time periods. This method represents a novel way to use size-at-age patterns from fishery-dependent or independent data to test hypotheses about growth dynamics while allowing for annual variation and measurement error.

D4. Title: Comparison of time-varying and non-time-varying growth in the Gulf of Mexico king mackerel stock assessment: a case study

Presenter: J. J. Isely

- Authors: J. J. Isely
- Abstract: In the recent Gulf of Mexico King Mackerel Stock Assessment, we compared four model configurations within Stock Synthesis. Model 1 was configured with catch per unit effort only. No length or age-at-length information was included, and sexspecific growth parameters were fixed at externally-calculated values. Model 2 added age at length, and freely estimated (no informed priors) sex-specific growth parameters. Model 4 fixed growth parameters at those estimated in in Model 3, but allowed for annual deviations in male and female L∞ and k. Model fit improved with each successive model. Further investigation identified a negative trend in size at age among older age classes across years. That is, older females appeared to be getting smaller through time. As there was no biological justification for the apparent change in growth, we selected Model 3 as the preferred model for management advice.
- **D5. Title**: Performance of a stock assessment model with misspecified time-varying growth
- Presenter: Y-J. Chang
- Authors: Y-J. Chang, B. Langseth, M. Maunder, F. Carvalho
- Abstract: Growth in fish can change over time and between cohorts due to many biotic and abiotic factors, yet temporal variability in fish growth is rarely accounted for in fisheries stock assessment models. Rather, stock assessment models commonly assume that growth is constant through time. We conducted a simulation study to evaluate the performance of a stock assessment model under various assumptions for time-varying growth. Fish populations under scenarios of year- and cohort-varying growth were simulated using an individual-based model (IBM), and formed the basis for sampling data used to fit a statistical catch-at-age model (Stock Synthesis version 3, SS). Four different configurations of SS were used in model estimation including (1) static growth, (2) time-varying growth parameters, (2) cohort growth deviations, and (4) empirical mass-at-age data. Bias in estimates of spawning stock biomass, fishing mortality, and key management quantities was recorded, and implications of various ways of handling time-varying growth using SS were discussed.

D6. Title: Interactions between spatial heterogeneity in growth and fishing mortality

Presenter: D. R. Hart

Authors: D. R. Hart, A. S. Chute

Abstract: Both growth and fishing effort can vary spatially, even though these variations are often ignored in fishery models. Areas of faster growth can be especially attractive to fishers. Fishing can thus reduce (apparent) mean growth by selectively removing fast

growers from the population. This phenomenon is demonstrated for the sea scallop (*Placopecten magellanicus*) fishery off the northeast U.S. coast. Growth is estimated in sea scallops using data from growth rings laid down on the shells and a mixed-effects model. Growth decreases with depth, likely due to reduced food supply. Scallops in shallow waters tend to fished harder than ones in deeper water at the same density and age. It is demonstrated that commercial-sized scallops in closed areas grow faster than those from areas that are moderately fished, which in turn grow faster than those that are intensively fished. This is likely due to selective fishing, since this relationship does not appear to hold for smaller scallops. This spatial pattern in fishing effort can induce reduced yield, since fast growers should optimally be fished less than slow growing scallops.

- **D7. Title**: Empirical weight-at-age vs. model-based estimation of time-varying growth: lessons from the evolution of Pacific Hake stock assessments
- Presenter: I. G. Taylor
- Authors: I. G. Taylor, I. J. Stewart, A. C. Hicks
- Abstract: Pacific Hake (*Merluccius productus*) is subject to a large and well-sampled fishery on the Pacific coast of the US and Canada. Since 1975, over 5 million length observations and 150,000 age readings with associated weight measurements have been amassed. The population has also been subjected to more than 20 stock assessments since early 1990s. The assessments have explored a variety of parametric treatments of growth including annual growth variations, cohort-specific growth patterns, and seasonal patterns in weight-length relationships, as well as nonparametric empirical weight-at-age measurements. This rich assessment history is drawn on to describe general issues and trade-offs associated with modeling complex growth processes using parametric relationships or empirical weight-at-age matrices. The need to explore these issues using simulation analyses is also discussed.
- **D8. Title**: An investigation of using empirical weight-at-age instead of modeling parametric growth in statistical age-structured population models
- Presenter: P. Kuriyama
- Authors: P. Kuriyama, A. Hicks, K. Johnson, I. Taylor, S. Anderson, F. Hurtado-Ferro, R. Licandeo, C. Monnahan, K. Ono, M. Rudd, C. Stawitz, J. Valero
- Abstract: Fisheries stock assessments typically assume fish grow according to a theoretical growth curve (e.g., von Bertalanffy, Richards, or Gompertz). In some cases, such as Pacific hake (*Merluccius productus*), growth is empirically incorporated into stock assessments with weight-at-age data from research surveys or fishery observations. Estimating growth and incorporating weight-at-age data into stock assessments may each bias fisheries reference points, provided to decision makers, but these biases have not been well studied. Monte Carlo simulations were used to identify conditions

under which using empirical weight-at-age in stock assessments provide more robust estimations of stock status and management reference points than when growth is internally estimated. Results of this research will provide guidance to fisheries scientists regarding under what circumstances (i.e., fishing pattern, life-history type, and data availability) it is most beneficial to estimate growth within a stock assessment rather than empirically incorporate growth data.

- **D9. Title**: Not the drunken sailor, but still bad: what can we do with spatially varying growth in a model that allows movement?
- **Presenter**: S. Harley
- Authors: S. Nicol, J. Hampton, S. Harley
- Abstract: We present evidence of spatially varying growth of bigeye tuna within the Western and Central Pacific Ocean based on both preliminary direct ageing data and catch-atsize data. Currently this stock is assessed using a spatially structured MULTIFAN-CL model which has time invariant, but seasonal and age-based movement, and only a single growth morph. We discuss some simple hypotheses that could explain the differences in growth that we observe and consider what is the best of some bad options to overcome this in a stock assessment modelling framework.

E. Modeling growth in tuna assessments

- **E1. Title**: Issues in modelling tuna growth
- Presenter: D. Kolody (Invited speaker)
- Authors: D. Kolody, R. Hillary, P. Eveson
- Abstract: We describe a number of challenges related to the use of growth curves in tuna Regional Fisheries Management Organization (tRFMO) stock assessments. The challenges are described in two broad categories: i) data and communication issues (e.g. age validation methods are still lacking for some species, biologists do not always understand how their data will be used in an assessment or the assessment analysts do not appreciate the limitations of the data that they are working with), and ii) failure of the assessment analysts to recognize and describe the uncertainty associated with violations to their modelling assumptions (this includes direct issues like temporal and spatial variation in growth, and indirect issues such as the interactions between growth and other uncertain model features like natural mortality). We argue that growth curve uncertainty should be examined in the context of management decision implications (e.g. ideally in the context of Management Strategy Evaluation, where alternative plausible growth models are admitted as possible). However, we speculate that for most tuna and tuna-like fisheries, the growth uncertainties are likely to be much less important than other fundamental problems, notably uncertainty in relative abundance indices derived from commercial CPUE and uncertain population connectivity.

- **E2. Title**: Estimates of growth from direct ageing and mark-recapture data for Pacific bluefin tuna
- Presenter: H. Fukuda
- Authors: H. Fukuda, T. Kitakado, I. Yamasaki, T. Ishihara, T. Ohta, M. Watai, N. Suzuki, Y. Takeuchi
- Abstract: Lengths at age and growth rate of Pacific bluefin tuna (PBF) have been estimated from direct readings of otolith annual rings which covered older than age-1. Therefore, the length at age-0 has been extrapolated before the data, and resulting estimates of smaller length than the observed length in fisheries. In the case of PBF, since the fisheries utilized from age-0 (about 2-3 months after the spawning season; ca. 20 cm in folk length [FL]) as a seedling for the aquaculture, so the estimation of accurate age at this stage is quite important for the stock assessment purpose. In this study, we challenged to integrate three different data sources, namely direct observation of otolith daily rings, annual rings, and a mark-recapture (M-R) experiment, to improve growth estimation especially in the young ages (age 0-1). The direct observation of otolith daily rings covered from 51 to 453 days after hatching (18.6-60.1 cm in FL; n = 143), and otolith annual rings data covered age 1 to 26 (70.5-260.5 cm in FL; n = 1,112). In the M-R experiment, FL of tagged fish at released are around 20-25 cm, and the time at liberty ranged from 14 to 2,218 days. The growth curve derived from integrated analysis had a larger growth rate than that from annual rings data only. Both the daily rings observation and M-R experiment data showed obvious tendency of seasonal change in the growth rate.

Appendix C: Focus questions

Focus questions and answers are presented under the five major topics of growth addressed during the workshop. It is important to note that it was beyond the scope of this workshop to produce an exhaustive list of questions/answers that have been thoroughly vetted and can serve as general consensus. Rather, researchers should consider this information in the context of initial steps to gain insight into appropriate practices for modeling growth in a variety of fishery settings, particularly those using contemporary integrated stock assessment models. See Background and Summary above for related information.

General

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

There are a number of examples where the von Bertalanffy (VB) size-age relationship does not appear to be adequate for modeling growth in an integrated stock assessment. Some species generally exhibit linear growth for a range of ages before growth slows rapidly, often associated with maturation. Such growth is not well described by the von Bertalanffy growth relationship. Other species exhibit temporary cessation in growth or multi-stanza growth over their lifetime. Another parametric growth relationship, such as the Richards growth curve, typically provides more flexibility for estimating size-at-age for a wide variety of species than possible using the VB growth relationship. A major problem with functional forms for describing growth curves is that data for any particular age can influence the estimated mean length-at-age for other ages. Often there are few observations available for modeling growth of very young or old fish and thus, information for intermediate ages is largely used to estimate mean length for young and old fish based on the VB curve, including in some cases, extrapolating outside the range of the sample data. This is often the case when fitting to length composition data and illustrates an inherent problem with model selection, parsimony, and estimating the growth curve outside the stock assessment model. If the more parsimonious model (fewer parameters) is selected, it may not represent the mean length of old fish and ultimately, resulting in potentially biased estimates useful to management due primarily to fitting to the length composition data. For example, inappropriately assuming a linear growth relationship in a length-structured assessment can produce an inflated average length for the oldest fish and a confounded result of a highly depleted population. 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?

Growth curves based on parametric functional forms are likely not flexible enough to estimate mean length-at-age for some species. Parametric forms are also unduly influenced by abundant

observations at intermediate ages, which typically characterize growth information available for many assessed species. On first principles, nonparametric methods should allow more flexibility, to some degree, for estimating growth in an integrated stock assessment. However, a potential limitation of nonparametric growth forms is determination of objective approaches for specifying asymptotic properties of the older ages. In general, nonparametric methods require parameterization regarding the amount of smoothness underlying the curve, which may be difficult to formally integrate within the statistical framework of 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, given most growth research has not examined the effect that the functional form has on the stock assessment results (e.g., how growth parameterization impacts 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 sexspecific size composition data, it is not possible to model selectivity differences between sexes. Thus, similar selectivity (age or size) will need to be assumed for both males and females, with results likely sensitive to such assumptions.

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

There are various methods available to diagnose model misspecification, including 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 diagnostics, and sensitivity analysis. However, none of these diagnostic methods are specifically designed to identify misspecified growth. Currently, the most reasonable approach is to visually examine patterns in residuals from fitting the length composition or age conditioned on length (conditional age-at-length) data, and determine if alternative growth assumptions/parameterization improves residual patterns. Also, it is important to note that there likely exists some amount of parameter tension between growth, selectivity, and other model parameters, which further confounds identifying estimation biases in residual patterns.

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 F_{MSY} 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. Catch-at-age models only require growth information to convert abundance (e.g., catch) in weight into numbers of fish. In these models, the length (or weight) of the most commonly sampled ages 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 asymptotic length estimates (vs. growth rate), as well as the variation of length-at-age of the oldest fish. The influence of growth on fits to size composition data can be influenced highly by interactions with the respective selectivity parameters. Ultimately, the relative effect of growth uncertainty compared to other population and fishing processes is probably application specific.

How do growth model assumptions interact with key management parameters?

Growth rate (K) estimates will impact 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 processes (e.g., growth, natural mortality, stock-recruitment relationship) and fishery operations (e.g., selectivity). The sensitivity of the shape of the production function (B_{MSY}/B_0 or equivalently, F_{MSY}) to growth is about the same as for natural mortality (M), but it is more sensitive to steepness of the stock-recruitment relationship. The productivity rate (MSY/B_{MSY}) is very sensitive to growth, natural mortality, and the steepness of the stock recruitment relationship. These management estimates are independent of the maximum length, however, due to the interaction with data used to fit the model (e.g., size compositions), estimates of L_{∞} will also influence derived management quantities generated from the model.

Should forecasts include trends in growth?

It is unusual for forecasts to include trends in growth, given an assumed trend would need some justification. For example, density dependence or genetic selection might be reasonable rationales to include trends in growth, whereas, broad climate change reasons are more likely speculative than objective at this time. It might be more reasonable to assume that growth rates are due to present environmental conditions that are more likely to persist into the near 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 fish 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 oldest ages (e.g., maximum age) can substantially influence bottom-line management results, but the largest sizes are often estimated based on the preponderance of data at intermediate ages. Therefore, model misspecification caused by simplifying assumptions can influence baseline results, particularly when fitting to size composition data and less so in age-structured models.

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. In particular, size-specific selectivity can introduce additional bias in the estimates of growth parameters. Integration of growth estimation within the stock assessment model will automatically account for selectivity effects 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 older fish?

Some researchers have fit growth models to age-length data giving equal weight to each age (e.g., fit to mean length-at-age time series, rather than to data for individual fish). However, this will necessarily over emphasize sparsely sampled ages in the overall data set. In addition, this approach does not estimate the variance 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 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, which is often 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 subsequently, their use has been limited to date.

Variation of length-at-age is important when fitting to size composition data. Variation of lengthat-age can be due to a number of factors, including individual variation, temporal variation, spatial variation, ageing error, protracted spawning periods, and different times of capture. Individual variation is only one component, so it may not be worth integrating methods that 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, resulting in more uncertain estimates from the assessment, but the relationship with age or size generally has to be assumed. 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.

How much does asymptotic growth vary between individuals and over time?

There is moderate variation in asymptotic length both over time and among individuals. There is roughly 10% variation in L_{∞} , but as much as 30% in W_{∞} .

Are finer time steps needed in the stock assessment model for modeling growth exhibited by highly productive, fast growing species?

The faster a species grows the more likely the length of a fish at a given age will change during 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 catch-at-length 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 are separated into shorter time periods. However, partitioning data into finer time steps will necessarily reduce the input sample sizes for each time period. Although, unless additional parameters are estimated in the stock assessment model 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 steps 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, particularly for models fitted to length compositions. Some applications simply run the same model on a time step shorter than a year (e.g., quarter), but this generally assumes recruitment takes place at each time step (e.g., tuna assessments), which may not be appropriate for some species that exhibit contracted spawning periods within a year. Other applications include a seasonal framework, whereby recruitment distribution can be assigned to one or more seasons within the year (e.g., Stock Synthesis). In these cases, attention to time step and recruitment apportionment assumptions is warranted, given results regarding derived quantities useful to management may be sensitive to such model dimension choices.

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

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_{∞}) can have 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 relatively high (or natural mortality is high or selectivity is dome-shaped). On the other hand, if many fish are observed at this length, the exploitation rates must be relatively low. L_{∞} estimates are often uncertain because for many species, older (larger) fish are more difficult to accurately age or sample sizes are low. It is unclear which approach should be used to deal with uncertainty in L_{∞} . Using the largest fish observed may not be a good choice because of inherent variation in length-at-age and thus, lengths of such fish would not strictly represent L_{∞} (average length of the oldest age). Also, note that in cases of high fishing mortality, there may be no fish that reach L_{∞} , which further complicates accurate determination of L_{∞} without good age data from validated methods.

A. Biological processes / ontogeny

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

Underlying processes may provide insight into the form of the growth equations and may indicate applications that deviate from the von Bertalanffy growth relationship. For example, species that expend large amounts of energy on reproduction might be expected to exhibit growth rate changes around the time of maturity. However, if able to be objectively determined, underlying processes are likely to be complex and thus, simplifying assumptions will be needed in most cases to more practically model growth in integrated stock assessments.

What are the most important mechanisms underlying growth (genetics, density dependence, environment) and how does this influence how growth is modeled in assessments that include movement parameters?

Growth rates appear to be relatively plastic and likely to be affected by immediate oceanographic conditions and variation in resources, with changes in growth expected as individuals move between different environments. This suggests that length-based population models with growth increments as a function of length might be the most appropriate assessment model to consider.

Is size-based genetic selection common in exploited species and does it warrant consideration in stock assessments and management?

Growth rates appear to be plastic and influenced to varying degrees by environmental factors, suggesting that genetics is not a single driving mechanism. Size-based genetic selection is probably a minor issue for most stock assessments and management relative to other issues.

What biological (e.g., natural mortality, maturity) and fishing (e.g., selectivity) processes 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, for most stocks, this affect is likely to be most influential for juvenile fish that are not vulnerable to the fishery, except for species that are still relatively small as adults (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 relationship between stock and recruitment for many species (i.e., steepness close to 1), this is unlikely to influence the dynamics of the population. However, it may affect 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 detectable and influential to bottom-line assessment results. In contrast, growth dynamics are likely to be influential in stock assessments using sized-based selectivity, particularly when fitting to size composition data, and can substantially influence results from the stock assessment model.

B. Specification and estimation: age-structured models

What is the best model for variation of length-at-age?

Variation of length-at-age can have a notable impact on assessment results when fitting to length composition data, particularly in regards to the maximum age in the model. Similar to L_{∞} , the variation of length-at-age largely determines the estimated maximum size of fish in the population. If variability is assumed (fixed) too low, so large fish are not expected in the analysis, estimated abundance will reflect a lightly depleted population. If growth variability is set too high, the expected larger fish will be unobserved, producing abundance estimates assuming a highly depleted stock.

Stock Synthesis has several linear-based formulations for addressing the variation of length-at-age, with the standard deviation (SD) or coefficient of variation (CV) treated as a linear function of age or mean length-at-age. The underlying relationship is based on parameters for a representative young and old age, respectively. The relationship is linear between the two ages and constant outside the age endpoints. It is unclear which relationship is most appropriate, however, using a constant CV as a function of age is likely not a robust assumption, given this practice can produce relatively large SDs for the older fish or very small, unrealistic SDs for the young fish. This outcome is due to growth rates declining with age and variation not expected to increase significantly at older ages, given growth has slowed. Also, note that in some cases, it might be reasonable to expect variation to increase as the fish grows to older ages. Therefore, if there is insufficient information to estimate a linear relationship, assuming a constant CV as a function of mean length may be most appropriate. However, the relationship may be complicated by a number of factors. For example, variability in birth dates may cause higher variation (CV) at younger ages. Further research is needed to identify good practices for treating growth variation in the integrated stock assessment model, e.g., conducting a meta-analysis that includes well-determined ages from 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, but other factors can also produce variation in length-at-age, e.g., ageing error, variability in birth dates, and temporal or spatial variation in growth. If the variation of length-at-age is fixed based on individual growth variation, it will lead to an underestimate of variation in length-at-age observed in the data, unless other processes are accounted for concurrently in the model.

How should age-length data be combined with growth increment data based on tagging studies to provide improved estimates of growth?

There are many stocks for which growth estimates are available from both age-length data and growth increment data from tagging experiments. Typically, these two types of data are analyzed separately and the results compared. Combining the results is difficult because the error structures assumed for each are different. However, Laslett et al. (2002) developed a method to combine the two types of data by treating the tagging data as age-length data and estimating the age-at-release of each tagged fish. Because the fish is measured twice, the tag data still contain some information after estimating its age, but information about absolute age is lacking and age-length data are still needed to calibrate the absolute age. This approach appears promising, but some issues remain unresolved, e.g., how should correlation between the length-at-release and length-at-recovery, ageing error, and altered growth rates due to tagging be addressed in the analysis.

How and when should ageing error be incorporated in the stock assessment model?

Between-reader error estimates may not be adequate for some applications, given unaccounted for 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, given there are clear modes for young ages in the survey length composition data that differ from the age-length data. However, notable modes are not as clear for older ages and extrapolation is typically implemented. Further research is needed to better assess inclusion of ageing error and its influence in growth estimation and derived quantities useful to management.

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 these data inside the stock assessment model. The advantages of internally estimating growth using these data include: 1) growth estimation utilizes additional information from other data (e.g., modes in the length composition time series); 2) uncertainty is automatically propagated throughout the analysis; 3) assumptions are consistent (e.g., selectivity is inherently taken into consideration); 4) sampling design is more explicitly considered (e.g., using age conditioned on length and length composition data). However, growth is typically a well-estimated quantity and integrating growth estimation in the stock assessment model may result in model misspecification (e.g., incorrect value of natural mortality) and biased estimates of growth, which lead to different estimates of management quantities. The statistical fit to the data can be about the same for different hypotheses (growth rate, natural mortality, fishing mortality, selectivity), but the policy implications differ. Some management policies may be more (effort limits) or less (minimum legal size) robust to variability in growth rates.

Is the assumption that length-at-age is normally distributed adequate?

Most age-structured models assume that length-at-age is normally distributed and the distribution reverts back to this form at each time step, even if there is high length-based fishing mortality. In a length-structured model, the implicit length-at-age distribution is adjusted. Changes in the length-at-age distribution can be approximated in an age-structured model using multiple growth groups (platoons or morphs in Stock Synthesis) that are modeled separately, with independently assigned growth curves. Normal, log-normal, and gamma distributions are often used, but with typically low CVs for length-at-age associated with most species, there is not likely to be notable differences between the shape of these distributions.

How does the choice of the age data plus group interact with growth specification and estimation?

There are two types of plus groups for age data 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, with all plus-group fish assumed to reflect similar biological (e.g., mean length-at-age, natural mortality, fecundity) and capture (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 size-at-age (length and weight) of the plus group is assumed to be equal to the mean size for the youngest fish in this combined group and thus, may underestimate the actual average associated with all fish included in the plus group. The actual mean will change with the exploitation rate, e.g., mean age decreasing as the exploitation rate increases. In Stock Synthesis, an adjustment is used to increase the mean length and weight of the plus group to account for growth within the plus group. It may be useful to set the plus group age old enough to minimize the potential for fish to continue growing or to ensure that in a virgin population (used for reference point calculations), very few fish are accumulated in the plus group. However, increasing the number of age classes in the analysis will lead to additional computational demands to varying degrees depending on the application. The second type of plus group is assigned for fitting the model to the composition data. If the bin size is too large, then the model may not be able to identify the relevant cohorts in the length composition data, with smaller bin sizes resulting in increased computational demands. Also, if the plus group size is set too small, it will preclude the length composition data from providing information regarding the asymptotic length of the growth curve. On the other hand, using a smaller size for the plus group may eliminate bias caused by misspecifying the asymptotic length of the growth curve, trading off less bias with more uncertainty (imprecision). Finally, a more robust practice may be to use a flexible growth

curve and estimate the asymptotic length inside the stock assessment model to better represent uncertainty.

What is the asymptotic length confounded with: a) specification of natural mortality; b) increased age-specific mortality for older fish; or c) selectivity of the oldest age class? Length composition data are particularly problematic because the absence of large fish in the composition data could be explained by several factors including high fishing or natural mortality, dome-shaped 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. This issue may be less of a problem for growth estimation if the model includes age conditioned on length data. Assuming asymptotic selectivity for at least one fishery or survey generally helps stabilize estimation in integrated stock assessment models. This is particularly true if growth or natural mortality is being estimated.

Is cohort slicing used in a VPA more or less sensitive to growth assumptions than for 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 more robust.

Can the distance between growth rings on hard parts (otoliths, spines, etc.) be used to model growth, and does it provide additional information on growth variability and relationships with density, environmental, and maturity?

Validation of the relationship between growth of the hard part and growth in body length is difficult and thus, the potential of the distance between growth rings on hard parts to provide additional information is unclear. However, if validated, there is huge potential for otolith growth data to provide information on temporal variability in body growth and relating it with density, environment, or other factors. The utility is probably species specific.

C. Specification and estimation: length-structured models

How should one choose the number and width of size classes (composition bins) when conducting size-structured assessments – should this issue be considered in terms of the amount of available 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 frequently, it should be practical with modern computers to handle the increased number of size classes to extract the most information from size composition data. Size classes that are too broad will prevent the model from extracting detailed information about the shape of the growth transition or the cohort strengths. Size classes that are too narrow 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, unless there are additional parameters added to the model for each size class, small size class drawbacks are not likely to be problematic. 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 fits if based on data condensed into fewer bins.

Tagging data are likely overdispersed – how can this be accounted for when tagging information is integrated into stock assessments?

There have been several methods used to account for overdispersion associated with tagging data for cases when tagging information is used for estimating biomass, but it is unclear if the same approach can be used for growth increment data from tagging studies. 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.

D. Spatial and temporal variation

When and how should temporal variation in growth be modeled?

There are a number of factors that could cause growth rates to vary over time, including changing environmental conditions and fishery operations that lead to population density fluctuations that influence underlying biological properties (e.g., growth, maturity, mortality). 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. Further simulation research is needed that includes stocks with relatively good growth data that would allow formulating and testing hypotheses based on the amount of temporal variation expected in the population.

How should spatial variation in growth rates be modeled in spatially-structured models?

For many species, it is clear that mean size-at-age varies spatially. Spatial models are being more frequently used in stock assessments. If movement is limited, then separate stock assessments with different growth rates may be adequate. If movement is moderate to substantial, then formally modeling movement may be needed to accommodate notable growth differences spatially. One main issue when considering movement within the population is uncertainty regarding the size and growth rate of a fish when it moves from one area to another. If the

difference in growth rates is environmentally driven, then the growth rate may change from area to area, but if genetics-based, then the growth rate may remain unchanged across areas. Magnitude of the change in growth rate will depend on the type of stock assessment. If the model does not fit to length composition data (fixed growth parameters), growth information is mainly used to convert catch in weight into numbers, and also used to convert numbers of fish-at-age into estimates of stock biomass. In this case, the influence of growth variation among areas may be limited. However, if the model is fit to length composition data, spatial variation in growth may influence the fit to the length composition data, resulting in more variable results from the model. In a simple spatially-structured/age-structured model without tracking the origin of a fish, the fish will grow or shrink to the new size-at-age as it moves areas, which is biologically unrealistic. In a length-structured model, fish transition to the correct length bin, but will reflect the 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 account for this phenomenon. Modeling genetic cohorts of the population, as well as length or age structure, may allow more flexibility for evaluating potential spatial variation in growth.

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

Temporal variation in growth should be considered in many cases, however, it is unclear if the amount of variation is meaningful and if ignored (constant), produces significantly biased results from the stock assessment model. Thus, robustness of model results to time varying growth assumptions will be application-specific and depend on the degree of temporal variation and types of data used in the assessment. Stock assessment models that fit to length composition data and assume constant growth over time will likely be 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 typically limits temporal variability. An ideal assessment configuration would include empirical weight-at-age data with low sampling and ageing error for all time periods and fisheries (which implies low observation error for age composition data collected in the field). In such cases, the obvious choice would be to essentially bypass growth estimation and use the empirical weight-at-age data in the model. However, as the sampling or ageing error increases, or when there are time periods without samples, explicitly modeling growth internally becomes a stronger consideration. Also, in applications when there are time periods or fisheries that have no age data and size composition data are used instead, growth estimation inside the model warrants consideration. The growth model can be configured to closely match the empirical data, but the

model may have increased computational demands and related convergence issues and thus, using empirical weight-at-age data would be more practical and straightforward.

E. Modeling growth in tuna assessments

Is there evidence for two stanza growth that has been proposed for tuna stocks?

For some species of tuna in some oceans, there appears to be unusual patterns observed in growth, where at intermediate ages, the growth slows down and then speeds up again within a relatively narrow age range. In other tuna species, growth is linear and 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 genetic-based, the result of physiological/ontogenetic changes or environmental conditions, or due to ageing methods (e.g., tagging effects on growth).

Appendix D: Participants

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Group photo from the CAPAM workshop on *Growth: theory, estimation, and application in fishery stock assessment models* (NOAA/NMFS/SWFSC, La Jolla, CA 92037, November 3-7, 2014).