Early life history growth in fish reflects consumption-mortality tradeoffs

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Abstract

Growth models used for adult fish are often inadequate to model early larval growth in the first weeks and days of life. However, growth rate during the earliest life stages may be a significant factor in determining survivorship, foraging success, transport, and settlement patterns. We fit growth models for the larvae of twelve grouper and snapper species from the families Lutjanidae and Serranidae, and conducted a survey of published early life growth models to explore growth pattern differences between taxonomic groups. The majority of these papers contained only larval stages but a few included early juvenile stages as well, so from here on we use the term "early life" to refer to larval and early juvenile stages. The majority of the grouper and snapper species are best represented by models with exponential growth patterns, which fits into the results from the literature survey. The surveyed growth literature included 31 papers which provide 94 models spanning 17 different fish families. In a meta-analysis of the growth models from the surveyed literature, exponential growth models were more often used for the early life of demersal fish, whereas linear growth models were more often used for the early life of pelagic fish. These results may indicate that early life growth patterns depend on the risk abatement strategies of each taxa.

Key words:

early life history, growth models, length-at-age, risk-mediation

1. Introduction

Early life stage survivorship is an important factor affecting population dynamics of exploited marine species. Larval fish must grow through a "window" where vulnerability to predators is high (Cowan et al. 1996, Meekan & Fortier 1996, Hinrichsen et al. 2002). After larvae reach a threshold length, the risk of predation decreases (Cowan et al. 1996). There are other motivations for understanding growth in larval fish. Hjort’s "critical feeding period" hypothesis posits that the end of yolk reserves is followed by a critical first feeding period in which larval fish must find food or die (Hjort 1914). Success in that first feeding may be due to hydrodynamic constraints and thus related to larval size (China &Holzman 2014). Finally, models of larval connectivity also require accurate models of early life stage growth to interpret length-based sampling data and understand migration behavior. Thus, larval growth is a key factor in determining predation mortality, starvation mortality, and spatiotemporal patterns of recruitment, all of which contribute to fisheries production and population viability.

Nevertheless, in many applications it is common to ignore deviations from predicted growth rates during the brief larval period. The ubiquitous von Bertalanffy growth function accurately describes growth across a wide range of taxa because growth rates are determined by predictable physiological relationships. Failure of the von Bertalanffy model to represent larval growth can be traced to the theoretical description of growth by von Bertalanffy (1938, 1951). He suggested that the growth in fish could be viewed as the difference between organic synthesis and destruction (eq 1).

$$\frac{dw}{dt} = HS - kw \qquad \text{Eq. 1}$$

The growth of a fish is represented as a change in weight per unit time (dw/dt). Von Bertalanffy proposed H and k as anabolic and catabolic coefficients and he suggested that synthesis and destruction were limited by the surface area for resorption of nutritive material (S) and by the weight of the organism (m), respectively. In answer to a criticism by Beverton and Holt (1957) concerning the anabolic term, Pauly (1981) suggested that respiration rate is limiting to growth, and that S should be viewed as a function of gill area instead of gut area. Thus, under isometric growth, surface area increases with the square of body length while weight increases with the cube. Scope for growth is therefore limited by a 2/3 power relationship that results in an asymptotic weight (eq 2).

$$\frac{dw}{dt} = Hw^{2/3} - kw \qquad \text{Eq. 2}$$

This offers a nearly universal growth model for fish, particularly when an additional allometric parameter is included. However, it also predicts the fastest growth rate at small body sizes, which is often not the case for larval fish. The poor fit of the von Bertalanffy growth model at larval ages is evidenced by an *ad hoc* additive factor t_0(the theoretical age at length zero), which is found in this familiar equation (eq 3).

$$W_t = W_\infty \left(1 - \exp\left(-K(t - t_0)\right)\right)^3 \qquad \text{Eq. 3}$$

A small negative value for t_0 is required to account for the fact that the von Bertalanffy growth model underestimates the rate of larval growth.$W_\infty$is an asymptotic weight and K is the growth constant. Larvae have been shown to have an exponentially increasing rate of growth, although this varies by species and larval condition (Jenkins 1990). Pauly (1981) maintains it is because larval fish can respirate through their skin and are therefore not bound to the 2/3 power relationship that limits the scope for growth at older ages. This continues until scale development thickens the skin. Thus, models with an initial exponential growth period that transition to asymptotic growth may better represent growth patterns throughout ontogeny.

Early exponential growth of this form is offered in some alternative growth models. Zweifel and Lasker (1976) showed that both fish egg development and larval growth could be adequately described by Gompertz-style curves (Gompertz 1825). They suggested that both the Laird-Gompertz and Logistic models are better options for fish growth than the von Bertalanffy growth model. These models both contain an initial exponential growth phase followed by an inflection point.

We propose that the exponential family of models may be more appropriate for representing the early life stages of some fish taxa because early growth may reflect feeding rate. Feeding rate could be affected by predation risk mediation. We suggest that the differences in larval and early juvenile growth between demersal/reef associated and pelagic fish may be related to strategies employed in predation risk mediation. Even though risk abatement strategies come into play at juvenile ages, the strong statistical differences in growth patterns between demersal and pelagic taxa at larval ages suggests that larval growth is indicative of the strategy to be employed later during the juvenile stage. Predation risk mediation behaviors establish the tradeoff between growth rate and predation mortality early in life, as younger fish move from safe or invulnerable areas to vulnerable areas to feed. Foraging arena theory articulates this idea (Walters & Juanes 1993, Ahrens et al. 2012). Vulnerable prey exist in the foraging arena and are at risk for predation, while invulnerable prey are in a refuge. The exchange rate between the vulnerable and invulnerable pools impacts the predation rate (Ahrens et al. 2012). Risk averse populations have higher survival but lower fecundity and consumption rates, while risk prone populations have lower survival but higher fecundity and consumption rates, with some optimal balance between the two extremes (Walters & Juanes 1993). Thus, maximum fitness occurs at a feeding time which balances the long-term survival gains with the risk of predation (Walters & Juanes 1993). Young fish achieve this balance by limiting their time outside of the refugia (Walters & Juanes 1993). As they get older, they become less vulnerable to predation and can spend more time feeding, potentially following an exponentially increasing rate of growth. Young fish that have access to refugia may therefore have the option to grow more slowly during the earlier and more vulnerable life stages, whereas young fish without access to refugia may need to grow more quickly to ensure that they are out of the gape range of predators.

A second possibility that would explain differences between groups showing exponential and linear growth relates to the seasonality of spawning. Seasonality impacts environmental factors driving larval development, such as temperature and productivity (Hernandez &Castro 2000). Larval growth rates may be highly sensitive to variable environmental conditions. Some variants to the von Bertalanffy growth model account for this by incorporating sinusoidal terms at seasonal or daily periodicities (Somers 1988, Campana & Hurley 1989, Campana & Jones 1992). A cohort that is born in the spring would show a growth pattern beginning on the upswing of a sinusoidal curve, whereas a cohort that is born in the fall would be on the downswing of a sinusoidal curve. We explore whether differences in growth patterns between taxa could be due to the seasonality of their spawning.

This study aims to determine the length at age relationship during early life history for twelve species of grouper and snapper. We chose these species based on the availability of length at age data in literature, and fit the data with the Von Bertalanffy, logistic, exponential, Laird-Gompertz, and linear growth models in order to determine which model best represented grouper and snapper growth during early life. These models have been used in the past to model early life history growth in different species (e.g. Houde & Schekter 1981, Jenkins & Davis 1990, Benetti 1992, Rae et al. 1999, Lozano et al. 2012, Luthy et al. 2005, Jayadi et al. 2017).

In addition to evaluating the best models to represent grouper and snapper larval growth, we conducted a meta-analysis examining previously published larval growth models from a wider variety of taxa in order to place the grouper and snapper growth models into a broader context. The meta-analysis examines whether differences in early life history growth patterns exist between taxa, and whether these differences relate to risk abatement feeding strategies. The null hypothesis for the meta-analysis is that early-linear and early-exponential growth models are independent of the fish family. We will make the case that changes in larval growth rate are indicative of risk abatement strategies during early life history.

2. Methods

2.1 Species-Level Analysis

We chose twelve grouper and snapper species based on the availability of early life growth data in literature and the temperatures at which those studies were conducted. The twelve species, study locations, spawning seasons, and publications in which they appear can be found in Table 1. Five of the species chosen were from the Gulf of Mexico and Caribbean, while the other seven are from studies that were conducted between 23-31°C. This is within the temperature range found in the Gulf of Mexico. Larval staging studies provide length at age data. Fish were reared under conditions similar to their natural environment. Typically, age is known and larvae are measured to obtain length data at designated time or stage intervals (e.g. Powell &Tucker 1992, Drass et al. 2000, Song et al. 2013). Thus, all species chosen for the species level analysis contained length at age data for similar temperature ranges. Models were then fit to the length at age data.

INSERT TABLE 1 HERE

2.2 Model Fitting and Selection

Larval fish are typically measured using standard length (Moser1996, Kahn et al. 2004). Standard length is measured from the snout to the base of the tail, which is the hypural bone or caudal peduncle (Kahn et al 2004). Body length is the same as standard or notochord length for larval fish (Drass et al 2000). Notochord length is the measurement from the snout to posterior end of the notochord (Drass et al 2000). After we extracted length at age data from the literature, we fit five types of growth models to each set of data: a linear model, an exponential model, a logistic model, the von Bertalanffy growth model, and a Laird-Gompertz growth model. The generic forms of each of these growth models are in Table 2. These five growth models for each species can be split into two groups, the exponential family and the linear family. The exponential family is comprised of the logistic, Laird-Gompertz, and exponential models, which have an increasing rate of growth at small body sizes. The linear family includes the linear and von Bertalanffy growth model.

INSERT TABLE 2 HERE

We fit the models with least squares regression using the R statistical software (R Core Team 2015, Maechler et al. 2017). Non-least squares regression with a Gauss-Newton fitting algorithm was used for all five model types for species with sample sizes of 15 or greater, with the exception of Longtooth Grouper. (R Core Team 2015, Elzhovet al. 2016). For the other species, we used a Levenberg-Marquardt algorithm to fit all models other than linear (Elzhov et al. 2016). Both types of algorithms yield identical results for large data sets.

Choosing a model from competing options requires a model selection criterion that assesses model parsimony. AICc is a corrected version of the Akaike Information Criterion, AIC, and has been shown to have a smaller bias than AIC. In some cases, it provides better model selection when the sample size is not large (Hurvich & Tsai 1991). We calculated the AICc for each model using the AICcmodavg package (Mazerolle 2016). Some species had multiple models with low AICc scores, so the models were ranked. In order to rank models, we calculated delta scores from the AICc according to the method outlined in Burnham and Anderson (2004). In this method (Eq. 5), the winning AIC score is subtracted from each of the other scores to produce a delta value for each model (Burnham & Anderson 2004). Delta values less than 2 represent substantially supported models that are not considered different from the most parsimonious model. A model with a delta score between 4 and 7 is less supported, and a model with a delta score greater than 10 is considered to have no support (Burnham &Anderson 2004). In order to use this method, we substituted AICc scores for AIC scores, so delta values were produced by subtracting the minimum AICc score from each of the other AICc scores. In Equation 4, AICi is the Akaike Information Criterion evaluated for model i, and AICmin is the minimum AIC value of all of the models. This means that the model for which AIC is lowest will have a delta value of zero (Burnham & Anderson 2004).

$$\Delta\, AICc_i = AICc_i - AICc_{min} \qquad \text{Eq. 4}$$

2.3 Meta-analysis

In order to place the grouper and snapper growth patterns into context with respect to other taxa, we conducted a survey of larval growth literature to examine the variability among published growth models for a variety of families (Supplemental Table 1). The majority of these studies are studies in which larvae are caught during a sampling trip and measured, then aged later using an otolith age-interval relationship (e.g., Lozano et al. 2012). To demonstrate these previously published models, we generated random test age data for 100 fish by generating 100 random ages between 1 and 40 days and plotted the models by family (Supplement Figures 1 through 6). We chose this age range to agree with the range of ages used earlier in the examination of grouper and snapper growth patterns. Ninety-four models for a range of species were included, some of which came from the same papers but refer to different cohorts, year classes, or locations. Length at age was plotted to visualize growth patterns within families.

In order to assess whether there was a difference in larval growth patterns between larval fish of demersal and pelagic taxa, we performed a chi-squared analysis. We gathered length at flexion and length at the transformation data from larval to juvenile stages for as many species as possible in the meta-analysis. The majority of these flexion and transformation lengths, as well as spawning information when possible, were found in Richards (2006), with remaining species filled in from larval fish guides, and technical memos on early life stages (Auditore et al. 1994, Moser 1996, Fahay et al. 1999, Richards 2006, Ré & Meneses 2008, Froese & Pauly 2019). We sorted each individual model into a demersal or pelagic group, and performed one tailed t-tests comparing flexion lengths and transformation lengths between the two groups. We gathered spawning dates and seasons for as many species in the meta-analysis as possible and we assigned the taxa a binary score for each season based on the spawning time of that fish: 1 for presence of spawning and 0 for absence of spawning. We calculated the total number of spawning presences in each season for demersal and pelagic groups, and then compared them using a chi-squared test. We also found spawning seasons for the grouper and snapper species in this paper (Hussain & Abdullah 1977, Jeyaseelan 1998, Richards 2006, Gaspare & Bryceson 2013, Bertucci et al. 2015, Froese & Pauly 2019).

3. Results

3.1 Grouper and Snapper Species-Level Analysis

In this analysis of grouper and snapper, the group of models with an exponential basis describes growth in early life better than the models with a linear basis. Model parameters and their associated p-values for all models and all species can be seen in Table 3 and the plots of all five models for every species can be found in Figure 1. Upon comparing AICc scores (Table 4), several patterns emerged in relation to both the winning scores and the order in which the delta values ranked under the winning scores. Ten of the twelve grouper and snapper species had a model with an exponential basis as their most parsimonious model, and in eight of those cases, multiple models with an exponential basis were shown to be at least somewhat supported. In contrast, only two species, Dusky Grouper and Gray Snapper, had the linear model as the most supported model, and in both of these cases, the second-best supported model was still relatively well supported and was from the exponential family of models. The model with the lowest AICc score for the most species was the exponential model. The von Bertalanffy ranked last or second to last in every species, and had delta scores indicative of completely unsupported models in all but two cases.

The demersal species Yellowtail Snapper, Sevenband Grouper, Mangrove Snapper, and Malabar Grouper were all best represented by the exponential model (Table 4, Fig 1). For Sevenband Grouper, the linear model was also supported with a delta AICc score less than 1. Four more demersal species, Nassau Grouper, Longtooth Grouper, Red Snapper, and Brown Spotted Grouper, were best represented by either the Laird-Gompertz or logistic model, with another model from the exponential family coming in second. Nassau Grouper and Longtooth Grouper showed two supported models, as they were best represented by the Laird-Gompertz model but also had the logistic model with a delta AICc score under 1 (Table 4, Fig 1). Of the remaining four species, two species were clearly represented by a single exponential-family model with no secondarily supported models. Blacktip Grouper showed a low AICc score for only the logistic model, while Red Grouper showed a low AICc score for only the exponential model (Table 4). Only two species, Dusky Grouper and Gray Snapper, had the linear model as the winner, with Dusky Grouper having a well-supported exponential runner up and Gray Snapper having well-supported logistic and Laird-Gompertz runners up (Table 4, Fig 1). Although the linear model is the most parsimonious for Dusky Grouper, it is clear from the plot that the growth pattern looks most similar to the von Bertalanffy. Dusky Grouper is the only species to exhibit a growth plateau in the time period covered by the data.

INSERT TABLE 3 HERE

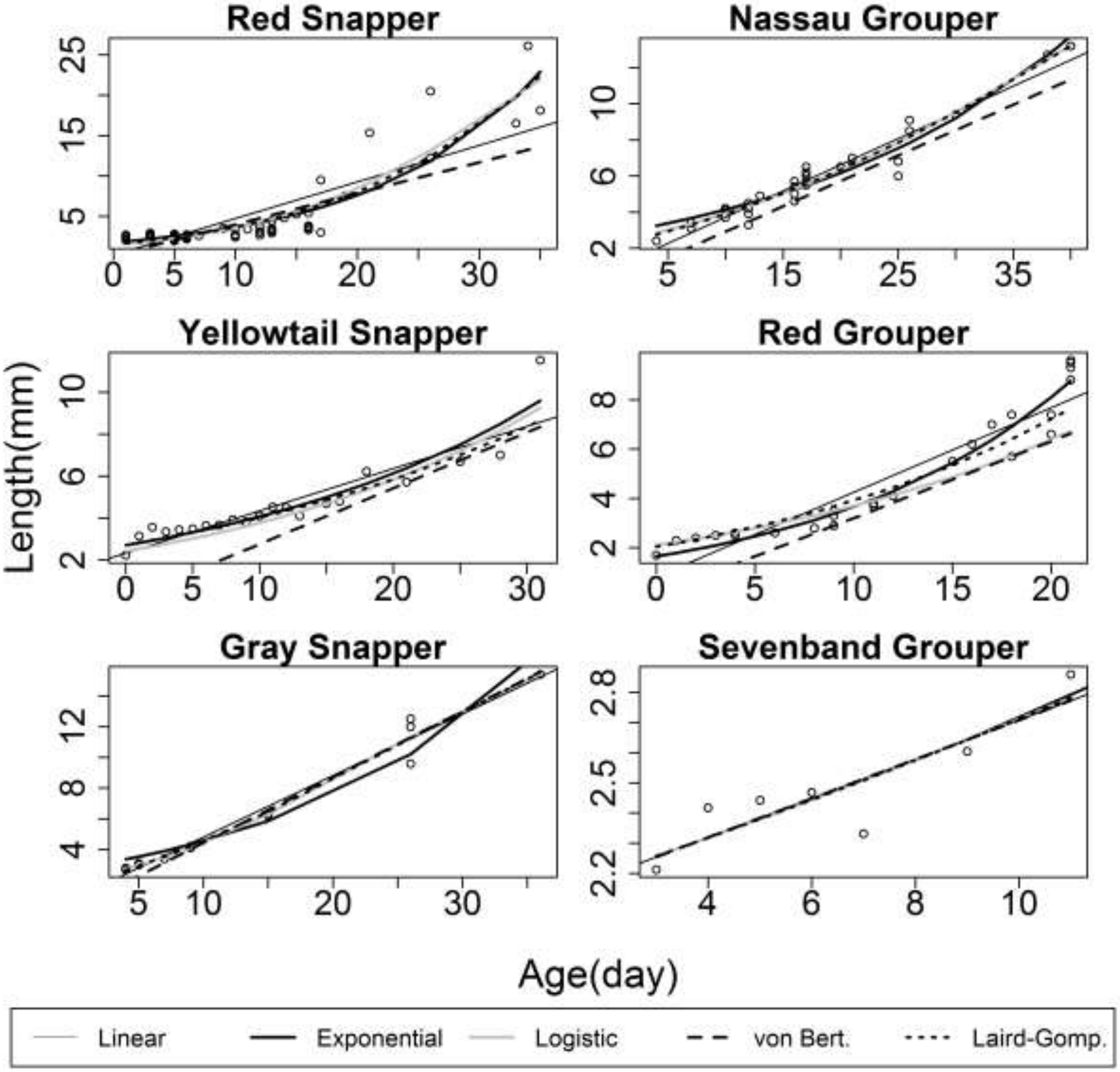

Figure 1: Fitted growth models plotted with length at age data.

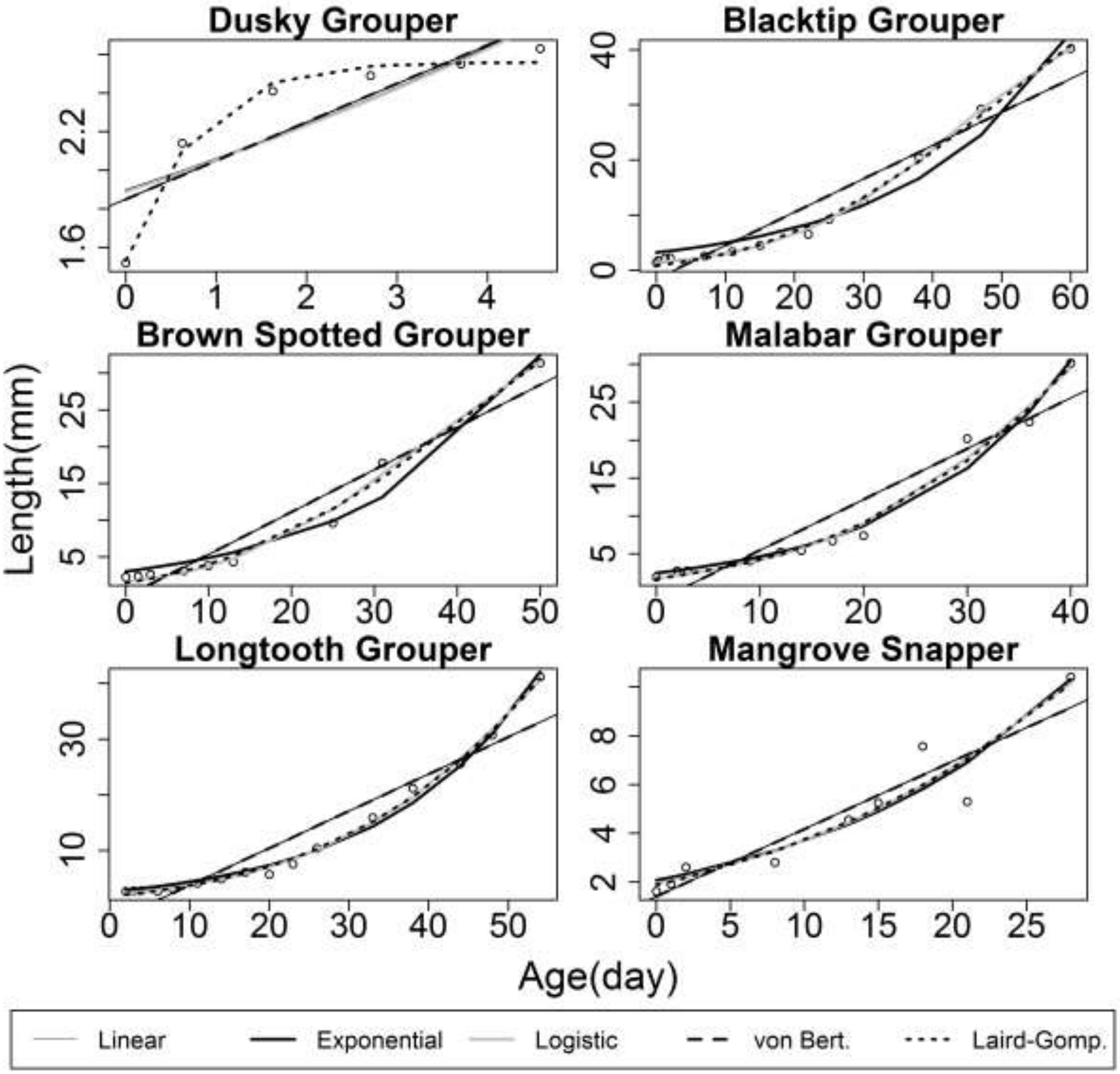

Figure 1 continued: Fitted growth models plotted with length at age data.

3.2 Grouper and Snapper: Seasonality and Spawning

The two species which had the linear model as the most parsimonious, Dusky Grouper and Gray Snapper, also have similar spawning seasons. They both begin spawning in the summer and continue spawning through fall, while the other grouper and snapper species we were able to find spawning information on showed different spawning patterns (Table 1). There are four patterns evident: 1) spawn starting in spring, 2) spawn year-round, 3) spawn from fall through winter, and 4) spawn from fall to winter and again from spring to summer (Hussain & Abdullah 1977, Jeyaseelan 1998, Richards 2006, Gaspare & Bryceson 2013, Bertucci et al. 2015, Froese & Pauly 2019).

INSERT TABLE 4 HERE

3.3 Meta-analysis

The surveyed growth literature included 31 papers which provide 94 models spanning 17 different fish families from around the globe. The majority of the ninety-four models used for the meta-analysis can be sorted into six families; and upon examination of the plotted models, marked differences between taxa emerged (Supplemental Plots 1-6). Demersal taxa included Serranidae, Notothen-iidae, Gadidae, Scianidae, Lutjanidae, Mugilidae, and Pleuronectidae. Pelagic taxa included Scombridae, Myctophidae, Istiophoridae, Carangidae, Coryphaenidae, Pomatomidae, and Xiphiidae. Forage taxa included Engraulidae, Clupeidae, Osmeridae. The models found for two demersal families, Gadidae and Pleuronectidae all had an exponential basis, as did additional models found for Lutjanids (Supplemental figures 2, 4, and 5).The Gadidae family contains Cod and Haddock, and the Pleuronectidae family contains flatfish such as Flounder and Sole. All models found for the Scombrid family, which contains Tuna, were linear (Supplemental Figure3). Other large pelagic taxa showed both linear and exponential patterns, but linear was more common. The chi-squared value calculated to compare the 59 models from demersal and pelagic families was well below the threshold needed to reject the null hypothesis that linear and exponential models were split between pelagic and demersal taxa proportionally (Table 5). When models including juvenile snapper in addition to larval snapper were added, the difference between demersal and pelagic families was still significant (Denit & Sponaugle 2004). Thus, of the ninety-four previously published models examined here, the models of early life growth in demersal taxa tended to have an exponential growth pattern, while models of early life growth in pelagic taxa tended to have a linear basis. Interestingly, previously published larval growth models of forage fish from the Engraulid and Clupeid family fell between these two groups, with a mixture of linear based and exponential based models in both families (Supplemental Plots 1 and 6).The one tailed t-tests comparing flexion lengths and transformation lengths in demersal and pelagic fish showed that demersal fish had significantly longer flexion lengths ($p = 0.037$) than pelagic fish, and that demersal fish had longer transformation lengths ($p = 0.074$) as well. There were no significant differences in seasonality of spawning patterns between the demersal and pelagic groups in the meta-analysis using the chi-squared analysis.

4. Discussion

Groupers and snappers were best modeled with equations having an exponential basis and we found a significant difference between the early life growth patterns of pelagic fish and demersal fish. These findings suggest that demersal and reef associated fish like Grouper, Snapper, Cod, Haddock, and flatfish follow an exponential growth curve early in life while pelagic fish like

Tuna more often follow a linear growth pattern. This supports our suggestion that differences in larval and early juvenile growth between taxa may relate to predation risk mediation tactics. As described in Foraging Arena Theory (Walters & Juanes 1993, Ahrens et al. 2012), predator-prey interactions are restricted in space and time, and prey are partitioned into vulnerable and invulnerable pools. Young fish may spend large amounts of time in refugia for protection from predation, but this limits the area in which they can feed (Walters & Juanes 1993, Ahrens et al. 2012). There is therefore an inherent trade-off between growth rate and predation risk (Walters & Juanes 1993, Ahrens et al. 2012). Exchange between these two pools impacts the overall predation rate and the form of the density dependent predation functional response (Walters & Juanes 1993, Walters &Christensen 2007, Ahrens et al. 2012). Increasing the exchange rate between pools allows for more feeding and faster growth but also increases risk of predation. Refugia can be thought of as microhabitats, and these may be present in differing degrees in the pelagic and demersal environments. Refugia may be available to both pelagic and demersal fish, but early life stages of demersal and reef associated species may have more refuge available in the form of physical structure and hiding places, whereas pelagic fish may have to rely on microhabitats such as the centers of schools. We suggest that demersal and reef associated species may rely on structural refugia to help mediate predation risk and gradually take on more risk and increase consumption as they increase in size, resulting in early exponential growth. In contrast, young pelagic fish that rear without available structural refugia need to grow large quickly to get out of the gape range of predators, or develop swimming skills quickly to increase mobility. The results of the flexion and transformation t-tests are consistent with this idea. They indicate that demersal fish may take longer to achieve these early life history milestones than pelagic fish. The refugia may allow them the luxury of remaining at small sizes for longer amounts of time, as they have the ability to utilize these hiding places until they grow out of the gape range of their predators. This could suggest that the life history strategies to either favor slow growth in protected habitat or fast growth in exposed habitat may manifest in the larval stage. Forage fish had a mixture of growth models in the linear and exponential families, which could indicate that the degree of refuge present is greater than that offered to other pelagic fish in the form of schooling, but lower than that available to demersal and reef fish that can utilize structural refuge. We found a strong distinction between the growth rates of pelagic and demersal fish, even at larval ages, which suggests that growth rate may show a low degree of plasticity throughout the early life history and is indicative of risk mediation strategy among juvenile fish. Even if larvae are not using these mediating strategies in the same way that older juveniles or adults would, the pattern supported in our results would still suggest that differences in larval growth patterns are tied to risk mediation behavior and may be indicative of physiology implications later in life. Unpublished predictive models indicate that larvae of different taxa inhabit different areas in the water column (Vasbinder, unpublished data). Larvae have been demonstrated to have the ability to make choices surrounding their movement behaviors, so we do not believe that the idea that larval stages can exhibit risk mediation behavior is out of the question (Codling et al. 2004).

The second possibility that we considered may be impacting growth rate was the seasonality of spawning time, which changes the season in which the young fish are growing and feeding. While there was not a clear case for this hypothesis in the meta-analysis, comparing spawning dates for grouper and snapper species did support this possibility as Dusky Grouper and Gray Snapper, which showed strong support for the linear family of growth models, have similar spawning seasons in the summer and fall (Richards 2006, Bertucci et al. 2015). It is possible that the statistical correlation between spawning date and the probability of exponential growth was not seen in the meta-analysis due to the wide breadth of climatic regimes included. Since the environmental factors at play in each of the ninety-one models included in the literature survey are different, these factors could impact the results of the survey. There are some other subtleties in the change in growth rates over age, such as discontinuous growth, that were not considered in the present study. Step changes between ontogenetic states can be represented by discontinuous growth functions. In fish and invertebrates whose growth rates are limited by oxygen availability, changes in habitat, feeding ecology, or physiology reveal strategies to decrease basal metabolic oxygen needs and increase scope for growth (Pauly 2010).

The impact of temperature on growth cannot be neglected in this conversation on comparative growth modeling. Temperature is one of the most important drivers of larval development before first feeding. It impacts several of the parameters commonly used in growth models including instantaneous growth rate, initial length or length at t=0, predicted length at metamorphosis, time to metamorphosis, and time of first feeding (Dulcic 1997, Pepin 1991, Benoit et al. 2000, Castello & Castello 2003). Temperature impacts on larval growth have been demonstrated in many species (Dulcic 1998, Folkvord 2004, Gracia-Lopez et al 2004, Fielder et al. 2005). In one study, differences in growth in sardine larvae from different locations were suggested to be the result of temperature (Dulcic 1995). All data for the grouper and snapper species modeled in this paper came from temperature ranges similar to the Gulf of Mexico. The literature surveyed in the meta-analysis includes a group of climatologically diverse regions, from the North Pacific and North Atlantic, to the Indian Ocean and the Gulf of Mexico. In an extensive review of marine fishes, Pepin (1991) concluded that increasing temperature led to increases in daily development rates and daily mortality rates, but led to decreases in stage specific mortality at very young stages. Higher temperatures also resulted in faster hatching, faster transition out of the yolk-sac stage, higher mean growth rates and increased growth rates of post larvae (Pepin 1991, Benoit et al. 2000). Thus, we should anticipate temperature differences between regions to impact the rate at which young fish grow and reach major developmental landmarks, but the shape of the growth curve may remain the same. Temperature can also change within a spawning season, which may lead to differences in growth rates among consecutively spawned cohorts (Hernandez &Castro 2000). If temperature increases throughout a season, young fish that grow in a linear growth pattern may begin to grow faster in response to temperature changes, leading to the appearance of an exponential growth pattern instead.

Surveying a wide range of published studies on early life growth and using those results to draw conclusions about larvae in the field raises another question: to what extent can laboratory reared larval growth studies inform our understanding of larval growth in the sea? This question has been addressed by Pepin (1991), who decided to use only use field studies when gathering development rates for a meta-analysis. Some authors use length at t_0 interchangeably with length at first feeding, and differences in this parameter between laboratory reared and field caught anchovy larvae have been observed (Dulcic 1997). Some growth studies have found that larvae grow faster in the field than in the lab, while others found no difference between wild caught fish and reared fish in their growth studies (Benoit et al. 2000, Jenkins 1987). In this paper, growth models from both wild caught and laboratory reared fish are included, which could be a potential source of error. Variability between models could also be impacted by the way in which length was measured as some studiesin the clupeid family used standard length while others used total length (eg, Geffen 2002, Luthy et al. 2012, Lozano et al. 2012). There is potential for error due to allometric growth, as the difference between standard length and total length increases as fish length increases (Beckman 1948). Another source of error could be the simplifying assumptions we made regarding the mortality regimes experienced by young fish in different stages. Fish undergo qualitative shifts as they grow, and we did not consider discrete changes in mortality regimes as fish participate in ontogenetic movement or behavioral or physiological changes. These are likely species or population specific, but because we were doing a broad survey, we did not fit or plot growth models for different stages. Ricker (1979) proposed the use of a sigmoidal curve called a “Sachs Cycle” (Ricker 1979), and suggested that ontogenetic growth is more accurately modeled in stages separated by “crises”, such as metamorphosis. A variety of other co-variates such as yolk-sac duration or pigmentation onset may have an effect as well. Although all co-variates cannot be eliminated, the highest source of error in this meta-analysis is that fitting techniques are not standardized between authors. Thus, while co-variates such as temperature, stage specific mortality, and measurement techniques cannot be controlled, controlling co-variates to this level of precision would be unwarranted by the level of precision in the data that comes from comparing models fit by different authors. Even with imperfect data sources, valuable observations of patterns between taxa can still be recognized and demonstrated statistically.

This paper also explores whether the same models can be used for young fish and adult fish. The von Bertalanffy growth model is typically the growth model chosen to represent adult fish growth, and has even been found to describe fish growth in fresh water taxa better than polynomial functions with three and four parameters for fish aged one year and older (Chen et al. 1992). The von Bertalanffy growth model ranked lowest or second lowest in all twelve grouper and snapper species, indicating that models commonly used to predict age or length in adult fish may not be appropriate for use with early life history data. At young ages, growth is not constrained by gill surface area in the same way that it is in adults (Pauly 1981). Young fish are not limited to an ever-diminishing scope for growth as is suggested by the von Bertalanffy growth model, so the linear or exponential growth models may be more appropriate. In addition, models that include exponential growth and an inflection point may be appropriate for early life stages because they allow the growth to slow as the fish approaches metamorphosis (e.g. logistic, Laird-Gompertz, generalized von Bertalanffy growth function), at least for demersal species that are able to regulate predation risk via a consumption-mortality trade off behavior. As fish get older, other growth models become more appropriate than those used in early life. For example, our meta-analysis showed that Scombrid fish in early life grow linearly. One of those linear models is for Bluefin Tuna (Malca et al. 2017). Juvenile Bluefin Tuna display a saturating growth rate at large sizes, eventually showing von Bertalanffy growth from one year onward (Cort 2002, Megalofonou et al. 2002). Thus, the appropriate growth model for Bluefin Tuna changes throughout ontogeny (Cort 2002, Megalofonou et al. 2002, Malca et al. 2017). These findings support the idea that early life history growth is best represented using different growth models than adult growth.

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Table 1: Species used, temperature or location of study, and citation for study

Species	Region/Temperature	Sample Size	Location Published	Spawning Season
Red Snapper *Lutjanus campechanus*	Texas and Alabama	n=96	Drass et al. (2000) Fish. Bull. (Wash. D. C.) 98(3): 507-527.	Late spring through fall with peaks in the warmer months (Richards 2006)
Nassau Grouper *Epinephelus striatus*	Grand Cayman	n=32	Powell & Tucker. 1992. Bull. Mar. Sci. 50(1): 171-185.	December to February at full moon (Richards 2006)
Yellowtail Snapper *Ocyurus chrysurus*	Florida Keys, FL, Corpus Christi, TX (27-28C)	n=21	Riley et al. 1995. Fish. Bull. (Wash. D. C.) 93: 179-185	Throughout the year with local peaks (Richards 2006)
Red Grouper *Epinephelus morio*	Gulf of Mexico (22-24C)	n=28	Colin et al. 1996. ICLARM Conf. Proc. 48: 399-414.	April through May in the Gulf of Mexico (Richards 2006)
Gray Snapper *Lutjanus griseus*	Florida Keys (26-28C)	n=15	Richards &Saksena. 1980. Bull. Of Mar. Sci. 30(2):515-522.	Summer through fall with a peak in August in some areas (Richards 2006)
Sevenband Grouper	Korea (25C)	n=7	Song et al. 2013. Dev.Reprod. 17(4):	Unknown

Epinephelus septemfasciatus			369-377.	
Dusky Grouper *Epinephelus marginatus*	Southeastern Adriatic (23C)	n=6	Glamuzina et al. 1998. Sci. Mar. 62 (4): 373-378	Spawning aggregations begin in May through July with spawning from late June to late September with peaks in July and August (Bertucci et al. 2015)
Blacktip Grouper *Epinephelus fasciatus*	Japan (22.5-27C).	n=13	Kawabe & Kohno. 2009. Fish. Sci. 75:1239–1251.	Unknown
Brown Spotted Grouper *Epinephelus tauvina*	Kuwait (22.6-30.4C)	n=9	Hussain & Higuchi. 1990. Aquaculture 19: 339-350	October through February and April through July (Froese and Pauly 2019)
Malabar Grouper *Epinephelus malabaricus*	Taiwan (26.1-26.88C)	n=11	Leu et al. 2008. J. Mar. Biol. Ass. U.K. 85: 1249-1254	September through February with a peak in November (Gaspare and Bryceson 2013)

Longtooth Grouper *Epinephelus bruneus*	Jeju Island, Korea (24.5-25.5C)	n=16	Song et al. 2005. Aquacult. Soc. 36(2):209-216	Unknown
Mangrove Snapper *Lutjanus argentimaculatus*	Panay Island, Central Philippines (28-31 C) Note:(28-31C) is for spawners, larvae were kept in ambient flow through tank in which all fish died by end of study	n=9	Emata et al. 1994. Aquaculture 121:381-387	Year round spawning (Froese and Pauly 2019)

Table 2: General Forms of Common Growth Models

Growth Model	General Form
von Bertalanffy	$Length = L_{\infty}(1 - e^{-K(age - t_0)})$
Linear	$Length = m * age + intercept$
Logistic*	$Length = \ Asym/(1 + e^{\frac{t_{mid} - age}{Scal}})$
Exponential**	$Length = Lo * e^{C * age}$
Laird-Gompertz***	$Length = Lo * e^{G * (1 - e^{-\alpha * age})}$

*Asym is the asymptote, t_{mid} is the age that corresponds to the inflection point of the curve, and Scal is a scale parameter

** L_o is the length at first feeding and C is the specific growth rate

*** Zweifel and Lasker 1976, as cited in Palomera et al 1988. L_o is the length at time 0 (first feeding), alpha is the instantaneous rate of decrease in growth rate, and G is a ratio of instantaneous growth rate to alpha.

Table 3: Model Parameters and associated p-values*** indicates highly significant p-value at <0.001,** indicates significance at 0.001,“**.**” indicates significance at 0.05.

“~” indicates lowest AICc

Red Snapper	**Coefficients**	**P-values**
Linear	$Length = 0.453 * age + 0.186$	Slope: < 2e-16 *** Intercept: 0.602
Exponential	$Length = 1.75 * e^{(0.0736*age)}$	Lo: < 2e-16 *** C: <2e-16 ***
Logistic ~	$Length = 40.1/(1+e^{(\frac{33.1-age}{9.96})})$	Asym: 0.00181 ** t_{mid}: 2.97e-07 *** Scal: 3.95e-13 ***
von Bertalanffy	$Length = 2.57 * 10^{+03} * (1 - e^{(-1.51 * 10^{-04} * (age - - 3.06 * 10^{-01}))})$	Linf: 0.993 K: 0.993 t0: 0.829
Laird-Gompertz	$Length = 1.52 * e^{8.39 * (1 - e^{(-0.0111 * age)})}$	G: 0.136 Alpha: 0.246 Lo: 6.86e-10 ***

Nassau Grouper	**Coefficients**	**P-values**
Linear	$Length = 0.291 * age + 0.800$	Slope: < 2e-16 *** Intercept: 0.00593 **
Exponential	$Length = 2.77 * e^{(0.0401 * age)}$	Lo: <2e-16 *** C: <2e-16 ***
Logistic	$Length = 24.5/(1+e^{(\frac{37.4-age}{16.5})})$	Asym: 0.003358 ** t_{mid}: 0.000809 *** Scal: 1.08e-06 ***
von Bertalanffy	$Length = 4.72 * 10^{+03} * (1 - e^{(-5.97 * 10^{-05} * (age - - 3.58 * 10^{-01}))})$	Linf: 0.997 K: 0.997 t0: 0.920
Laird-Gompertz ~	$Length = 2.134 * e^{3.31 * (1 - e^{(-0.0200 * age)})}$	G: 0.000121 *** Alpha: 0.0275 * Lo: 5.51e-08 ***

Yellowtail Snapper	**Coefficients**	**P-values**
Linear	$Length\ =\ 0.201 * age + 2.33$	Slope: 1.79e-08 *** Intercept: 5.69e-07 ***
Exponential ~	$Length =\ 2.71 *\ e^{(0.0408 * age)}$	Lo: 4.79e-12 *** C: 6.65e-11 ***
Logistic	$Length =\ 105/(1 + e^{\left(\frac{82.6 - age}{22.1}\right)})$	Asym: 0.916 t_{mid}: 0.745 Scal: 0.0721 .
von Bertalanffy	$Length\ =\ 4.97 * 10^{+03}\ * \left(1\ - e^{\left(-5.36 * 10^{-05} * \left(age - - 3.46 * 10^{-01}\right)\right)}\right)$	Linf: 0.999 K: 0.999 t0: 0.932
Laird-Gompertz	$Length\ =\ \ 2.72\ *\ e^{8.33 * (1 - e^{(-0.00483 * age)})}$	G: 0.835 Alpha: 0.848 Lo: 3.32e-07 ***

Red Grouper	**Coefficients**	**P-values**
Linear	$Length\ =\ 0.342 *\ age\ +\ 0.829$	Slope: 9.77e-14 *** Intercept: 0.016 *
Exponential ~	$Length\ =\ 1.65 *\ e^{(0.0794 * age)}$	Lo: 1.94e-13 *** C: < 2e-16 ***
Logistic	$Length =\ 103/(1 + e^{\left(\frac{67.4 - age}{17.4}\right)})$	Asym: 0.967 t_{mid}: 0.894 Scal: 0.379
von Bertalanffy	$Length\ =\ 3.63 * 10^{+03}\ * \left(1\ - e^{\left(-8.57 * 10^{-05} * \left(age - - 3.11 * 10^{-01}\right)\right)}\right)$	Linf: 0.999 K: 0.999 t0: 0.912
Laird-Gompertz	$Length\ =\ \ 2.05\ *\ \ e^{10.3 * (1 - e^{(-0.00653\ * age)}\ )}$	G: 0.838 Alpha: 0.852 Lo: 1.01e-05 ***

Gray Snapper	**Coefficients**	**P-values**
Linear ~	$Length\ =\ 0.401 * age +\ 0.795$	Slope: 8.32e-12 *** Intercept: 0.0186 *
Exponential	$Length\ =\ 2.75 * e^{(0.0505 * age)}$	Lo: 1.1e-07 *** C: 2.1e-09 ***
Logistic	$Length =\ 19.8/(1 + e^{\left(\frac{22.9 - age}{10.4}\right)})$	Asym: 5.08e-06 *** t_{mid}: 1.02e-05 *** Scal: 1.77e-06 ***
von Bertalanffy	$Length\ =\ 2.61 * 10^{+03}\ * \left(1\ - e^{\left(-1.65 * 10^{-04} * \left(age - - 3.18 * 10^{-01}\right)\right)}\right)$	Linf: 0.990 K: 0.990 t0: 0.844
Laird-Gompertz	$Length\ =\ \ 1.71 *\ e^{2.82 * (1 - e^{(-0.0425\ * age)}\ )}$	G: 1.09e-08 *** Alpha: 0.00149 ** Lo: 3.78e-05 ***

Sevenband Grouper	**Coefficients**	**P-values**
Linear	$Length = 0.0649 * age + 2.06$	Slope:7.09e-06 *** Intercept:0.00853 **
Exponential ~	$Length = 2.09 * e^{(0.0262 * age)}$	Lo: 2.84e-06 *** C: 0.00695 **
Logistic	$Length = 38.2/(1 + e^{\left(\frac{101 - age}{25.7}\right)})$	Asym: 0.993 t_{mid}: 0.985 Scal: 0.905
von Bertalanffy	$Length = 8.22 * 10^{+02} * \left(1 - e^{\left(-7.92 * 10^{-05} * \left(age - - 3.17 * 10^{-01}\right)\right)}\right)$	Linf: 1.000 K: 1.000 t0: 0.856
Laird-Gompertz	$Length = 2.08 * e^{6.18 * (1 - e^{(-0.00436 * age)})}$	G: 0.98464 Alpha: 0.98511 Lo: 0.00186 **

Dusky Grouper	**Coefficients**	**P-values**
Linear ~	$Length = 0.200 * age + 1.85$	Slope: 0.027840 * Intercept: 0.000336 ***
Exponential	$Length = 1.89 * e^{(0.0823 * age)}$	Lo: 0.00031 *** C: 0.04144 *
Logistic	$Length = 22.5/(1 + e^{\left(\frac{26.0 - age}{10.9}\right)})$	Asym: 0.987 t_{mid}: 0.978 Scal: 0.891
von Bertalanffy	$Length = 4.59 * 10^{+02} * \left(1 - e^{\left(-4.37 * 10^{-04} * (age - - 9.24)\right)}\right)$	Linf: 0.999 K: 0.999 t0: 0.811
Laird-Gompertz	$Length = 1.53 * e^{0.513 * (1 - e^{(-1.53 * age)})}$	G: 0.00104 ** Alpha: 0.00955 ** Lo: 0.00013 ***

Blacktip Grouper	**Coefficients**	**P-values**
Linear	$Length = 0.605 * age - 1.58$	Slope:2.45e-07 *** Intercept:0.306
Exponential	$Length = 3.21 * e^{(0.0433 * age)}$	Lo: 7.42e-05 *** C: 2.59e-08 ***
Logistic ~	$Length = 50.0/(1 + e^{\left(\frac{42.9 - age}{12.0}\right)})$	Asym:2.13e-11 *** t_{mid}:8.43e-13 *** Scal:4.12e-11 ***
von Bertalanffy	$Length = 1.66 * 10^{+04} * \left(1 - e^{\left(-3.66 * 10^{-05} * (age - - 2.62)\right)}\right)$	Linf: 0.997 K: 0.997 t0: 0.336
Laird-Gompertz	$Length = 0.923 * e^{4.62 * (1 - e^{(-0.0286 * age)})}$	G: 7.11e-11 *** Linf:2.24e-05 *** Lo: 0.00419 **

Brown Spotted Grouper	**Coefficients**	**P-values**
Linear	$Length\ =\ 0.577 * age\ - 0.430$	Slope:2.07e-05 *** Intercept:0.745
Exponential	$Length\ =\ 3.03 * e^{(0.0474\ *age)}$	Lo:0.00102 ** C:8.72e-06 ***
Logistic ~	$Length =\ 39.5/(1 + e^{\left(\frac{34.9-age}{11.0}\right)})$	Asym:6.60e-05 *** $\mathrm{t}_{\mathrm{mid}}$:2.86e-05 *** Scal: 0.00015 ***
von Bertalanffy	$Length\ =\ 2.50 * 10^{+04}\ *\ \left(1\ - e^{\left(-2.31\ *10^{-05} * (age - - 0.746)\right)}\right)$	Linf:0.999 K:0.999 t0:0.800
Laird-Gompertz	$Length\ =\ \ 1.47 *\ e^{4.03* (1 - e^{(-0.0286\ * age)}\ )}$	G:1.28e-05 *** Alpha:0.0146 * Lo: 0.0259 *

Malabar Grouper	**Coefficients**	**P-values**
Linear	$Length\ =\ 0.670 * age\ - 1.24$	Slope:7.11e-06 *** Intercept:0.44
Exponential ~	$Length\ = 2.47 *\ e^{(0.0629 * age)}$	Lo:7.29e-05 *** C: 9.14e-08 ***
Logistic	$Length =\ 57.8/(1 + e^{\left(\frac{39.6-age}{11.6}\right)})$	Asym:0.053701 . $\mathrm{t}_{\mathrm{mid}}$:0.003654 ** Scal:0.000538 ***
von Bertalanffy	$Length\ =\ 1.49 * 10^{+04}\ *\ \left(1\ - e^{\left(-4.51\ *10^{-05} * (age - - 1.86)\right)}\right)$	Linf:0.998 K:0.998 t0:0.512
Laird-Gompertz	$Length\ =\ \ 1.72 *\ e^{5.80* (1 - e^{(-0.0169\ * age)}\ )}$	G:0.0468 * Alpha: 0.2148 Lo:0.0204 *

Longtooth Grouper	**Coefficients**	**P-values**
Linear	$Length = 0.666 * age - 2.88$	Slope:1.12e-08 *** Intercept: 0.0815 .
Exponential	$Length = 2.65 * e^{(0.0512 * age)}$	Lo:2.33e-09 *** C:1.59e-14 ***
Logistic	$Length = 96.1/(1 + e^{\left(\frac{58.8 - age}{15.3}\right)})$	Asym:0.000387 *** t_{mid}:9.78e-08 *** Scal:6.63e-10 ***
von Bertalanffy	$Length = 1.56 * 10^{+04} * \left(1 - e^{\left(-4.26*10^{-05} * (age - - 4.35)\right)}\right)$	Linf:0.9974 K:0.9974 t0: 0.0977 .
Laird-Gompertz ~	$Length = 1.78 * e^{6.66 * (1 - e^{(-0.0118 * age)})}$	G: 2.39e-05 *** Alpha:0.00238 ** Lo:6.24e-06 ***

Mangrove Snapper	**Coefficients**	**P-values**
Linear	$Length = 0.27717 * age + 1.39778$	Slope:0.000189 *** Intercept:0.047162 *
Exponential ~	$Length = 2.070469 * e^{(0.057342 * age)}$	Lo: 0.000639 *** C:0.000151 ***
Logistic	$Length = 32.981 /(1 + e^{\left(\frac{39.6 - age}{14.3}\right)})$	Asym: 0.677 t_{mid}:0.475 Scal:0.110
von Bertalanffy	$Length = 4.48 * 10^{+03} * \left(1 - e^{\left(-6.19*10^{-05} * (age - - 5.04)\right)}\right)$	Linf:0.999 K:0.999 T0: 0.355
Laird-Gompertz	$Length = 1.88 * e^{5.15 * (1 - e^{(-0.0141 * age)})}$	G:0.5816 Alpha:0.6699 Lo:0.0166 *

Table 4: AICc scores and Delta Scores

Red Snapper	AICc_Scores	DeltAICc
Logistic	368.7	0
Exponential	371.9	3.2
Laird-Gompertz	372.6	3.8
Linear	433.0	64.3
von Bertalanffy	446.4	77.7

Nassau Grouper	AICc_Scores	DeltAICc
Laird-Gompertz	63.1	0
Logistic	63.9	0.7
Exponential	65.7	2.6
Linear	66.8	3.7
von Bertalanffy	104.6	41.4

Yellowtail Snapper	AICc_Scores	DeltAICc
Exponential	49.1	0
Logistic	56.6	7.5
Laird-Gompertz	56.7	7.7
Linear	58.7	9.7
von Bertalanffy	94.3	45.2

Red Grouper	AICc_Scores	DeltAICc
Exponential	51.4	0
Laird-Gompertz	75.5	24.1
Linear	76.7	25.4
Logistic	95.9	44.6
vonBertalanffy	107.9	56.5

Gray Snapper	AICc_Scores	DeltAICc
Linear	37.4	0
Logistic	37.7	0.3
Laird-Gompertz	38.3	0.8
von Bertalanffy	46.1	8.7
Exponential	49.2	11.8

Sevenband Grouper	AICc_Scores	DeltAICc
Exponential	-0.1	0
Linear	0.2	0.3
Logistic	13.9	14.0
Laird-Gompertz	13.9	14.1
von Bertalanffy	14.2	14.3

Dusky Grouper	AICc_Scores	DeltAICc
Linear	15.2	0
Exponential	16.1	0.8
Laird-Gompertz	27.2	12.0
von Bertalanffy	45.2	30.0
Logistic	45.9	30.7

Blacktip Grouper	AICc_Scores	DeltAICc
Logistic	26.7	0
Laird-Gompertz	44.7	18.0
Exponential	66.9	40.1
Linear	77.0	50.3
von Bertalanffy	81.4	54.7

721

Brown-Spotted Grouper	AICc_Scores	DeltAICc
Logistic	41.2	0
Laird-Gompertz	44.6	3.4
Exponential	46.8	5.6
Linear	52.0	10.8
von Bertalanffy	59.2	18.0

Malabar	AICc_Scores	DeltAICc
Exponential	47.2	0
Logistic	49.5	2.3
Laird-Gompertz	50.1	3.0
Linear	63.7	16.6
von Bertalanffy	69.0	21.8

722

Longtooth Grouper	AICc_Scores	DeltAICc
Laird-Gompertz	46.2	0
Logistic	46.7	0.5
Exponential	54.4	8.2
Linear	93.2	47.0
von Bertalanffy	96.8	50.6

Mangrove Snapper	AICc_Scores	DeltAICc
Exponential	33.3	0
Linear	35.4	2.1
Laird-Gompertz	40.3	6.9
Logistic	40.3	7.0
von Bertalanffy	42.6	9.3

723

724

Table 5: Chi-squared Comparison of Linear and Exponential Models among Pelagic and Demersal Groups

Observed Values	Exponential	Linear	Total	Expected Values	Exponential	linear	Total
Demersal	31	16	47	Demersal	27.084	19.915	47
Pelagic	3	9	12	Pelagic	6.915	5.085	12
Total	34	25	59	Total	34	25	59
				Chi-Squared Value p-value	6.567 0.0104		

Observed: Expected: