Good practices for estimating and using length-at-age in integrated stock assessments

HuiHua Lee[1,2], Mark N. Maunder[3,4] and Kevin R. Piner[5]

[1]Corresponding author at: NOAA Fisheries, Southwest Fisheries Science Center, Fisheries Resources Division 8901 La Jolla Shores Drive, La Jolla Ca. USA

E-mail address: huihua.Lee@noaa.gov

[2]NOAA Fisheries, Southwest Fisheries Science Center, Fisheries Resources Division 8901 La Jolla Shores Drive, La Jolla Ca. USA

[3]Inter-American Tropical Tuna Commission 8901 La Jolla Shores Drive, La Jolla Ca. USA

[4]Center for the Advancement of Population Assessment Methodology, Scripps Institution of Oceanography, La Jolla, CA, USA

[5]NOAA Fisheries, Southwest Fisheries Science Center, Fisheries Resources Division 8901 La Jolla Shores Drive, La Jolla Ca. USA (retired)

Abstract

Estimating growth (increase in size with age) is an integral component of fish population assessment. The use of integrated assessment models combined with the influence of misfitting size composition data on results have led to renewed interest in how growth is modeled in the assessment process. The types of data available to describe the growth process control how the length-at-age relationship will be estimated. Many factors contribute to the complexity of estimating length-at-age, including multiple sources of biological variability and difficulties in getting representative samples. The growth process in the population dynamics model is linked to all other processes and data but most directly influences the assessment model through 1) converting numbers into weight and vice versa, 2) productivity, and 3) modifying fits of size composition data. In some cases, an assessment may be insensitive to moderate levels of misspecification of the growth process, and therefore, relatively simple treatments may be adequate. However, in many cases, especially those where the fit of size composition is influential in estimating scale, a more thorough treatment of the growth process is needed. A complete treatment of growth will estimate the most important forms of biological variability, including individual, sex-specific, temporal, and spatial variability. Several types of sampling bias, including selectivity, length-stratified sampling, and spatial and measurement error, will likely also need to be addressed. When sufficient data are available, assessment authors should consider estimating the growth process as part of the integrated assessment model or consider empirical approaches for situations with high biological variability and sampling bias.

Keywords: Growth, Length-at-age, Integrated stock assessments

1. Introduction

The field popularly known as ‘age and growth’ has often served as the gateway for biologists into the broader arena of population assessment. Understanding fish growth patterns plays a key role in more than just the applied fields. Growth patterns have been used to assert evolutionary processes (Roff, 1984; 1993; 2000; Hendry et al., 2000; Haugen and Vøllestad, 2001), to infer less easily observed life history traits (Pauly, 1980; Griffiths and Harrod, 2007), connectivity between areas (Helser, 1996; Swain and Foote, 1999), and movement (McDaniel et al., 2016). However, it could be argued that growth studies play one of their most crucial roles in the population assessment of exploited stocks.

The increasing use of integrated assessment models (i.e., those that combine several sources of data into a single model) combined with the influence on assessment results from misfitting size composition data (Francis, 2016) has led to renewed interest in the applied understanding of fish growth. It was once presumed that because growth models are simple and data can be readily gathered, the estimation of this biological process is relatively uncomplicated. However, this assumption has proven to be far from reality as the difficulties faced in collecting representative growth data are the same as for any data sources used in stock assessments. Despite the importance of age and growth research, there has been surprisingly little change in the applied approaches used in assessments to depict growth. The von Bertalanffy Growth function (VBGF; Beverton and Holt, 1957; von Bertalanffy, 1957) remains (by far) the most commonly used growth model (Flinn and Midway, 2021). Relatively little attention has been paid by stock assessors to the many sources of variability in growth (Lorenzen, 2016). A workshop (Maunder et al., 2016) aimed at providing guidelines for treating the length-at-age relationship in age-structured models (Francis, 2016) outlines many of the issues, but no clear consensus could be developed for using growth modeling in applied population assessments.

In this paper, we attempt to expand upon the conceptual framework of Francis (2016) and summarize the current level of understanding of fish growth. Additionally, we will provide some advice to assessment scientists about the process of fish growth, explicitly covering how the estimates of size-at-age affect integrated population dynamics modeling and methods of its estimation. We focus on length-at-age as it relates to integrated age-structured population models because of their widespread use and because length-at-age is especially important in fitting size composition data. However, many of the same considerations could apply to other types of assessment models and other forms of fish growth (e.g., length-weight).

2. Biology

The terms "growth" and "size-at-age" are often used interchangeably. However, for the sake of simplicity in the remainder of this paper, we will define "growth" as the action of changing length over time, "length-at-age" as an expression of that action, and the "growth process" as the mathematical relationship between length and age.

2.1. Theoretical model

The biological model underpinning growth generally assumes that nutrients are metabolized over time, making growth age-dependent. Fish are somewhat unique among vertebrates in that growth can be indeterminate in maximum length (Talbot, 1993) and quite variable (Lorenzen, 2016). Variability arises because local factors that affect nutrient availability, metabolism, or anabolism will ultimately affect the local expression of length-at-age.

2.1.1. Nutrient availability

Nutrient availability affects growth and maximum fish size (Yoneda and Wright, 2005; Auer et al., 2015; Kuzuhara et al., 2019), influenced by both biotic and abiotic factors (Eker-Develi et al., 2022). Ecological processes like hypoxia (Eby et al., 2005; Campbell and Rice, 2014) impact actual nutrients available to a fish, and density-dependent competition affects growth in both juvenile (Lorenzen and Enberg, 2002) and adult stages (van Gemert and Andersen, 2018).

2.1.2. Metabolism

Abiotic factors, such as temperature, have been shown to influence individual metabolism (Campana et al., 1995; Gillooly et al., 2001). It is widely agreed that metabolism and growth peak within an optimal temperature range and decline as temperature departs from that range (Little and Seebacher, 2021). However, the effects of temperature on growth can be complex, as increased growth rates may cause early maturation, which may ultimately decrease the maximum length-at-age (Daufresne et al., 2009). Salinity (Bœuf and Payan, 2001), pH (Mota et al., 2018), and oxygen intake (Pauly, 2021) also affect metabolism (Bœuf and Payan, 2001; Mota et al., 2018).

2.1.3. Anabolism

The process of synthesizing new tissue in fish is complex, variable, and influenced by multiple factors that interact with each other. Age is often the primary factor affecting the growth rate in fish (Denechaud et al., 2020). Maturation, which may also be influenced by age, often has a negative impact on somatic growth (Roff, 1983; 2000) as more metabolized nutrients are allocated to reproduction (Minte-Vera et al., 2016). However, these effects can vary among individuals and are influenced by environmental factors (van Poorten and Walters, 2016).

2.2. Does understanding biology even matter?

The complexity and interactions of factors that simultaneously influence nutrient availability and metabolism make a mechanistic understanding of the drivers of growth and its variability difficult and beyond the scope of the typical stock assessment. Consequently, it is reasonable to ask if a mechanistic understanding of the growth process is necessary (van Poorten and Walters, 2016). Most population assessment work is descriptive, involving recreating the past population abundances. The role of fishing in determining those dynamics may not require a mechanistic understanding of growth drivers. In some cases, a reasonably accurate description of length-at-age may suffice. However, in cases where fine-scale estimates of growth are important and observations of length-at-age are incomplete or where we need to forecast beyond the observation period, a mechanistic understanding may improve predictions. This is particularly evident in long-term projections, where length-at-age may be related to potential environmental changes (Lee et al., 2018; Denechaud et al., 2020). However, a high bar should be placed on such studies for informing management, as the mechanistic growth drivers are likely more complicated than generally acknowledged. Therefore, the key question for applied work is what constitutes a "reasonably accurate" representation of length-at-age for the questions being asked and how we can achieve it.

3. Data

Before discussing how to or what is an accurate estimate of length-at-age, the most basic consideration governing the growth process estimation is what data is available. Although when estimated inside the population dynamics model, information on the process may come from indirect sources (Sippel et al., 2017), for this paper there are several categories of direct sources. These direct sources generally consist of size measurements and associated measures of time. Time can be either an age or an increment of time. In most instances where an age is associated with a length, that age is derived from counting and validating daily or annual rings from hard parts such as otoliths, fin rays, spines, or vertebrae, although other products of metabolism have also been used (Kilada and Driscoll, 2017). Increments of time are typically derived from capture and recapture events without necessarily knowing the age. The following is a brief discussion of the most common types of data used in routine stock assessment.

3.1. Length composition (length modes)

Length composition, though not directly associated with age or time increment, can reveal cohort information through modal structures (Leigh and Hearn, 2000), which suggests time as a relative age. More complicated methods have been developed to decompose less obvious structures (usually larger sizes) into age groups (Pauly, 1987; Fournier et al., 1990; Laslett et al., 2004). Seasonal modal changes can offer insight into cohort growth rates.

3.2. Paired age-length observations

The most commonly used data to estimate the length-at-age relation are paired observations of length and age. Francis (2016) described two ways these paired observations could be treated, which relate to whether length or age can be considered representative of a given value of the other. The more traditional use of paired age-length data assumes that lengths are representative of a given age (random-at-age). Alternatively, the same type of data can be used with an estimation procedure that assumes that the ages are representative of a length (random-at-length). Random-at-length data is also sometimes referred to as conditional age-at-length.

3.3. Mean length at age

A variation of the paired length and age data is observations of mean length at age. This type of data is similar to random-at-age data, but it has the drawback that the growth pattern is summarized, and information on the individual variability is missing. The use of mean length-at-age is often because the information is taken from a report, and the individual data is not available. Alternatively, mean length-at-age could be used when the analyst does not want a large number of samples from small or intermediate-aged fish to have too much influence and wants to give equal weight to each age.

3.4. Tagging

Tagging offers direct growth observations (Francis, 1988; Hearn and Polacheck, 2003; Francis et al., 2016), through measurements taken between capture and recapture increments of time. However, tagging can be costly, suffer from sparse recaptures across regions/ages/size groups, and may lack age information. Concerns also exist about the stress effects on growth rates due to tagging, making them not representative of the actual population (Smircich and Kelly, 2014; Vollset et al., 2020). Typically, estimating the growth process and length-at-age requires some method or other data to derive the fish's age (e.g., Eveson et al., 2004).

4. Why is estimating the growth process so complicated?

With the range of data available and potentially no imperative to understand the mechanistic drivers, why does it remain so difficult to get a complete and reasonably accurate representation of a population's length-at-age? Many factors contribute to the complexity of estimating this process, including the biological variability in the growth pattern itself and a multitude of sampling biases in the data. What follows is only a partial list of some of the key types of biological variability and sampling biases.

4.1. Biological variability/system processes

Biological variability is the natural variation in length-at-age and should ideally be included in the assessment model as a system model process along with its associated variability (Maunder and Piner, 2015). When estimating length-at-age for an assessment, ideally, many sources of variability should be considered separately. However, in practice, these multiple sources of variability are often not specifically addressed with separate components of the system model process but are subsumed into other types of variability, model processes, or observation error (Maunder and Piner, 2017; Piner et al., 2018).

4.1.1. Individual variability

The most basic source of biological variability is the individual variability in the lengths for a given age, but it is not always fully considered. When it is estimated, there is no real consensus on how it should be modeled, such as whether it should be modeled as a constant (standard deviation) or proportional (coefficient of variation) across ages (or length) or how it changes with age (constant, linear, or a functional form) or the shape of the distribution of lengths for a given age (normal, lognormal). Simulation studies indicate that even when individual variability is estimated, the variability may be underestimated (Schemmel et al., 2022) and almost always oversimplified.

Furthermore, the observed individual variability is not the same as that expressed in the system processes of the assessment model. In most integrated assessments, synthetic length distributions are created at discrete time step intervals (e.g., year, quarter) to compare to the observed length composition collected over that interval. Thus, the individual variability in the growth process of the model should include variability due to the continuous growth during the interval in addition to the natural variability. The shorter the model's time step interval and the slower the growth of fish, the smaller the contribution from growth over the interval will be to the individual variability parameters. Individual variability in spawning time and larval survival can also contribute to the variation (see 4.1.4 below).

4.1.2. Sexual dimorphism

Even under the same environmental conditions, fish of the same species often show some sexual dimorphism. The onset of sexual differences in length-at-age often becomes apparent after maturation (Hüssy et al., 2012), with multiple hypotheses for this phenomenon (Slatkin, 1984). Assessment and growth models that are not sex-specific (one-sex models) often implicitly include (intended or not) sex-specific differences in length-at-age as an additional contribution to individual variability.

4.1.3. Temporal (annual/cohort) variability

Surprisingly, few studies aimed at length-at-age estimates for integrated assessment consider that the length-at-age relationship can change across years (although those for Cohort Analysis and Virtual Population Analysis applications often do). This temporal variability includes long-term trends or interannual variability. When temporal variability is estimated, it is usually attributed to either annual changes in the growth pattern or cohort growth differences (Thorson and Minte-Vera, 2016; Correa et al., 2021). Annual changes may occur when environmental conditions within a year cause growth pattern aberrations to more than one age class in the population. Cohort growth differences arise when cohorts display a different growth pattern that may also be associated with environmental factors, which may be spatially dependent or density-dependent. For instance, Denechaud et al. (2020) demonstrated density-dependent cohort-specific growth patterns for Atlantic cod. However, potential changes to the individual variability, rather than or in addition to changes in mean length-at-age, have received relatively less attention.

4.1.4. Timing of spawning/hatching

The spawning seasons are not fixed points in time and exhibit variability in both the timing of peak spawning and the duration of spawning. When a fixed birthdate assumption is made in the assessment or growth model in conjunction with variability in peak spawning, it may appear as temporal differences in the length-at-age of young fish even when the growth pattern is unchanged. Durham and Wilde (2005) demonstrated this phenomenon, although the persistence of such apparent differences in length-at-age across the lifespan of the cohorts is uncertain. Variability in the duration of spawning likely impacts the spread of lengths for young fish. Because spawning timing and duration variability primarily affect young fish, these sources of variability may be subsumed in the individual variability parameter(s) of young ages. However, it is not clear whether expanding the individual variability will lead to accurate estimates of young fish length-at-age when hatch dates vary, and the growth process is assumed to be time-invariant.

4.1.5. Seasonal variability

Fish do not grow at the same rate throughout the year due to changes in nutrient availability, temperature, and other factors affecting metabolism (Pauly, 1990; Bacon et al., 2005). Length-at-age estimation models that account for seasonal effects have been available for decades (Pitcher and Macdonald, 1973). However, routine stock assessment rarely incorporates these seasonal growth effects.

4.1.6. Spatial variability

Spatial differences in length-at-age can arise due to regional variations in growth patterns. Campana et al. (1995) demonstrated that Atlantic Cod (*Gadus morhua*) could exhibit up to a 3-fold difference in lengths-at-age across the stock distribution. Regional growth rates are likely related to either nutrient availability or factors affecting metabolism within specific geographical areas. In the case of Atlantic cod, the authors surmised that local temperatures likely contributed to the difference. However, it is unclear if these differences in growth rates are maintained if fish move from one region to another. Despite this potential source of variation, these spatial patterns in length-at-age are not routinely included in stock assessment models (including spatially explicit assessments). Instead, spatial variability may be implicitly approximated using estimates of other biological process variability, model processes, or observation error (e.g., McGarvey et al., 2007). Nevertheless, even knowing the contribution of genetic and environmentally driven components still may not produce accurate estimates of length-at-age for all regions.

4.1.7. Fishing-induced variability

The consequences of fishing have been shown to alter length-at-age at different spatial and temporal scales (Kristiansen and Svåsand, 1998; Hilborn and Minte-Vera, 2008; Andersen and Brander, 2009; Eikeset et al., 2016). Over shorter periods, high fishing mortality in conjunction with size-selective gears can lead to temporal changes in cohort mean length-at-age and its associated variability (Lee, 1912). The typical assessment with a time-invariant growth process does not account for this effect, as expected lengths in a time interval are a function of the growth process and its individual variability (typically assumed to be normally distributed), without keeping track of cumulative removals of faster-growing fish. Thus, the effect of size-selective removals on the population size structure is lost between time intervals in the model. Beyond short-term effects, decadal fishing pressures have been theorized to permanently alter life history characteristics such as maturation and growth processes (Audzijonyte et al., 2013). However, the common assertion that fishing will inevitably cause a slowing of growth due to the removal of faster-growing individuals has been challenged (Enberg et al., 2012). These decadal effects are likely to show up as temporal variability or trends in the growth process.

4.1.8. Shrinkage

The general model of fish growth assumes growth over any unit of time. However, limited studies have documented that vertebrates can shrink in length under harsh environments. The mechanisms for such a survival strategy are not clear, but observational studies in fish (Huusko et al., 2011), amphibians (Bendik and Gluesenkamp, 2013), and laboratory studies of crustaceans (Marinovic and Mangel, 1999) have documented length shrinkage. Despite its assumed rarity, in practical work, observations of fish shrinkage have likely been attributed to some form of observation error (e.g., data entry error) or rigor mortis.

4.2. Sampling Biases/observational processes

Estimates of population lengths-at-age, along with their associated variability, are further complicated by various sampling biases. Within the assessment model, sampling bias is approximated by estimating observation processes (e.g., selectivity), accounting for bias in the observation error (e.g., the effective sample sizes used in the likelihood for length composition data), or absorbed by other model processes (e.g., natural mortality; Maunder and Piner, 2017). Sampling biases can affect the representativeness of estimated growth rates, observed lengths, observed ages, or a combination of all these factors.

4.2.1. Gear

The effects of fishery gear selectivity (Maunder et al., 2014; Sampson, 2014) are perhaps the best study of observational biases. Fishing gear does not operate randomly with respect to the size/age of the fish captured. Selectivity bias in the growth parameter estimates has been well-studied, and several estimation methods are available to deal with this issue (Frater and Stefansson, 2020). However, the effects of fishermen-directed choices on the size/age of fish captured in fishing operations are much less studied. Purse seine fishermen have been shown to avoid capturing unwanted species or sizes of targeted species (Marçalo et al., 2019). These decisions can be based on regulations, market forces, or fishermen's preferences and can be adjusted within short time frames. In most assessments, these non-gear selection decisions are likely subsumed in the gear selectivity estimates. The extent to which this approach will account for such effects is not well-studied. It has generally been regarded that gear effects are more consequential for length-at-age estimation methods assuming lengths are random-at-age, as pre-selection of age seems less likely than selection based on length.

4.2.2. Discarding

Discarding (Rochet and Trenkel, 2005) is a post-operational decision that can affect the sizes of fish ultimately sampled from commercial fisheries (Catchpole et al., 2014). Both market forces and regulation often contribute to size-selective discarding (Aarts and Poos, 2009), which can influence the length-at-age similarly to gear selectivity. Some popular assessment models enable the estimation of retention curves to approximate the discarding process. However, this estimation requires observations of discarded fish or the imposition of strong assumptions about the discard process itself.

4.2.3. Spatial patterns in size/age

Spatial patterns in observed length-at-age can arise even when the population exhibits a single common growth pattern across regions, but each region contains different segments of the population's length or age structure. These spatial patterns can be attributed to fish behaviors (McDaniel et al., 2016) or exploitation patterns (Frank et al., 2018). High and low regional levels of exploitation with size-selective gear can result in different observed lengths-at-age by area. Patterns in larval settling influence the observed regional length-at-age. Perhaps the most common cause of these observational spatial patterns is fish movements. Size-based movements (Nøttestad et al., 1999) are thought to arise from the differential swimming speeds associated with size, thus influencing observed lengths-at-age across migratory space. Age-based seasonal migrations were documented by McDaniel et al. (2016) in Pacific sardine (*Sardinop sagax*), influencing regional ages-at-length. Similar to migration, age-specific habitat selection, possibly due to maturation, can make some segments of the age structure less available to fishing gear (Tao et al., 2021). Spatially explicit assessment models with an estimation of movement or potentially estimating the appropriate form of availability in a fleets-as-areas model have been shown to approximate these observational spatial effects (Lee et al., 2017).

4.2.4. Sampling

Size-selective onboard or dockside sample collection can affect the observed length-at-age similar to size-selective gears. In some instances, researchers try to address the lack of data on certain poorly observed size classes (often the largest sizes) by adding additional samples to understand length-at-age better (Xu et al., 2016). In other instances, sampling strategies are used to improve estimates of length-at-age for stratified estimation methods. Random sampling, fixed sampling, and proportional sampling strategies have been studied via simulations, with methods fairing differently depending on factors such as fishery selectivity, sample size, and life history characteristics (Goodyear, 2019; Schemmel et al., 2022). Several growth estimation methods (Goodyear, 2019; Lusk et al., 2021) have been developed specifically for these stratified designs (Kimura, 1977). Although sampling methods can affect all length-at-age estimation methods, random-at-age methods are the most likely impacted as age selection strategies are less often used (Piner et al., 2016; Lee et al., 2017).

4.2.5. Measurement error

Measurement errors can occur in both age estimates and length measurements. Aging error is generally regarded as the larger of the two sources of errors. Not all structures used to age fish are confirmed to produce annual rings, and the interpretability of these structures can be quite variable (Cailliet et al., 2001; Campana, 2001). For example, age determination becomes difficult when annual marks are reabsorbed in fin spines (Rodríguez-Marín et al., 2012). Multiple methods have been developed to quantify the reliability/interpretability (aging error) for stock assessment purposes (Richards et al., 1992; Punt et al., 2008). However, in most applied situations, this interpretability is not the true error; instead, it is usually some measure of reader-to-reader variability. Even when that measure of interpretability is measured against the true age, correcting observed ages requires an estimation of the population age structure or an assumption that the observed ages are a random sample of the population.

Although generally thought less critical, error also exists in the length measurement (Page et al., 2004). In some examples, this error increases with fish size and may be related to human tendencies to prefer recording digits ending in 0 or 5 (Bunch et al., 2013). The issue of measurement error will be compounded when measurements are taken on difficult-to-measure fish (e.g., live releases for tagging, large sharks released alive) or when measurements are taken under challenging conditions (e.g., rough seas or using flexible tape measures). In cases where lengths are a conversion from one metric to another, such as fork length to total length (Hansen et al., 2020), the conversion itself can introduce additional variability and bias. Even when fish length is measured accurately, post-mortem shrinkage has been shown to occur in relatively short periods (Morison et al., 2003; Morison, 2004). Measurement and aging errors likely impact all length-at-age estimation methods.

Estimation of the growth process may include fitting data that requires conversion from one type of size measurement to another (e.g., length from weight). This conversion adds an additional source of variability and modeling complexity. The variability in the weight-length relationship, which includes similar components as those described for length-at-age, also needs to be incorporated into all the model components. Some models also fit weight frequency data, often in conjunction with length composition data, but the variation in the weight-length relationship is often overlooked, causing a biased estimation of the variation in the length-at-age. Conversion from processed weight to whole weight, a common practice for some species, adds additional variation to the estimation process.

4.2.6. Learned behaviors/avoidance

A nearly completely overlooked bias in some length-at-age estimation methods (and stock assessments in general) is a behavioral adaptation to fishing. Behavior has been described as a combination of innate (hard-wired) and learned responses to environmental stimuli (Kieffer and Colgan, 1992). Experimental evidence suggests that fish behaviors can be modified by repeated exposure to environmental stimuli. Yue et al. (2004) demonstrated that fish learn from impacts with fishing gears, and long-term memory of that event leads to avoidance behaviors. Similarly, largemouth bass (*Micropeterus salmoides*) have demonstrated lure avoidance through experience-based learning rather than from conspecifics mimicking (Louison et al., 2019). Learned behaviors are likely an age-based process because the number of experiences leading to learning will likely increase with age. Other age-based patterns, such as age-related habitat choices (Tao et al., 2021) or movements (McDaniel et al., 2016), may be learned rather than innate behaviors. If the learned responses (e.g., avoidance) lead to a lower probability of capture, then assumptions about the representativeness of random-at-length data are in question.

5. How influential is growth on assessment results?

Before moving to estimating the growth process, it may be helpful to investigate its influence on assessment models (e.g., Wang et al., 2015; Stawitz et al., 2019; Correa et al., 2021) to help assess what might be a 'reasonably accurate' representation. In integrated population dynamics modeling, the growth process is linked to all other processes and data. However, to characterize its influence on assessment results, we are simplifying this complexity into the specific subunits of the model that are likely the most directly influenced by length-at-age estimates. Length-at-age most directly influences the assessment model through 1) converting weight into numbers and vice versa, 2) its contribution to the production function, and 3) modifying fits of size composition data. Relatively simple sensitivity diagnostics can help gauge the magnitude of assessment errors resulting from each growth process misspecification (see an example of each misspecification applied in Appendix A).

5.1. Converting weight into numbers and vice versa

Most integrated stock assessment models are formulated in terms of numbers of fish at each modeled age, but the catch is often recorded in weight. The total catch in weight needs to be converted into numbers-at-age in the age-structured models. The conversion is done through a series of population dynamic equations, including the selectivity curve, the growth curve (length-at-age relationship), the length-weight relationship, and the observed catch composition (assuming here it is size composition). If the growth process is misspecified, the incorrect numbers of fish are removed from the population, which will bias estimates of derived quantities. Indices of abundance are also often recorded in biomass and have to be scaled to the numbers in the stock assessment model. Similarly, the management quantities are often specified as biomass and will be biased because the numbers-at-age often have to be converted back into some form of a population biomass measure (e.g., spawning biomass, maximum sustainable yield). We generally believe that for size classes when fish are growing, there is usually adequate information about length-at-age. However, it may be common that the length-at-age of the old fish is misspecified due to the low number of specimens and the difficulty in distinguishing growth zones in the otoliths of older fish. Because old fish often make up a small proportion of the catch and the biomass, the misspecification of growth in terms of converting numbers into weight and vice versa may be a relatively minor impact compared to the way the growth process interacts with other model sub-units. One exception is that, in an unexploited population, old individuals make up a larger proportion of the population. Therefore, estimates of depletion may be more impacted by bias in the length estimates for old individuals.

5.2. Production function, estimation of absolute abundance, and management quantities

The growth process also informs yield-per-recruit, which is a tradeoff between growth and natural mortality and, in conjunction with the stock-recruitment relationship, controls the shape of the production function. The absolute abundance, depletion, and productivity determine how the catch impacts the population and therefore determine how the model fits to the indices of relative abundance (Figure 1). Misspecified growth will result in biased estimates of absolute abundance or depletion level. The absolute abundance and productivity also determine the maximum sustainable yield and related management quantities. Therefore, a misspecified growth process will also bias estimates of MSY-based management quantities. A key question to assess is how much misspecification of the growth process affects absolute abundance estimates.

5.3. Fits to length composition and estimation of absolute abundance

Misspecification of the growth process may most influence the fit to length-composition data and its effect on estimates of abundance. The decline in the proportion of numbers-at-age in the population resulting from a combination of natural and fishing mortality is mediated through the selectivity to produce the catch-at-age (Figure 2). The smaller the proportion of old fish observed in the catch, given the selectivity curve and natural mortality, the higher the estimated exploitation rate. In models fit to length composition data, the catch-at-age is translated into catch-at-length through the estimated lengths-at-ages. So, the fewer large fish in the catch, the higher the exploitation rate. Estimates of exploitation rate and catch correlate to population abundance. Because the catch is usually assumed to be known with little or no error, if the growth curve is misspecified, the estimates of population abundance will also be biased. The effects of misspecification of the growth process are not confined to large fish, as fits to intermediate lengths will also influence estimates of abundance. The role of intermediate sizes is more difficult to conceptualize and may be less influential. However, these considerations should be evaluated for each specific situation.

5.4. Length-structured models

Prior discussions have focused on the influence of the growth process on age-structured models, with emphasis on those that fit length composition data. Although beyond the scope of this work, length-structured models are also used for stock assessment (Punt et al., 2013). Those models are particularly used in situations where aging is impossible or when the fishing mortality significantly changes the length-at-age distribution (i.e., it is not normally distributed due to high fishing mortality and/or minimum legal size). In length-structured models, misspecification of the growth curve (e.g., the length transition matrix) can also influence the productivity of the stock and the fits to the indices of relative abundance and length composition data. Age and length-structured models or hybrids (McGarvey et al., 2007; Methot and Wetzel, 2013; Punt et al., 2013) are impacted similarly.

6. Methods of estimation

Several decisions need to be made about the methods used to estimate the growth process and those decisions will be influenced by the available data, the complexity of biological variation and sampling biases, and consideration as to what is a reasonably accurate representation. The two basic decisions about methods are the functional forms of the growth process and its variability (structural choice) and the statistical methods (procedural choice) used to estimate it (Francis, 2016).

6.1. Structural decisions

One would think that the choice of the functional form of the growth process would be the simplest and most biologically based decision in applied work. In contrast, the types of biological variability to be estimated may be a somewhat more complex choice. Despite theoretical work suggesting that the VBGF may not always be the most appropriate functional form (Day and Taylor, 1997), a recent review of published growth studies (196) found that the VBGF is by far the most commonly used growth model (Flinn and Midway, 2021). Other popular functional forms included the three-parameter Gompertz model and the three-parameter logistic model. Newer growth models that explicitly consider the cost of reproduction have also been proposed (Minte-Vera et al., 2016). Undoubtedly, even more forms will be proposed and available for consideration. Several authors have made a case for some form of model averaging or multi-model inference (Katsanevakis, 2006) because the preferred functional form by model selection criteria (e.g., AIC) may not always provide the most accurate predictions of length-at-age (Thorson and Simpfendorfer, 2009). However, Vincenzi et al. (2020) argued that with good data, the predicted length-at-age might not be functionally different when estimated using different approaches. It is also not clear how model averaged length-at-age estimates could be used in some popular stock assessment model packages. Examination of data, data fit and realism of results across spatial and temporal scales are important and should guide these structural choices.

The dominance of the VBGF for applied work is in part rooted in both tradition and the current limitations in choices of functional forms supported by widely used assessment packages. Issues related to assessment model support will likely diminish with the development of the next generation of assessment models (Punt et al., 2020), with more open code facilitating inclusion and experimentation with alternative functional forms. Perhaps the larger issue in applied assessment is the general practice of ignoring biological variability in the length-at-age (Lorenzen, 2016). This reluctance may be due to data limitations or estimation complexity as much as the availability of these features in assessment packages. Assessments often ignore variability in all life history traits and implicitly account for the error in other components of the model. This practice causes either additional observational error, process variability in recruitment, or selectivity. It is often unclear how this practice has influenced assessment results (Maunder and Piner, 2017).

6.2. Procedural decisions

After deciding on the functional form of the growth process and what variability to include, the next decision is what method will be used to estimate it. This research area has seen the development of a host of new statistical methods to estimate length-at-age. The different procedures are usually developed in response to specific sampling biases, improved statistical methods, or to make use of alternate forms of data. We divide the methods into external estimation (the estimation is done external to the assessment model and results brought into the model) and internal estimation (the estimation is done as part of the assessment model itself).

6.2.1. External estimates

Most length-at-age estimates are derived from standalone methods. These approaches often are designed to account for at least one of the observational biases, forms of system variability, or types of data that can be used. They generally solve their specific issues by making a set of assumptions; thus, each approach may be good for one situation and inappropriate for another. Knowledge of the potential data biases is needed to evaluate which approach, given its assumption, may be most appropriate. The studies available are too many to summarize here. However, we give a few examples of approaches designed to solve some of the complex issues described in Section 4 or use data described in Section 3.

6.2.1.1. Length-only methods

There are many methods for estimating length-at-age using length-frequency data (Schnute and Fournier, 1980; Mildenberger et al., 2017), with the Multifan program (Fournier, 1990; Fournier et al., 1998) perhaps being the best known of the statistically rigorous approaches. The use of lengths only has not been without criticism (Wang, 1994), as the reliability of asserting an age with length-only data becomes more difficult as the growth slows and the modal structure becomes less apparent. Even younger ages can be difficult to determine as spawning seasons become more diffuse (Batts et al., 2019). As with all methods, careful consideration of the assumptions of that method should be made. For example, Wang and Somers (1996) described an alternative method to estimate growth using length frequency for a short-lived prawn dealing with protracted spawning. However, the method overcomes the bias due to protracted spawning by assuming a known maximum size at recruitment.

6.2.1.2. Methods that deal with selectivity bias

Because bias caused by size selection in fisheries has been known for more than 100 years, methods that attempt to account for length-based selection are perhaps the most common. A seldom used but innovative approach described by Taylor et al. (2005) accounted for size-selective gears. Their method, however, must assume strong information on the fishing history and selectivity shape. The use of random-at-length data has also been shown to account for size selectivity but at the cost of approximately knowing the age structure of the sampled population (Piner et al., 2016).

6.2.1.3. Methods that use length-stratified samples

The advantage of stratifying samples used to estimate length-at-age is ensuring good coverage of all sizes of fish. Several methods have been developed using these length-stratified samples (Perreault et al., 2020). However, the same issues related to assumptions about gear selection and spatial availability will apply.

6.2.1.4. Methods incorporate aging error

Cope and Punt (2007) demonstrated a method incorporating aging error that assumes knowledge of the population's age structure and reader-to-reader ageing precision using random effects methods to estimate length-at-age. As with methods that use knowledge of the age-structure of the population, any age-based biases that affect the representativeness of the age structure may bias estimates. As the approach assumes random-at-age, length-based sampling issues will also affect the estimates.

6.2.1.5. Meta-analysis

Meta-analytical methods have been used in fisheries to estimate various life history characteristics (Thorson et al., 2014). They have been used specifically to estimate individual growth variability (Pilling et al., 2002), variability in growth between populations of a species (Helser and Lai, 2004), and estimate growth across closely related taxa (Helser et al., 2007). For applied work, the advantage of these methods is to improve parameter estimation for units with weaker data by borrowing information from the more data-rich populations. The estimation procedure used to estimate the length-at-age relationship will be subject to the same biases associated with that method, and improvements due to borrowing information will be only as good as the representativeness of those populations for the unit of interest.

6.2.1.6. Methods incorporating covariates

Estimating the length-at-age relationship has included other explanatory variables such as water depth, spatial location, and cohorts (Helser et al., 2007; Kimura, 2008). The evaluation of covariates is often for larger ecological questions; however, it could be helpful for applied assessment where observations are sparse. In those cases, the covariate may help inform the estimate. However, in those situations where there is enough information to explore covariates, there was likely enough information to estimate length-at-age without the covariate. Perhaps, covariates may be most useful in forecasting future changes in growth in response to hypothesized changes in the environment.

6.2.1.7. Methods that combine multiple data types

We normally think of integrating multiple data types as the exclusive purview of the integrated population dynamics model, but several approaches have been developed to use multiple data types to estimate growth. Several papers have been developed that integrate the direct observation of growth from tagging and direct observations of length-at-age from paired age-length data (Eveson et al., 2004; Aires-da-Silva et al., 2015; Scherrer et al., 2021). Much like other growth estimation methods, specific sampling biases and biological sources of variability may still need to be addressed and may differ among the different data sets used in the analysis.

6.2.1.8. Back calculation methods

When paired age and length samples are particularly sparse, back-calculated lengths-at-age are sometimes used to estimate the growth process. Back-calculation typically involves establishing a relationship between fish size and otolith size and subsequently using that relationship to predict a younger fish size than observed. Often done to fill in missing ages, it has also been used to create repeated measures on the same fish. Jones (2000) developed methods accounting for the lack of independence of the repeated measures, and Francis (1990) created a review of available estimation methods and caveats.

6.2.1.9. Random-at-length methods

Although treating the paired age and length data as random-at-length is less commonly used, random-at-length estimation procedures are not affected by length sampling biases. Some evidence suggests that estimates of individual variability are improved when paired age-length data is treated as random at length (Piner et al., 2016). Lee et al. (2019) showed that age sampling biases that are not properly accounted for will cause biased growth estimates. As lengths are conditioned on the ages of the population, this approach needs an estimate of the age structure of the population. Although approximate methods were developed (Piner et al., 2016), this approach depends on a good approximation of the population age structure and has generally been constrained to use within the population dynamics model (see Section 6.2.2).

6.2.1.10. Empirical transition matrices/age-length keys

Although these approaches are not used to estimate the growth process, they are observed measures of the age distribution for a length or the length distribution for an age (less often). In applied work, these approaches are most commonly used for converting length composition into age composition, which is then used in the assessment model. Empirical approaches do not need to assume some functional relationship between length and age and are unaffected by selectivity issues in the conversion when only used to represent the fishery/survey unit. Ailloud and Hoenig (2019) provide a good overview of both forward (estimate ages for a length) and inverse (estimate lengths for an age) keys, as well as a method to combine both. Much like with growth estimation methods, this approach has a larger literature background that we can present here: an example is Babyn et al. (2021), who provided methods for estimating spatial keys. In this paper, we lump this method with empirical weight at age (discussed below 6.2.2.2) as empirical approaches.

6.2.2. As part of the dynamic model

6.2.2.1. Internal

The growth process is increasingly estimated as part of the integrated population dynamic model (Zhu et al., 2016). In theory, estimation inside the assessment model offers many clear advantages over external methods. Integrated population dynamics models can incorporate many (if not all) data types and potentially draw information from indirect sources, such as the linkage between catch and indices via the production function (Sippel et al., 2017). Additionally, incorporating the growth process estimation as part of the assessment model may provide a better estimate of the total assessment uncertainty. The most often cited advantage of estimating length-at-age in these models is that they can estimate the relevant systems and observational processes needed to match both random-at-age and random-at-length assumptions. Spatial availability and age-based effects can be separated from length-based gear and sampling selection (Lee et al., 2017; Piner et al., 2018). Aging error and random-at-length data are most adeptly handled inside the population model as an estimate of the population age structure can be combined with measures of aging precision. In a separate application, Stewart and Piner (2007) used known age samples as data to estimate aging bias. Integrated assessment models can also incorporate (or estimate) much of the biological variability, such as individual, sexual dimorphism, and temporal variability. However, spatial patterns in the growth process and movement of fish with those patterns from one area to another are still somewhat of an unknown problem.

Despite the obvious advantages of estimating length-at-age as part of the assessment model, many applied assessments still specify this process based on external estimates. Although the external estimates of length-at-age must rely on assumptions that may be estimable in the assessment model, estimating the growth processes as part of the assessment is far from straightforward. The correct observation and system processes need to be estimated. Piner et al. (2018) demonstrated that estimating only length-based selection patterns in a fleets-as-areas model, when gear selection is length-based and availability is age-based, will result in biased estimates of mean length-at-age. In this case the model may incorrectly approximate the age-based availability effect as length-based selection. Care should also be taken when adding additional data sets to the integrated model with the only purpose of better informing growth. These additional data sets require that different model processes (both observation and systems) be estimated linking that data to the dynamics, or bias can be introduced to the dynamics themselves. Lee et al. (2019) demonstrated that conditional age-at-length data (random-at-length) also have direct information on the age structure of the population. If the appropriate age-based observation or systems processes are not estimated (including potentially temporal variability in the growth process), that data provides bias not only on the growth process but the population age structure itself. Additionally, in assessments that estimate the growth process, it is common to assume at least one fleet is represented by an asymptotic selectivity to inform the model that the very largest fish are observed. However, the validity of this assumption may be questionable (Sampson, 2014), and erroneously invoking it may lead to biased results. In information-limited systems, estimating the growth process may lead to convergence issues and will likely increase run times substantially when fitting length composition data. These issues will be even more pronounced when several forms of biological variability in the growth process are also estimated. There is some hope that incorporating random effects into next generation assessment models will aid in the estimation of these time-varying processes.

6.2.2.2. Bypassing the growth process

A number of integrated assessments bypass the growth process for some or all sub-components of the assessment model. In some sense, this could be seen as abandoning the conceptual approach of integrated modeling; however, depending on the circumstance it may provide more reliable assessment results. As already mentioned, empirical age-length keys bypass the growth process in converting observed lengths to ages. The advantage of this empirical approach is that multiple sources of process variability that may be difficult to estimate may be adequately addressed with appropriate samples. Empirical weight-at-age approaches take this concept further by bypassing the length-at-age relationship entirely by inputting observed weights-at-age for each fleet as model structure. Empirical weight-at-age models are age-based (age composition data) and can be combined with the use of age-length keys if composition data are lengths. This approach to dealing with length-at-age has several advantages, especially for highly variable populations. Changes in lengths-at-age due to all relevant biological processes are embedded in the observed weights-at-age and thus do not need to be estimated. Using the empirical approach can also account for some aspects of spatial variation in length-at-age. Because the weight-at-age represents each fleet, size-based selectivity is already incorporated and doesn't need to be estimated (although an age-based selection is needed to link to the underlying numbers-at-age). However, aging error may be problematic in developing the weights-at-age observations because population numbers-at-age are still needed to correctly interpret aging error. This may be a more significant problem for very young fish as the aging error will be unidirectional and compounded if age-related weight gains are rapid. For example, aging errors will lead to some age 1+ fish being misclassified as age 0, which may substantially bias the weight of age 0 fish. In addition, to calculate the total population weight-at-age, one fleet or survey is usually assumed to be representative of the population, and size-selectivity may lead to biased population biomass. Although this approach is intended to be observation-based, some level of imputation/estimation of missing weights-at-age may be necessary. This replacing of missing or unrealistic weights-at-ages might be considered a form of growth process estimation and may be subject to a separate set of assumptions. As with length-at-age estimation, these assumptions will be somewhat subjective; for example, within a cohort, fish may shrink from one year to the next, and decisions about shrinking (Huusko et al., 2011; Bendik and Gluesenkamp, 2013) versus sampling issues may have to be addressed. Finally, because much of the ‘estimation’ in empirical methods is done outside the assessment model, total assessment uncertainty will likely be reduced relative to internal estimation.

7. Good practices

The previous sections have highlighted our understanding of length-at-age and the difficulties in estimating and using this system model process. What follows is our general conclusions (in bullet points) regarding estimating and using the growth process in applied age-structured integrated assessment models. We provide guidance by the same sections as given above and include the underlying rationale. We also provide an additional section on expressing length-at-age uncertainty in the total assessment uncertainty.

7.1. Data - Good Practices

- Include all relevant data when the important sampling biases can be identified and adequately addressed.

Rationale

In principle, increasing the amount and types of data used should add information to the estimation of the growth process and its variability. Different data types have been shown to have better information on either mean length, growth or individual variability, and for different ages. When estimating length-at-age in the integrated assessment model, care should be taken to include only data where important sampling biases are identified and can be adequately addressed. Within the integrated assessment model, unmodelled observational processes will lead to biased estimates not only of the growth process but also the population dynamics. In cases where a single time-invariant growth curve is estimated in the assessment model, consider if adding multiple years of data such as random-at-length is needed as this may greatly increase the amount of observational and systems processes that need estimation.

7.2. Biological variability - Good Practices

- Estimate all relevant biological variability whenever possible, focusing on individual, sex-specific and temporal variability.
- Be explicit about what forms of variability will be subsumed into the individual variability parameters. If the individual variability is specified, care should be taken to match the specified variability with fish growth over the time step interval used in the assessment model.
- When fish growth is rapid and the growth process is estimated inside the assessment model, consider modeling smaller timestep intervals in the assessment.
- Investigate possible spatial variability and if regional growth patterns are found to be important to assessment results consider empirical methods, separate assessments for each area or spatially explicit assessments with regional growth processes.

Rationale

Individual, sex-specific, temporal, and potentially spatial variability are likely sources of biological variability for many stocks. Individual, sex-specific, and temporal variability offer no real impediments to estimation and should be investigated in most assessments. Estimating individual and temporal variability inside the assessment model also offers some advantages with dealing with other forms of biological variability. If individual variability is estimated inside the assessment model, it will likely account for variability from the duration of spawning and growth within the time step interval of the assessment model. For fast growing fish, smaller model time step intervals can reduce the potential errors from continuous growth over the interval. If temporal variability is estimated, it will likely account for variability from spawning timing and fishing induced variability. Spatial variability due to regional growth patterns may present the most problems for the assessment model as a common growth process with inflated individual variability may not provide good predictions of regional length composition. In cases with impactful levels of biological spatial variability, empirical approaches should be considered. If movement between areas is low, separate assessments for each area or spatially explicit assessments with regional growth processes could be considered.

7.3. Sampling biases/observational processes - Good Practices

- When estimating the growth process internally, estimate all the appropriate observational and/or system processes linking data to the estimated dynamics. When using external growth estimation methods, choose the methods that best deal with the important sampling biases.
- As the number of important sampling biases increase, estimate the growth process as part of the integrated model.
- If sampling biases are difficult to address consider empirical approaches.

Rationale

We consider the major sources of sampling bias common to most assessments are gear selectivity, length stratified sampling, spatial patterns, and measurement error. More than one form of sampling bias can exist for any particular data set and may change over time. Observational processes may need to be estimated in age, length, or both to deal with the sampling bias. Because aging error requires some measure of population age structure, it will be most easily handled as part of the assessment model. As more and different types of important sampling biases are identified, estimate the growth process as part of the integrated assessment model or consider empirical approaches.

7.4. Influence of growth on assessment - Good Practices

- Investigate how length-at-age estimates will influence the assessment models results through sensitivity diagnostics. The greater the influence of misspecification on results, the more accurate the estimates of both the growth process and its biological variability will be needed.
- The growth process is likely to be influential when composition data are lengths and they are used to provide information about abundance. In cases when growth is uncertain and there is other reliable information on absolute abundance, consideration should be given to managing the influence of length-composition data (e.g., data weighting or observational model processes estimated)
- In cases where misspecification of the growth process will affect assessment results but estimation of all relevant variability is not possible, consider empirical methods.

Rationale

The sensitivity of assessment results to the misspecification of the growth process will influence what is considered reasonably accurate in the representation of the length-at-age and its associated variability. A determination of the minimum level of growth process complexity in the stock does not set an upper bound to the level of growth complexity incorporated into the assessment. The maximum level of complexity will likely be influenced by data availability, knowledge of the system, and analyst time. There may also be a cost to the estimation of less consequential processes or variability as it could lead to issues in the estimation of more consequential processes and their variability (e.g., selectivity, M etc.).

For cases where misspecification of the growth process will have limited influence on the estimated dynamics, a time-invariant estimate of length-at-age may be the minimum resolution required to get a reliable assessment result. These situations will likely be when the population scale is not derived from fitting to length composition data. This could occur when a strong production function explains the depletion in an index of relative abundance caused by catch or when an absolute biomass survey is part of the assessment. Reduced model sensitivity to the growth process may be reinforced when catches come from young fish, age composition data are available, or when catches are recorded in numbers rather than weights. Model diagnostics and sensitivity type analyses will be helpful in the impact of the growth process misspecification.

For cases where fitting length composition is used to estimate population abundance, a more accurate and, therefore more complex/complete treatment of the growth process may be needed. This includes accounting for all forms of observational bias and estimating the relevant biological process variability. However, estimating all those observational and system processes may become challenging. Alternatively, empirical methods may be used if appropriate samples are present and with consideration of the issues mentioned.

7.5. Methods

7.5.1. Structural Decisions - Good Practices

- Use the most appropriate functional form for the data with consideration of what the assessment package used will support.

Rationale

Structural decisions about the functional form of the growth process should be made based upon the best evidence but may have to conform to the forms available in the assessment models used. Care should be taken not to use a highly constrained growth model that is not appropriate because the typically abundant data for young fish can control the estimates of mean length-at-age for old fish and the fit to length frequency data represented by old fish (the large lengths) often influences the estimates of absolute abundance.

7.5.2. Procedural Decisions - Good Practices

- In situations where the growth process will not be influential on results an external estimate may be appropriate, but internal estimation should still be considered.
- In complex situations with multiple sources of biological variability and sampling biases, estimate the growth process as part of the integrated assessment model where possible.
- If the growth process is too complex to be estimated as part of the assessment model, consider empirical methods.
- If growth varies by area and movement among areas is low, consider assessing each area separately using the regional growth process or use empirical methods.

Rationale

Although external methods of estimating length-at-age can be used to handle multiple forms of biological variability, internal estimation may be more appropriate for situations where accurate estimates of length-at-age and its variation is needed. Internal estimation will better account for multiple sources of sampling bias and add to the assessment estimate of uncertainty. Estimating temporal variability and individual variability will likely account for other sources like spawning timing and growth during the time step interval of the model. When external estimates are deemed sufficient, use the most appropriate method that deals best with the sampling bias identified. Consider empirical estimates when biological variability is important but too complex to adequately estimate inside the assessment model. Modeling of spatial difference in growth is complicated in age-structured population dynamics models and when movement rates are low it may be adequate to assess each region separately.

7.6. Incorporating uncertainty in the growth process into characterizing assessment uncertainty - Good Practices

- Estimate the growth process as part of the dynamic model.
- All key sources of biological variability should be appropriately accounted for and estimated.
- Consider a more flexible growth form to represent the uncertainty in the growth form beyond the VBGF.
- When the estimates of length-at-age influence model results and the growth process is estimated externally, consider an ensemble modeling approach or a joint prior on the growth parameters to incorporate growth process uncertainty.

- Further research is needed to understand the appropriate approaches to represent uncertainty when using empirical methods.

Rationale

Estimating key biological processes as part of the assessment model will likely provide a more complete estimate of the total uncertainty. This includes all the relevant sources of biological variability. Despite the popularity of the VB growth function, it often is relatively limited in dealing with growth patterns of very young fish, and given the general abundance of young fish samples can result in biased estimates of mean length-at-age for old fish. Developers of the next generation of assessment models should make it a priority to provide more flexible options. As empirical approaches become more popular with integrated assessment modelers, some thoughts should be given to how to incorporate uncertainty in the unmodeled growth processes into the total assessment uncertainty. When growth misspecification is a key source of uncertainty in assessment results and not estimated as part of the assessment model, ensemble approaches or the use of a joint prior on the growth parameters may be needed to incorporate this uncertainty into assessment results. The joint prior accounts for the common correlation between estimates of the asymptotic length and the growth rate parameter.

8. Final Thoughts and Future Research

The general recommendation of this work is to use either empirical approaches or to estimate the growth process and all its biological variability as part of the assessment model. The authors recognize that this is a ‘best case’ recommendation and many (if not most) assessments will not have the complete age data for the empirical approach or the information load to estimate the growth process and all its complexity. Estimation of the growth process will be even more problematic due to likely parameter confounding if good practices recommend estimating other model processes (e.g., M, selectivity etc.) with both flexibility and including process variation.

If information constrains growth process estimation then perhaps the more important question for the typical assessment is what to do if reasonably accurate estimates of the length-at-age or complete age data are not available. Because so many assessments rely on size composition data, more research needs to focus on how best to approach modeling length composition data. This is especially crucial when size composition data are used to estimate abundance, as these models tend to be data rich and information poor. Even in information rich situations, more work needs to be done on the best approaches to deal with the seemingly inevitable misfit to length composition data arising from incomplete growth modeling. The relative roles of data weighting/observation error, estimation of alternative observational processes or alternative modeling approaches (like empirical weight-at-age) should be investigated. This research needs to be done with the understanding that variability in other system processes (e.g., natural mortality) and observation processes (e.g., selectivity) may be more important to estimate.

CRediT authorship contribution statement

Huihua Lee: Writing − original draft preparation, Writing − review & editing preparation, Analyses, Visualization.

Kevin Piner: Conceptualization, Writing − original draft preparation, Writing − review & editing preparation.

Mark Maunder: Writing − review & editing preparation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

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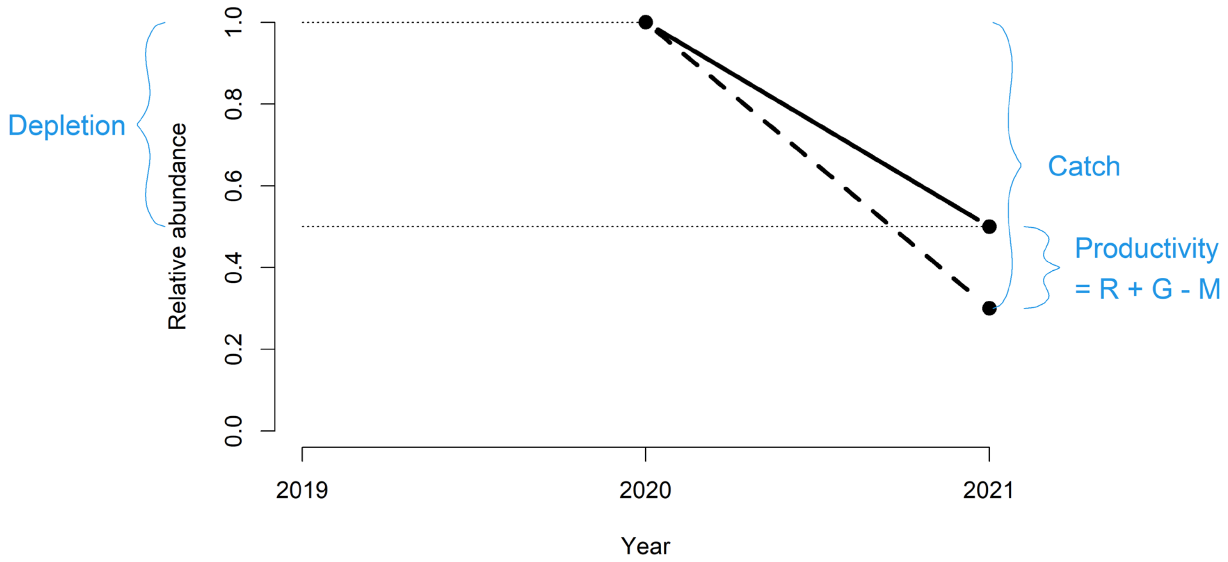

Figure 1. Illustration of the absolute abundance information contained the systems model process of the production function, catch, and index of relative abundance. The solid and dashed lines represent depletion in the presence and the absence of biological processes, respectively. *R* is recruitment, *G* is growth, and *M* is natural mortality.

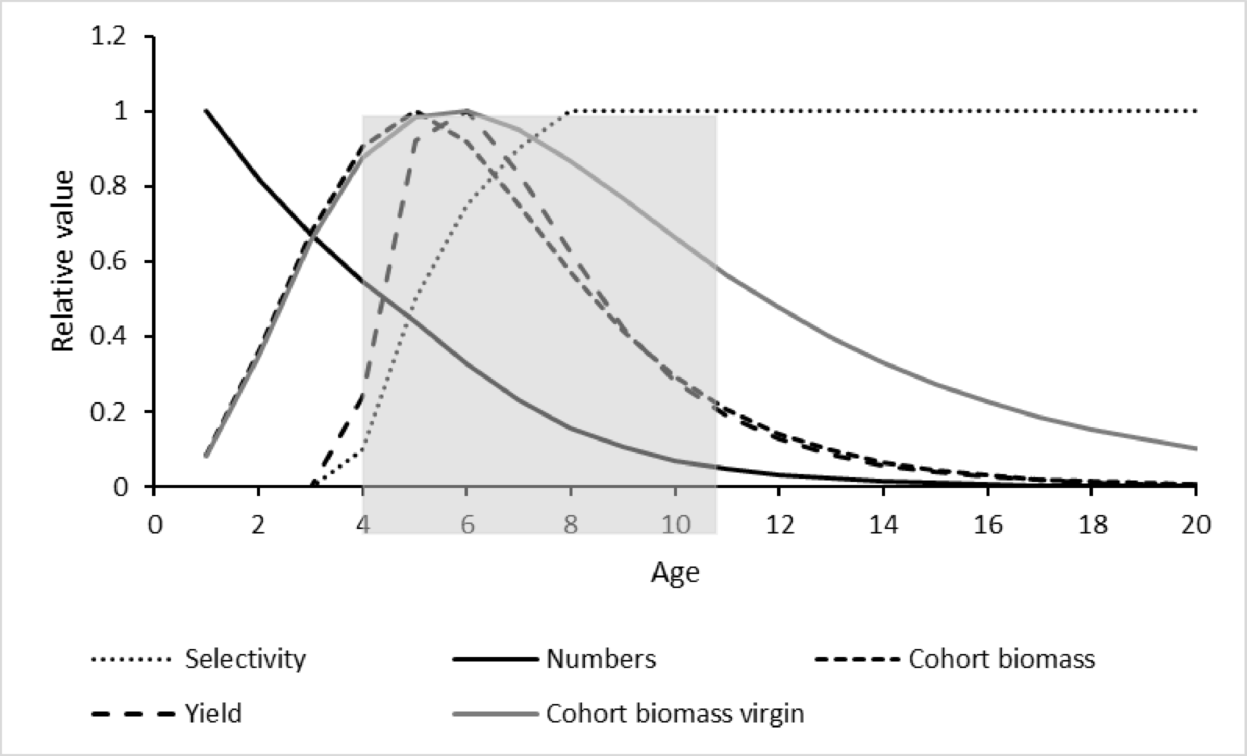

Figure 2. Illustration of the roles of both systems model and observational processes on the abundance of a cohort and catch-at -age.

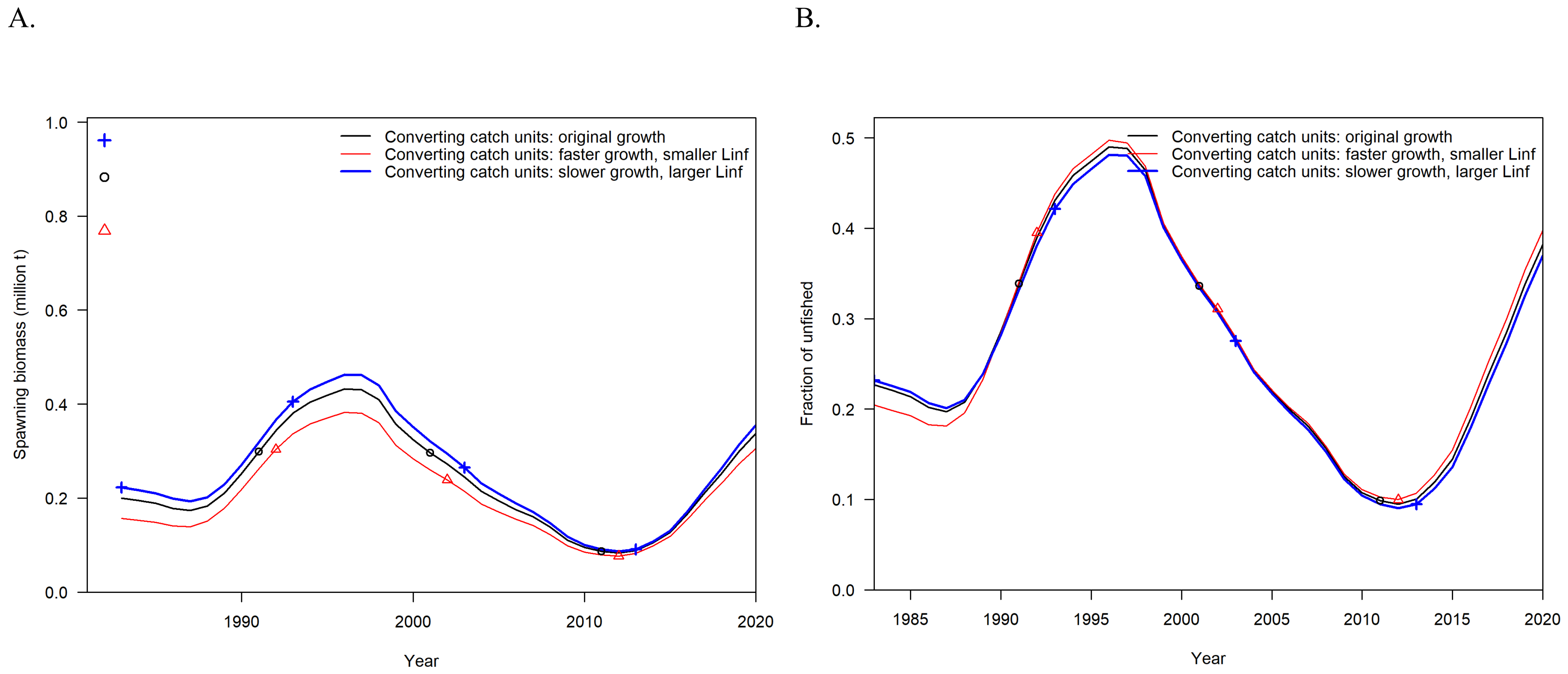

Figure 4. Sensitivity diagnostic results from misspecifying the growth process on converting numbers into weight in the Pacific Bluefin tuna stock assessment. Panel A is spawning biomass and B is fraction unfished (depletion level). The three lines in each plot are ASPM models specifying faster growth and smaller Linf (red), original length-at-age (black), and slower growth and larger Linf (blue). Unfished spawning biomass estimates for model runs are given in panel A as triangle, circle and cross, respectively.

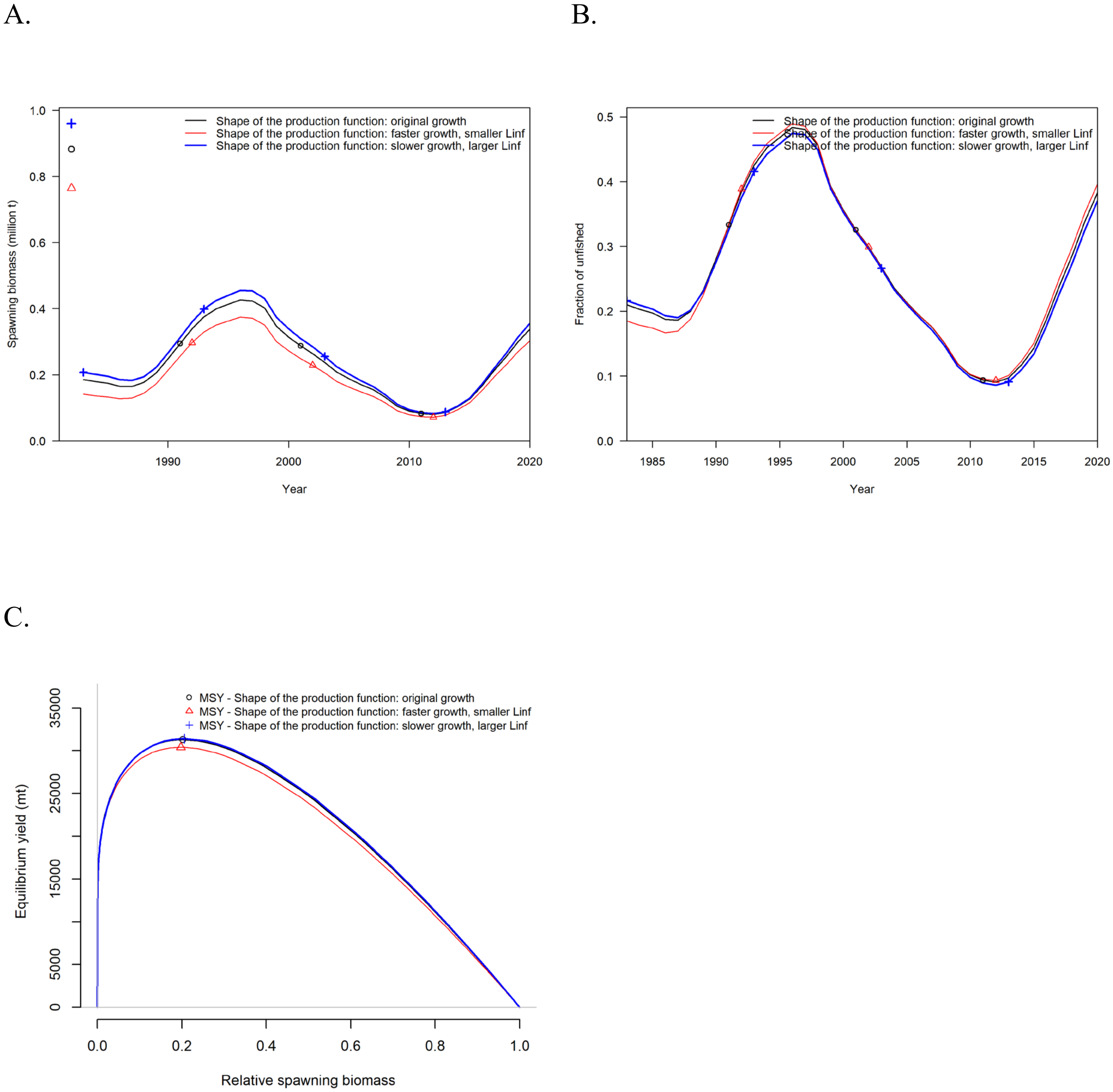

Figure 5. Sensitivity diagnostic results from misspecifying the growth process on the shape of the production function and calculation of biomass from model estimates of numbers-at-age. Panel A is spawning biomass, B is fraction unfished (depletion level), and C is the production curve. The three lines in each plot are ASPM models specifying faster growing and smaller Linf

(red), original length-at-age (black), and slower growth and larger Linf (blue). Unfished spawning biomass estimates for model runs are given in panel A as triangle, circle and cross, respectively.

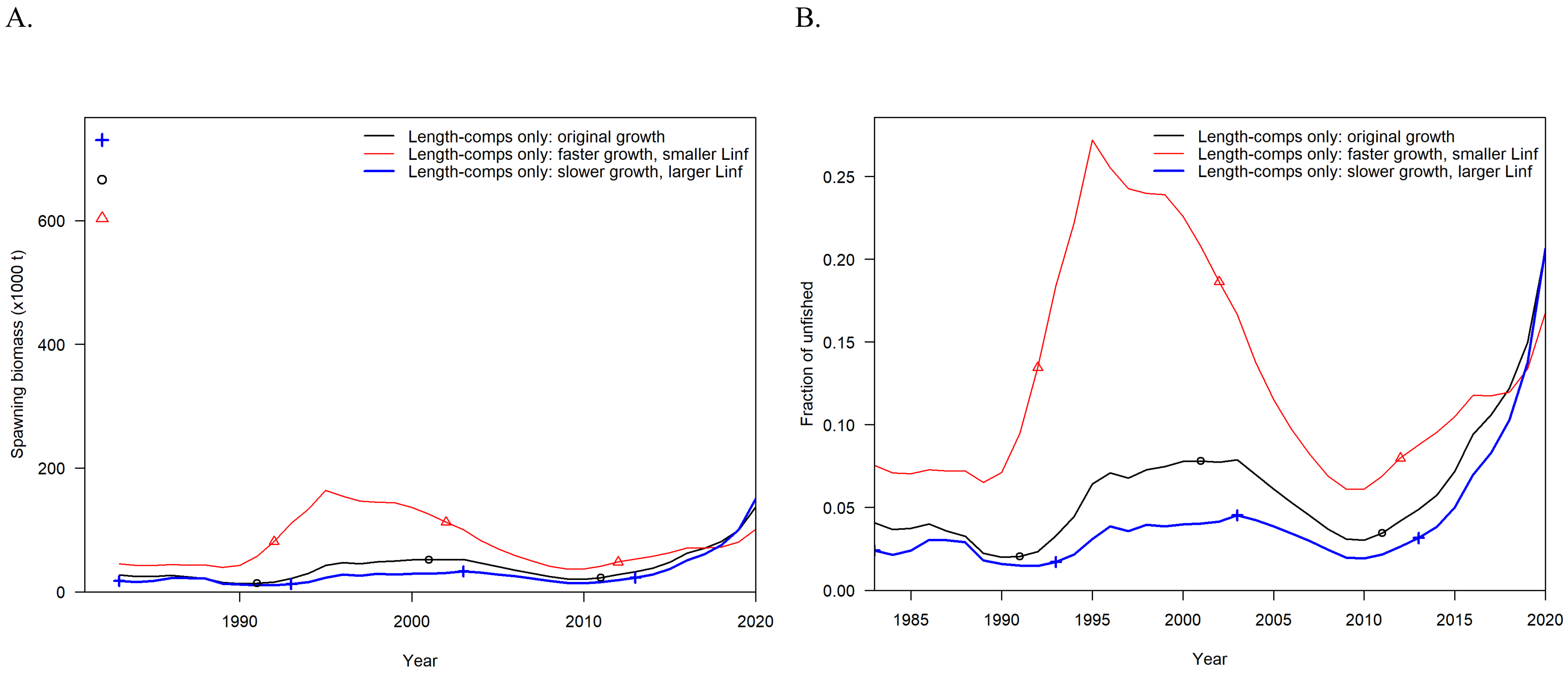

Figure 6. Sensitivity diagnostic results from misspecifying the growth process in the Pacific Bluefin tuna stock assessment that fits to length compositions only. Panel A is spawning biomass and B is fraction unfished (depletion level). The three lines in each plot are the models specifying faster growth and smaller Linf (red), original length-at-age (black), and slower growth and larger Linf (blue). Unfished spawning biomass estimates for model runs are given in panel A as triangle, circle and cross, respectively.