

# Trends in Growth Modeling in Fisheries Science

Shane A. Flinn<sup>1,2</sup> and Stephen R. Midway<sup>1,\*</sup> 

<sup>1</sup> Department of Oceanography and Coastal Sciences, College of the Coast and Environment, Louisiana State University, Baton Rouge, LA 70803, USA; flinnsha@msu.edu

<sup>2</sup> Quantitative Fisheries Center, Department of Fisheries and Wildlife, College of Agriculture and Natural Resources, Michigan State University, East Lansing, MI 48824, USA

\* Correspondence: smidway@lsu.edu; Tel.: +1-225-578-6458

**Abstract:** Growth models estimate life history parameters (e.g., growth rates and asymptotic size) that are used in the management of fisheries stocks. Traditionally in fisheries science, it was common to fit one growth model—the von Bertalanffy growth model—to size-at-age data. However, in recent years, fisheries science has seen an increase in the number of growth models available and the evaluation of multiple growth models for a given species or study. We reviewed  $n = 196$  peer-reviewed age and growth studies and  $n = 50$  NOAA (National Oceanic and Atmospheric Administration) regional stock assessments to examine trends in the use of growth models and model selection in fisheries over time. Our results indicate that the total number of age and growth studies increased annually since 1988 with a slight proportional increase in the use of multi-model frameworks. Information theoretic approaches are replacing goodness-of-fit and a priori model selection in fisheries studies; however, this trend is not reflected in NOAA stock assessments, which almost exclusively rely on the von Bertalanffy growth model. Covariates such as system (e.g., marine or fresh), location of study, diet, family, maximum age, and range of age data used in model fitting did not contribute to which model was ultimately the best fitting, suggesting that there are no large-scale patterns of specific growth models being applied to species with common life histories or other attributes. Given the importance and ubiquity of growth modeling to fisheries science, a historical and contemporary understanding of the practice is critical to evaluate improvements that have been made and future challenges.



**Citation:** Flinn, S.A.; Midway, S.R. Trends in Growth Modeling in Fisheries Science. *Fishes* **2021**, *6*, 1. <https://doi.org/10.3390/fishes6010001>

**Keywords:** Akaike's information criteria (AIC); fish growth; model selection; multi-model inference; stock assessment; von Bertalanffy

Received: 30 October 2020

Accepted: 7 January 2021

Published: 19 January 2021

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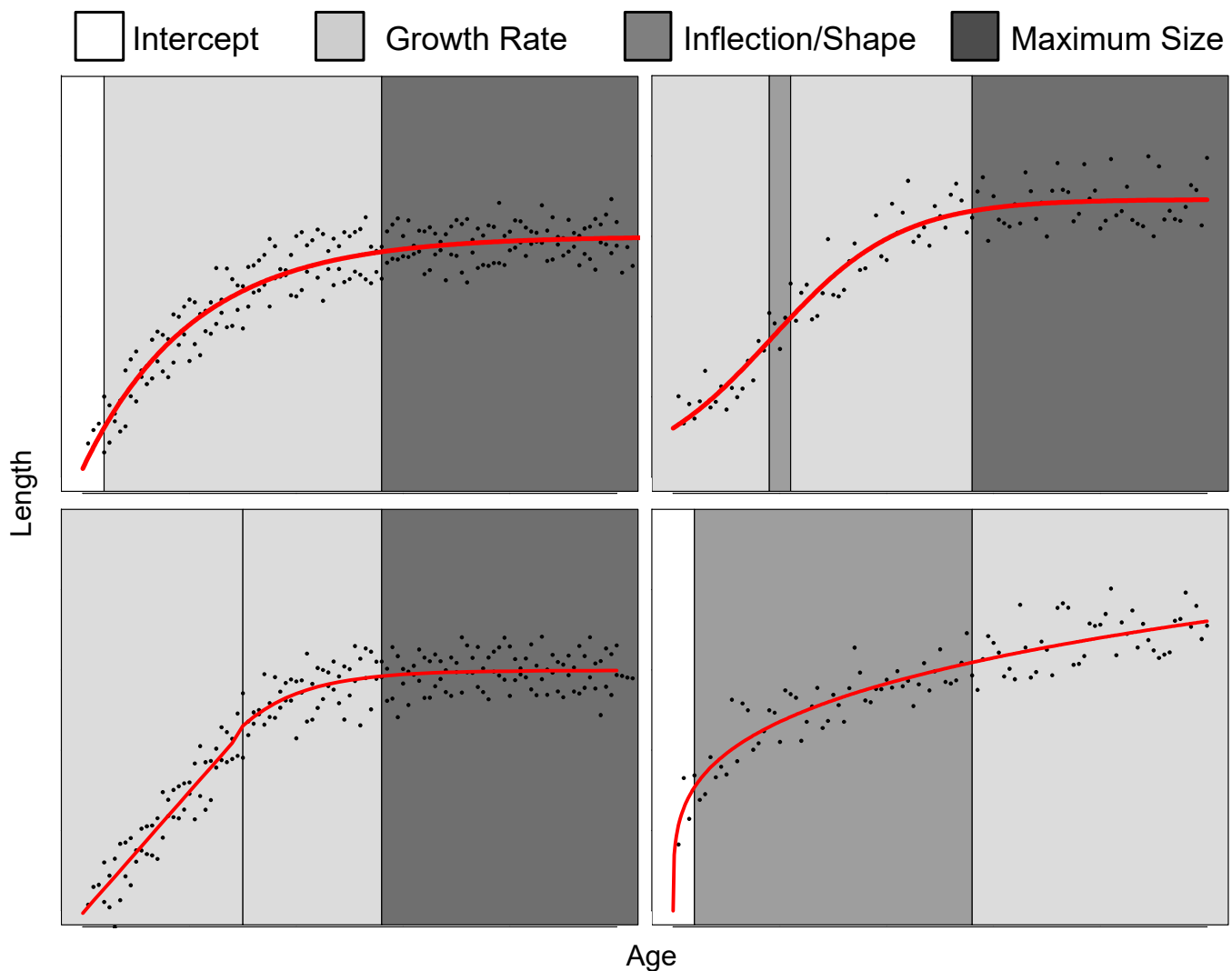
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## 1. Introduction

Growth—the change in organism size with age—is a basic yet critically important biological process that integrates numerous processes and shapes the life history of fishes. Growth can be directly linked to other life history traits such as natural mortality and fecundity [1–3]. The ability to accurately model fish growth has a wide range of applications in population dynamics [4]. Outside of recruitment, increases in the biomass of a (closed) stock come about by the growth of individuals. Mathematical models relating the size (typically length) of a fish species to its age are necessary inputs to other models such as those used in stock assessments that are used to monitor a population and inform management decisions such as length limits for harvest and other regulatory measures. Furthermore, growth data can be used to assess the status of a fishery and determine how fisheries have responded or will respond to exploitation [5]. For example, growth parameter estimates can be used to compare different populations (or stocks) over time as a tool to evaluate density-dependence or prey availability [6,7]. Growth of fishes often varies by species and within species along gradients (e.g., latitude, temperature), and the use of mathematical models to represent growth allows for comparison [8–10].

Traditionally, in fisheries science, it was common to fit one growth model to size-at-age data. However, many model types have been proposed and evaluated to estimate the

growth of fishes. Most are asymptotic, sigmoidal, or biphasic (having two growth phases) in shape, but other model types such as linear [11,12] and polynomial functions [13] have also been used to describe growth of some species (Figure 1). There is a wide variety of functional responses that have been used to model growth, but many of the equations for these functions also exist in different forms known as reparameterizations. Reparameterizations have been developed over time as putative advantages have been identified with different descriptions of a function. For example, some reparameterizations better allow for a visual interpretation of parameters, while other reparameterizations improve model fitting or decrease correlation between and among parameters [14].



**Figure 1.** Four common growth functions used to model fish growth. The von Bertalanffy growth function (**upper left**), logistic growth function (**upper right**), Lester biphasic growth function (**lower left**), and power growth function (**lower right**) are shown to illustrate the differences among models. Data (black dots) were simulated from the same model parameterization that fit the individual growth functions (red lines). The shaded background areas correspond to parameter interpretations, although they are approximate because these models are general examples, and the parameter interpretations are clearer for some models (and their parameters) than for others. Please refer to specific growth equations for details.

In 1938, von Bertalanffy derived his well-known growth equation that balances the catabolic and anabolic processes of growth to relate organism size based on its age. Beverton and Holt [15] modified and introduced the von Bertalanffy growth model (VBGM) to fisheries and it has received much attention and use in the following decades. Prior to the introduction of the VBGM, growth parameters were not estimated in size-at-age studies;

instead, observed (or mean) size-at-age data were plotted to visualize the trajectory of growth and make inferences. However, size-at-age studies were very inaccurate prior to otolith aging; for example, Pearson [16] estimated the maximum age of red drum (*Sciaenops ocellatus*) to be between 3 and 6 years, yet a later study estimated the maximum age to be around 50 years [17]. Since 1957, the VBGM has been the most widely used growth model in fisheries. However, other commonly used growth models now include the Gompertz growth model [18], the logistic model [19], and the generalized VBGM [20]. More complex models also exist, such as the Schnute–Richards model [21], in which different size-at-age models are effectively nested sub-models (i.e., continuous model expansion) and the resulting model fit has implicitly included some model selection, as opposed to traditional binary model selection. Additionally, many stock assessment models (e.g., [22]) use mean length-at-age and conditional age-at-length models to account for variation in size at age resulting from phenomena such as Rosa Lee [23]. While conditional age-at-length models are important for estimating growth parameters for many stock assessment models, this topic is not explored in this study.

Using a sub-optimal growth model may result in sub-optimal parameter estimates that will continue to carry error throughout subsequent modeling—such as in stock assessment. Although a sensitivity analysis looking at multiple models for the species in question will provide the exact loss of information germane to a specific analysis, it has been shown that using the wrong growth model can be problematic [24,25]. The uncertainty around how well different growth models predict growth of different organisms has driven the introduction of new methods, models, and model selection procedures. Today, it is often common for fisheries researchers to fit multiple growth models to size-at-age data and use information theoretic (IT) procedures to select the best-fitting model. Model selection and averaging using IT is a relatively new practice in biological sciences that has emerged as one way to account for the uncertainty surrounding the a priori use of growth models [26,27]. The most widely used IT for model selection is Akaike’s Information Criterion (AIC; [28]). Other IT criteria such as Bayesian Information Criterion (BIC; [29]), small-sample bias-corrected form of AIC (AIC<sub>c</sub>; [30]), and Akaike weight [26,27,31] have also been used in fisheries studies to select best-fitting growth models.

With a variety of estimation methods, growth models, and model selection and averaging procedures available to researchers, focus has turned towards refining the biology [25] of a species in question using models that estimate biological meaningful parameters. As such, certain growth model forms may prove to be more likely for certain species or families by better explaining their growth trajectory. Additionally, covariates such as study location, species maximum age, diet, and environment (marine or fresh) may play a role in the approach (e.g., models chosen) to growth modeling. Some growth models may be more common for species in a given location or environment and life history traits such as maximum age and diet may also tend towards specific growth trajectories that are best modeled with specific growth models.

We reviewed the peer-reviewed literature to examine how the use of growth models and model selection has changed over time, and whether any trends can be determined in the approach to growth modeling. We also considered (i) whether certain models have been used more frequently or have been shown to be better fitting for certain species or families and (ii) how the approach to growth modeling changes as a function of different covariates, such as species maximum age, the range of ages used in model fitting, location (e.g., developed vs. undeveloped countries), system (e.g., marine or freshwater), or diet. Additionally, we reviewed recent stock assessments from NOAA regional fisheries management councils (FMC) to analyze whether or not the trends in growth modeling in the peer-reviewed literature are reflected in stock assessments.

## 2. Results

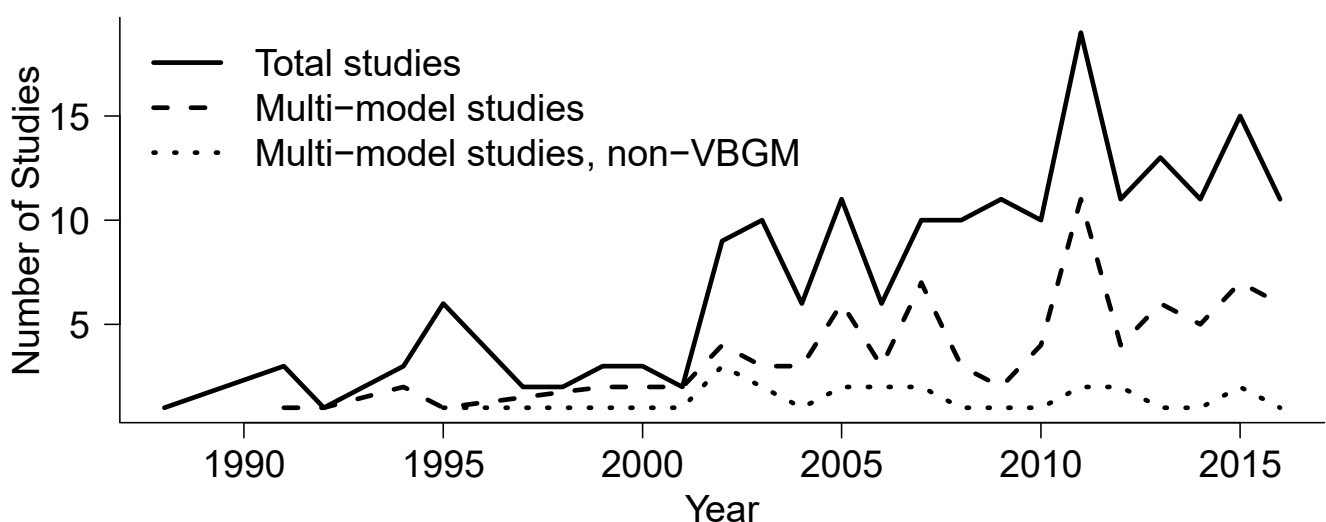
### 2.1. Peer-Reviewed Studies

We reviewed 196 peer-reviewed studies published between 1988 and 2016 that reported use of a fish growth model. Only 14% of the studies we reviewed occurred before 2000. The most commonly reported estimation method was least squares or maximum likelihood (49%), while 32% of studies did not explicitly report their estimation method. Bayesian estimation was reported in 2% of studies. Only 14% of studies added covariates to growth equations to attribute effects (e.g., environmental covariates) on growth, and 58% separated sexes for growth modeling.

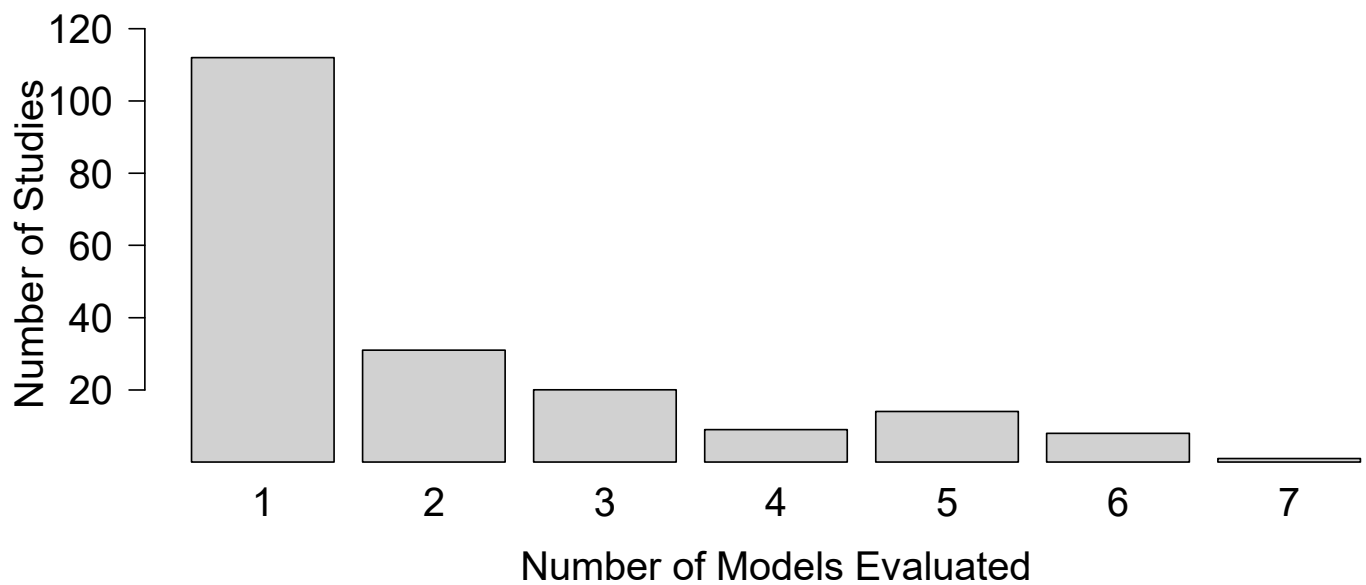
The most represented families were Scombridae and Sciaenidae ( $n = 16$  studies each), and the most represented species was albacore (*Thunnus alalunga*) ( $n = 4$ ). About 60% of the studies were of piscivorous fish and nearly 75% were of marine species. The longest-lived species studied was orange roughy (*Hoplostethus atlanticus*) with a reported maximum age of 149 years. The mean maximum age of all fish studied was 31, and the median was 22.5. An ANOVA found no significant differences in best-fit model or number of models evaluated as a function of maximum age or the range of ages used for model fitting. The geographic location with the most studies was North America ( $n = 66$ ), followed by Australia ( $n = 36$ ) and Europe ( $n = 35$ ).

#### 2.1.1. Growth Modeling

Between 1988 and 2016, the total number of age and growth studies increased, with a slight proportional increase in the use of multi-model frameworks (Figure 2). Aside from one outlier in 1992 (one study that evaluated six growth models), the annual average inclusion of growth models increased from about one throughout the 1990s to 2.5 in 2016. Between 1988 and 2016, only 42% of studies considered more than one candidate growth model (Figure 3). The largest number of models evaluated by one study was seven, and the mean number of models evaluated among all studies was two (median = 1). Among all peer-reviewed studies, the most common models to be considered as candidate models were the three-parameter VBGM (95% of studies), followed by the three-parameter Gompertz model (21%) and the three-parameter logistic model (16%). Some studies (22%) evaluated one or more candidate models that did not fall into our discrete categories (because of extremely low usage) and were thus classified as other (Figure 4).



**Figure 2.** Trends in the total number of age and growth studies (solid line), multi-model ( $\geq 2$  models) studies (dashed line), and multi-model studies not including the von Bertalanffy growth model (VBGM) to be the best-fitting model (dotted line), based on peer-reviewed literature between 1988 and 2016.



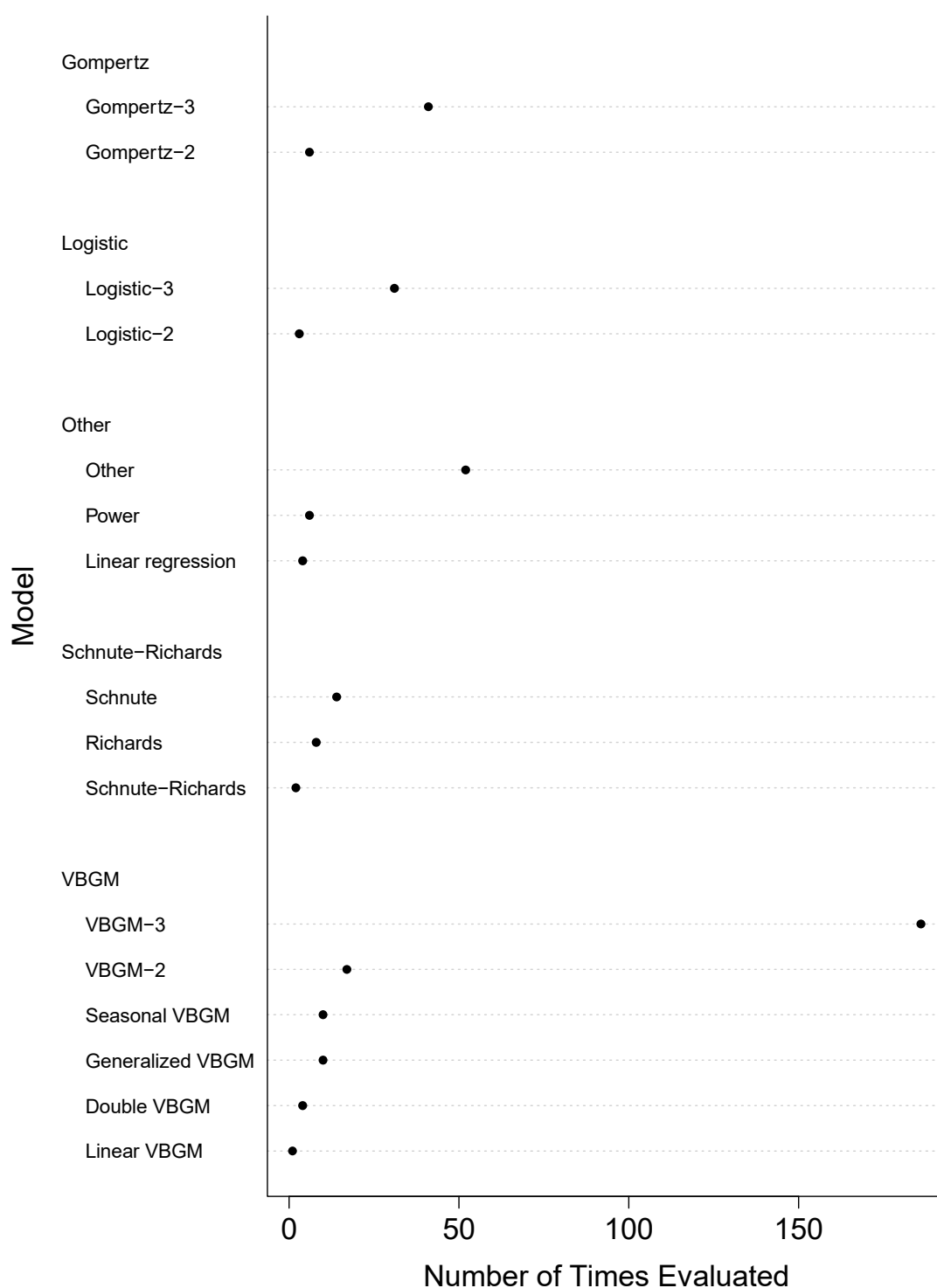
**Figure 3.** Counts of the number of studies evaluating different numbers of growth models based on 196 peer-reviewed age and growth studies between 1988 and 2016.

#### 2.1.2. Multi-Model Framework Studies

The three-parameter VBGM was evaluated as a candidate model in 96% of multi-model framework studies ( $n = 83$ ) compared to the three-parameter Gompertz model (48%), the three-parameter logistic model (37%), the Schnute model (17%), and the generalized VBGM and linear VBGM (12% each). When multiple models were evaluated, the three-parameter VBGM was selected as best-fit 39% of the time (Table 1). The mean number of models evaluated for studies evaluating multiple models was 3.4 (median = 3). The families with the most multi-model framework studies were Sciaenidae ( $n = 9$ ), Carcharhinidae ( $n = 6$ ), Serranidae ( $n = 6$ ), Scombridae ( $n = 5$ ), and Rajidae ( $n = 4$ ). The species with the most multi-model framework studies was spotted seatrout (*Cynoscion nebulosus*;  $n = 3$ ).

**Table 1.** Selection rate (percentage) of various growth models from multi-model studies (2+ models evaluated).

Model	Evaluated	Selected	Selection Rate
Schnute–Richards	2	2	100%
Double VBGM	4	3	75%
Seasonal VBGM	10	5	50%
Three-parameter VBGM	79	31	39%
Other	32	12	38%
Power	6	2	33%
Richards	8	1	13%
Two-parameter VBGM	17	2	12%
Three-parameter Gompertz	40	4	10%
Schnute	14	1	7%
Three-parameter Logistic	31	2	6%
Generalized VBGM	10	0	0%
Two-parameter Gompertz	6	0	0%
Two-parameter Logistic	3	0	0%
Linear VBGM	1	0	0%



**Figure 4.** Total number of times individual models were evaluated within 196 peer-reviewed studies from 1988 to 2016. Model types are clustered within a model family (e.g., Gompertz, Logistic), in which models are further described and where numbers correspond to parameters in a specific version of that model. Other (within the Other category) refers to models or model variations that had low usage and were therefore grouped together.

Studies of species in marine systems tended to evaluate multiple models more frequently, with 48% ( $n = 71$ ) of studies in marine systems using a multi-model framework compared to 20% ( $n = 8$ ) in freshwater systems. Marine studies also tended to evaluate a wider range of candidate models (Table 2). The number of models evaluated ranged from

1 to 7 in marine systems (mean = 2.17, median = 1) and ranged from 1 to 6 in freshwater systems (mean = 1.5, median = 1).

**Table 2.** Best-fitting models by system type. Migratory refers to species living in both marine and freshwater systems in a single life cycle (e.g., catadromous and anadromous fishes). Specific refers to studies that found multiple models to be best-fitting based on sex, species, location, or some other factor.

Model	Migratory	Fresh	Marine
Double VBGM	0	0	3
Gompertz	0	1	4
Linear Regression	1	0	1
Logistic	0	0	3
Power	0	0	2
Schnute-Richards	0	0	5
Seasonal VBGM	0	1	5
Specific	0	1	10
VBGM	8	35	107

### 2.1.3. Multi-Model Non-VBGM Studies

When multiple models were evaluated and the three-parameter VBGM or a variation of the VBGM was not selected as the best-fitting model ( $n = 14$ ), the Gompertz ( $n = 4$ ) and the Schnute–Richards ( $n = 4$ ) models tended to be selected, while the logistic ( $n = 2$ ) and power ( $n = 2$ ) models along with linear regression ( $n = 2$ ) tended to be selected less (Table 1). For example, out of the three multi-model framework studies of spotted seatrout, two studies found that the VBGM was not the best-fit model; this was the highest number of studies to find models other than the VBGM to be best fit for any one species. One spotted seatrout study [32] found the Gompertz and linear regression to best fit females and males, respectively, and another study [33] found the logistic growth model to be the best fit. The families demonstrating non-VBGM selected as best fit were Sciaenidae ( $n = 5$ ), Carcharhinidae ( $n = 2$ ), and Scombridae ( $n = 2$ ). Of the studies that found a model other than the VBGM (or variation) to be best fitting, 89% were in marine systems.

### 2.1.4. Model Selection

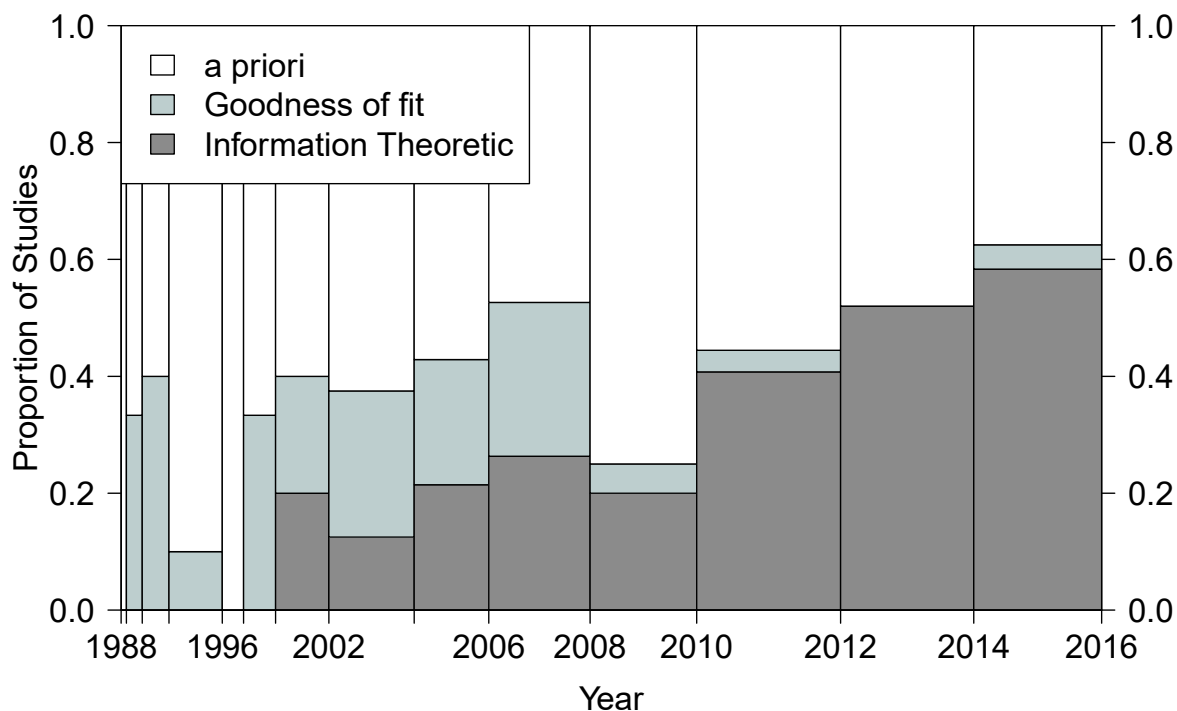
Among all peer-reviewed studies, 55% chose growth models a priori ( $n = 106$ ). Of the 106 studies in which models were chosen a priori, the three-parameter VBGM (or variation) was used in 103 studies compared to one time each for linear regression, the seasonal VBGM, and a sinusoidal Schnute model. The family with the most a priori use of growth models was Scombridae ( $n = 10$ ); however, the a priori use of growth models was also common for studies modeling the growth of multiple species (or families). In freshwater systems, 72% of studies used growth models a priori, compared to just under 50% in marine environments. Of those studies using a priori model selection, 42% did not report their estimation method.

Among peer-reviewed studies, 11% used goodness of fit (GOF, which describes how well a model fits observed data) to select the best model. The most common GOF method was  $R^2$ , followed by log-likelihood. The use of GOF has decreased over time, especially after 2008 (Figure 5). The a priori use of growth models and GOF for model selection were common throughout the 1990s, but since then, GOF methods of model selection have seen a sharp decline.

Some form of IT criteria was used for model selection in 28% of studies. AIC was the most common IT criteria for model selection, followed by  $AIC_c$ . The first uses of IT criteria in our dataset occurred in 2002 [34,35]. After that point, a marked increase in use of IT criteria is apparent (Figure 5). The first use of IT in our dataset was AIC, and since that time, additional IT methods such as  $AIC_c$  and Akaike weight have become more common in fisheries research. Both BIC and DIC (Deviance information criterion) were only reported



in two studies, and both of the studies reporting BIC also reported AIC, suggesting BIC and DIC are not commonly used model selection routines. The two most common model selection methods today are a priori and IT, although the use of a priori model selection seems to be declining in recent years.



**Figure 5.** Model selection procedure usage over time. The width of the annual bars corresponds to the relative frequencies of sample sizes (number of studies) binned by two years. Specific definitions and examples within the three categories—a priori, goodness of fit, and information theoretic—are described in the text.

## 2.2. Stock Assessments

We also reviewed a total of 50 stock assessments that were the most up-to-date for each species, all of which included growth estimation. The results of this search were less variable than our search of peer-reviewed studies, with only three stock assessments using a model other than the traditional three-parameter VBGM. The Pacific FMC used a Schnute parameterized version of the VBGM to model the growth of three species: Kelp Greenling (*Hexagrammos decagrammus*), Blue Rockfish (*Sebastes mystinus*), and Starry Flounder (*Platichthys stellatus*), although it was not explicitly stated why that model was used. The most assessed family was Pleuronectidae ( $n = 10$ , or 20% of total stock assessments). The regional FMC with the most stock assessments was by far the Pacific ( $n = 20$ , or 40% of total stock assessments), followed by the North Pacific ( $n = 10$ , or 20% of total stock assessments). Sexes were separated for growth modeling in 66% of the stock assessments we reviewed. Model selection was never mentioned in any of the stock assessments; thus, all were assumed to be selected a priori.

## 3. Discussion

### 3.1. Growth Modeling

Our results suggest that covariates such as system, maximum age, range of ages used in model fitting, diet, family, and location were not significant in determining which models are evaluated or found to be best fit. We found that marine systems have more multi-model framework studies and also tend to evaluate a wider range of models. The maximum age, range of ages used in model fitting, system, and diet of fish species appear to not be strong factors. Although species biology and growth is often specific and tends toward a specific



growth function, it could be that within these grouping factors, a sufficient diversity of growth forms prevents the emergence of strong patterns. Location also appears to not be a significant factor, although our results suggest that countries with more developed management infrastructure will have more complex modeling methods; however, we realize the bias towards North American studies in our sample which arises from our limitation to studies published in English. In many cases, studies in developing regions are more concerned in providing a baseline for fisheries in some given areas, and the VBGM is used due to ease of fitting and comparability to other studies.

We found that the families Sciaenidae, Scombridae, and Carcharhinidae are more frequently found to have models besides the VBGM selected as best fit. In fact, a few multi-model studies did not even include VBGM as an option (e.g., [11]), perhaps because the nature of the species' biological growth did not conform well to VBGM. Spotted seatrout, for example, tend to grow very quickly and also keep growing rather than asymptote, like many fish species. However, not reporting VBGM as the best fit may also be because some species were evaluated with more models than other families, and furthermore, it is unclear whether these studies resulted in more accurate size-at-age estimates and, ultimately, better management. Smart et al. [4] found that although multi-model framework studies are now common in elasmobranch studies, length-at-age estimates of 74 elasmobranch studies were only marginally affected by the approach, and the VBGM was equally as likely to be best fit as other candidate models. Furthermore, fixed-parameter models (categorized as other in this study) are a common candidate model choice in chondrichthyan age and growth studies, and varying degrees of support for this practice exist in the literature [24,36].

Growth is variable by species and within species along gradients such as temperature; therefore, it seems logical to conclude that no one model—the VBGM—could accurately describe the growth of all fish species, and furthermore, there have been criticisms of how well growth models capture the plasticity of growth in nature [37]. However, we found it surprising that nearly half of the time, the VBGM (or variation thereof, i.e., double or seasonal VBGM) was selected as the best-fitting model when multiple growth models were evaluated. We found that between 1988 and 2016, the total number of studies increased substantially, with a slight increase in the proportional use of multi-model frameworks in peer-reviewed fisheries studies. Despite the slight increase in multi-model framework studies, there was no increase with time in non-VBGM models being determined to be better fit. Therefore, our results suggest that the VBGM performs quite well when tested against many candidate models and seems to be a good general model to use. In fact, one could argue that VBGM parameters should be reported alongside better-fitting model parameters because the long history of VBGM use affords the ability to compare between studies. However, the VBGM is not without weaknesses—for example, this study excluded larval and juvenile studies; however, a major criticism of the VBGM is that it does not model the first year of growth well, and the Gompertz model has been used to model the growth of young fish [38]. Regardless of its shortcomings, we found it surprising how frequently peer-reviewed studies that evaluated multiple growth models found the VBGM to be best fit.

Although our study has found that the VBGM performs quite well when evaluated against candidate models in model selection routines, the use of multi-model frameworks when modeling the growth of fishes can be beneficial. Whether in continuous model expansion (e.g., [39]) or traditional binary model selection, the result of not considering potentially applicable models is that it cannot be known if there is a better model to describe growth for a given stock or species. We found that the seasonal VBGM (which adds a seasonal component to growth but maintains the overall VBGM shape) tends to perform well in multi-model frameworks; therefore, the ability to improve growth modeling in fisheries may lie in incorporating seasonal variation in growth into commonly used growth models. The seasonal VBGM was suggested as being a strong candidate model for long-lived fish [38] and it has since been used to model the growth of economically important fish species such as red drum in Louisiana [35], sardine (*Sardina pilchardus*) in the Mediterranean

and northeast Atlantic [40], and bonito (*Sarda australis*) in Australia [41]. Not only has the seasonal VBGM been shown to perform well on a variety of fish species, it is rooted in ecological and biological theory whereby fish grow faster in warmer conditions and slower in colder conditions. However, a major limitation to the wide use of this model (and other more complex models) is the amount of data needed. For example, in order to model the seasonal growth of fish throughout the year, samples need be collected throughout the entire year and age data must be fractional (i.e., not whole year). This requires a level of investment that few species have devoted to them. Therefore, a major limitation to adopting more complex modeling methods is less about computational or statistical power and more about the workforce needed to meet increased data demands. Furthermore, complex models may have a difficult time converging on parameter estimates when data are sparse (i.e., few individuals sampled) or sampling is incomplete for all life history stages, which can be the case when dealing with fisheries data. Considering this, models that can be fit to coarse (i.e., whole age) and sparse data to produce reasonable estimates that are biologically relevant are most likely to become widely used in fisheries.

One area that remains unclear and was not analyzed in this study is how many of the studies we reviewed that used a multi-model framework actually began with a biologically relevant reason to evaluate multiple models. Because growth models can capture different life history dynamics, researchers that are evaluating multiple models should have clear biologically relevant reasons to test multiple models, otherwise the modeling of fish growth becomes nothing more than a statistical ritual. We suggest that unless a biologically relevant reason exists or the VBGM has previously been shown to be a poor fit, fish age and growth modelers should use the VBGM initially. Additionally, if multiple models are fit and a model besides the VBGM is found to be best fit, the VBGM parameter estimates should be reported alongside estimates of a better-fitting model.

Our review and analysis only considered studies that were estimating growth using length-at-age data and excluded studies using tag recapture and length data. However, length-at-age data may be difficult to obtain, especially for tropical and migratory stocks; thus, length-based or tag recapture data may be used to estimate the age structure of a population, which may lead to biases in growth estimates [42]. Francis [43] identified a comparability problem between age-based and length-based data, and methods have since been developed to combine the two types of disparate data for growth modeling [44]. Furthermore, biases in growth estimation can result from using data from a single gear type, restricted range of life history (e.g., only adult fish), or even from slight sexual dimorphism. When estimating growth using data collected by multiple gears, the data are more representative of the actual population rather than the population vulnerable to the sampling gear [45]. Additionally, the sampling protocol and associated biases need to be considered. Goodyear [46] found that random and age-stratified sampling accurately reproduced known growth model parameters, while size-stratified sampling caused biases in estimates of length-at-age and growth model parameters. Better-fitting growth models are not enough to overcome biases in data; therefore, consideration should be given to the biases caused by uneven sampling and combining disparate datasets. Despite this importance, the topic is not explored further in this study; we focus on reporting growth model use for studies estimating growth using length-at-age data.

### 3.2. Model Selection

Between 1988 and 2016, IT criteria emerged as the most common process by which to select growth models. The use of IT criteria increased beginning around 2000—corresponding to the publishing of Burnham and Anderson [47], which advocated and popularized methods for the use of this IT approach. The use of IT criteria in fisheries also follows the general trend of other ecological fields [48,49]. With the increase in IT approaches, a decline was seen in GOF methods. This is likely due to advances in statistical programming packages that made it relatively easy to obtain AIC values for model comparison.

Statistical model selection in fisheries appears to have two dominant paradigms, GOF and IT. Despite this recent movement towards the use of IT criteria, there have been criticisms that the IT approach only amounts to a substitution of one statistical ritual for another and that ecology, not statistics, should be at the forefront of all ecological studies [48]. Furthermore, there have been criticisms of the IT approach (specifically AIC) because it takes into account model parsimony, such that models with fewer parameters will be preferentially selected [24]. However, others have argued for AIC biases in the opposite direction—such that more complex models (i.e., models with more parameters) are too often selected (see [50]). Zhu et al. [5] compared six model selection approaches of fish growth models and found that AIC<sub>c</sub> and BIC performed best for small and large datasets, respectively. Brewer [51] also found AIC<sub>c</sub> and BIC to be the best model selection methods when unobserved heterogeneity was small and large, respectively, and suggested the use of multiple model selection methods.

While the type of model selection used is an important consideration, perhaps more important is that the model that is being statistically chosen as best fit is also a biologically good fit. For example, linear models may fit the data better over some intermediate range-of-age and length data for a given species; however, we know that biologically, fish do not grow linearly and instead reach an asymptotic size or grow more slowly with age. Furthermore, even if a model selection method suggests a linear model over a more biologically relevant model, the researcher should consider the value of a better statistical fit versus a better biological fit. Serra-Pereira et al. [52] chose the VBGM over the Gompertz model for thornback ray (*Raja clavata*) because the estimate of  $L_{\infty}$  (mean asymptotic length) was more biologically reasonable when fit statistics (e.g., AIC) provided support for both models. In fact, the VBGM has been used with a biological intercept (e.g., [53]), which can approximate the actual growth trajectory and also improve biological realism. Fisheries professionals should not sacrifice biologically reasonable parameter estimates for improved statistical fit.

### 3.3. Stock Assessments

Even though many growth models are available, it is rare for stock assessments to test multiple candidate models [37]. We found our results surprising as NOAA regional FMCs tended to use the VBGM almost exclusively a priori in stock assessments, even when better-fitting models had been found for the species in peer-reviewed studies. For example, we found three stock assessments for species that have peer-reviewed studies which showed a model other than the traditional VBGM to be best fit, i.e., gag grouper (*Mycteroperca microlepis*) [54], spiny dogfish (*Squalus acanthias*) [55], and red snapper [56], and would be interested if the Schnute–Richards model expansion approach were used to choose the VBGM models for the stock assessment. Initially, we interpreted our results comparing growth model use between peer-reviewed age and growth studies and stock assessments as a potential disconnect between research and management; however, upon further consideration, we determined that peer-reviewed age and growth studies and stock assessments performed by management agencies have fundamentally different purposes.

Although growth models other than the VBGM may be shown to fit data best for some species in peer-reviewed age and growth studies, there can be good reasons why such models are not rapidly integrated into stock assessments. The objectives of the age and growth studies we evaluated in the peer-reviewed literature varied widely (e.g., evaluating sexual dimorphism, how environmental factors affect growth, etc.), while the objectives of the stock assessments consistently were to evaluate the status of a fishery and prescribe management actions such as total allowable catch. However, growth models were not used in the same way across all stock assessments. For example, some stock assessments model the change in length distributions as a function of size-selective mortality and account for among-individual variation in growth. Changing growth models in this context can be complex and would not generally be undertaken without clearly identified benefits. In addition, some assessments use well-established relationships between VBGM parameters

(e.g.,  $k$ ) which are correlated to other life history attributes that are more difficult to estimate (e.g., natural mortality, recruitment compensation; [57]). Similarly, although the effects of environmental covariates, ontogenetic shifts, and spatial and temporal variation are known to be important for growth, incorporating them into stock assessment models can be difficult, especially for more complex models than the VBGM [57]. Furthermore, stock assessment scientists are surrounded by uncertainty in their analyses, and in some cases, even a poor-fitting VBGM may seem acceptable considering other sources of uncertainty and its relative contribution to the stock assessment results. For example, another critical component of a stock assessment is the stock–recruitment relationship. However, stock–recruitment curves (e.g., the Beverton–Holt function) are notoriously poor-fit; therefore, the choice of growth model is often a small part of the uncertainty that stock assessment scientists are confronted with, yet they still must fit models and make management recommendations. The relative importance of growth uncertainties is also dependent on the type of stock assessment model and the type of data being analyzed [57]. Stock assessments fit to size composition data are highly sensitive to growth estimates; therefore, an area for researchers to explore in the future is how incorporating different growth models into stock assessments that use size composition data could result in changes to management decisions.

It is also useful to consider the fact that a model used for assessment and a model used to study the biological process of growth may be different models. Statistical models can be used for understanding, prediction, or both [58]. Often, an inquiry into the biological process of growth may be undertaken more for understanding than prediction, and this may also lead to more complex models or models with more predictors that have some relation to growth. On the other hand, an assessment may place a greater value on prediction than understanding, and as such, a growth model that optimizes some fit statistic or prediction exercise could be selected (see Midway et al. [59] for an example of model understanding vs. prediction for fish maturity data). In reality, there is often substantial overlap for models that explain processes and make predictions, so it might not be expected that most fish would have different models for understanding and prediction; however, it is a possibility and should be considered. Furthermore, although assessment models sometimes explore environmental variation in growth (e.g., [60]), it can be easier to fit multiple models than to test whether the inclusion of an environmental linkage results in an expected improvement in model performance. To this end, parsimony or GOF may not be the best model performance metric and biology and management procedures should also factor into which model is “best” [25]. Additionally, from the perspective of long-term assessment, the benefit of the consistency of one model (VBGM) over time may outweigh the cost of not using the best-fitting model for a shorter time.

In studying historic and recent trends in fish growth modeling, it was apparent that while some approaches remained constant over time (a priori use of VBGM), there is still a large amount of variability in how fisheries scientists evaluate growth. The current state of growth modeling in fisheries is dynamic and is increasingly becoming more complex and computationally demanding as models are created that account for variability in growth due to a variety of factors (environment, maturity, etc.; [61–63]). Hierarchical Bayesian models are now being used in many cases because they have made advancements in growth comparisons [9], changes in growth over time [64], and accounting for spatial variability [10]. Conditional age-at-length approaches and measurement error models also show promise as a way to explicitly include observer (aging) error into growth models [65].

Despite statistical advances, it is sometimes unclear how often growth models other than the VBGM are incorporated into stock assessment models. For some assessments, there may be latent model selection (e.g., the Richards model, where certain combinations of parameter values result in functional forms of different growth models without the explicit model selection of different models) and consideration of conditional age-at-length and non-constant coefficients of variation that ultimately improve the realism of the model. Although there has been an increase in attempts to find better-fitting models, the VBGM

is often chosen as best fit, and thus, this lack of advancement may be inconsequential to stock status. Furthermore, our results suggest that newly developed or highly specialized growth models (“other” models in this study) will not only not be used for stock assessment but will likely not be adopted by fisheries researchers. We found that the VBGM performs well when evaluated against other growth models; therefore, newly developed models should attempt to balance computational simplicity and biological relevance if they are to be widely adopted by fisheries professionals. More accurate estimates of growth have the potential to improve management and protection of stocks for the future and improve our understanding of the underlying mechanisms of fish growth. Thus, we should continue to evaluate and develop new models regardless of whether or not these new models will ultimately be used in stock assessment and the decision-making process of fisheries managers.

#### 4. Materials and Methods

##### 4.1. Peer-Reviewed Literature

We used Web of Science (an academic research database maintained by Clarivate Analytics) to conduct peer-reviewed literature searches. We first used the search terms, Title: “growth” AND Topic: “models” AND Topic: “fish” NOT Publication Name: “aquaculture”. Subsequently, we searched, Topic: “growth” AND Topic: “models” AND Topic: “fish” NOT Publication Name: “aquaculture”. The change of “growth” from being a title search to a topic search allowed us to increase our search to include papers that might report on growth, but in a way that was not reflected in the title of the paper. The results of both searches were refined by Web of Science Categories, “fisheries”. The first search was conducted on 17 October 2016, and produced 769 results. The second search was conducted on 25 January 2017, and produced 2666 results. In our first search, “growth” was included in the title, whereas in our second search, “growth” was included as the topic. This change in the search terms allowed us to gain a larger sample size after our first search left us with what we thought to be a low sample size.

To evaluate trends in the use of growth models, model fit, and model selection, criteria were used to construct a dataset based on our search. We chose to only include studies that were estimating the growth of a group (e.g., stock or population) of wild fishes using length-at-age data. Therefore, mark-recapture, aquaculture, larval, and juvenile growth studies were excluded. We recorded information for the lead author, year of publication, species name, species family, location of the study population, the number and type of candidate growth models evaluated in the study, the best fit model, the range of age data used for model fitting, the model selection process used, what estimation process was used (if reported; e.g., least squares, maximum likelihood, Bayesian, etc.), whether or not the model took into account effects on growth (defined by the addition of model parameters), and whether or not separate growth models were ultimately fit for males and females. From FishBase [66], we also collected any available diet (e.g., benthivorous, piscivorous, etc.), system (freshwater or marine), and maximum age information for species from each study. We also examined the covariate of location and grouped locations broadly by continent.

Based upon our review, we identified 16 heuristic categories of growth models: two-parameter VBGM, three-parameter VBGM, two-parameter Gompertz, three-parameter Gompertz, two-parameter logistic, three-parameter logistic, Schnute, Richards, Schnute-Richards, double VBGM, generalized VBGM, linear VBGM, seasonal VBGM, power, linear regression, and other (Table 3). Some models that were evaluated by individual studies were obscure, having low usage in the literature, and therefore could not be placed into one of our discrete categories; thus, we classified these models as other. Most of these models were fixed-parameter, specialized, or modified variations of more common growth models, such as the VBGM. Likewise, there was a large amount of variation among individual studies and our other variables of interest (e.g., best-fitting model ( $n = 40$  unique entries) and model selection procedure ( $n = 26$  unique entries)); thus, we aggregated certain variables based on the following criteria. For best-fitting model, we included a second variable



that more broadly aggregated (coarsened) the models into one of six groups: either the Gompertz, logistic, VBGM, double VBGM, seasonal VBGM, or Schnute–Richards. These aggregated groups included two-parameter, three-parameter, seasonal, and other variations of the five parent model types and were designed to obtain higher-level information about models used. The seasonal and double VBGM models were kept separate from the VBGM group because they each had high selection as best-fit (50% and 75% of the time evaluated, respectively) relative to other variations of traditional models (Table 2). We also aggregated model selection such that only IT, goodness-of-fit (GOF), and a priori were considered as model selection types. Information theoretic consisted of AIC, AIC<sub>c</sub>, Akaike weight, BIC, and DIC. Goodness of fit consisted of R<sup>2</sup>, log-likelihood, residual sum of squares, mean squared error, likelihood ratio tests, and principle component analysis, while a priori consisted of those studies that only evaluated and used one growth model in their respective study.

**Table 3.** Model equations, parameter descriptions, and references for the most commonly evaluated growth models in our dataset. References in bold refer to original usage or formulation of the model and subsequent references serve as examples of its use. Many variations and reparameterizations have been excluded for brevity.

Model Name	Model Equation	Parameter Description	Reference(s)
Two-parameter VBGM	$L(t) = L_{\infty} \left(1 - e^{-k_1(t)}\right)$	$L_{\infty}$ = asymptotic length $t$ = age $L(t)$ = length at age $t$ $k_1$ = Brody growth parameter	[56]
Three-parameter VBGM	$L(t) = L_{\infty} \left(1 - e^{-k_1(t-t_0)}\right)$	$t_0$ = age at zero length	[15]
Two-parameter Gompertz	$L(t) = L_0 e^{G(1-e^{-k_2 t})}$ , $G = \ln \frac{L_{\infty}}{L_0}$	$L_0$ = length at birth	[55,67]
Three-parameter Gompertz	$L(t) = L_{\infty} e^{-\frac{1}{k_2} e^{-k_2(t-\alpha)}}$	$k_2$ = rate of exponential decrease of relative growth with age	[18,55]
Three-parameter Gompertz	$L(t) = L_{\infty} e^{-e^{(-k_2(t-\alpha))}}$	$\alpha$ = inflection point of the sigmoid curve	[19,55]
Three-parameter Logistic	$L(t) = \frac{L_{\infty}}{(1 + e^{-k_3(t-\alpha)})}$	$k_3$ = relative growth rate parameter	[55,68]
Linear VBGM	$L(t) = (b_0 + b_1 t) \left(1 - e^{-k_1(t-t_0)}\right)$	$b_0, b_1$ = linear coefficients; $b_0$ (intercept), $b_1$ (slope)	[35,69,70]
Double VBGM	$L(t) = \begin{cases} L_{\infty} \left(1 - e^{-k_4(t-t_1)}\right) & \text{if } t < t_p \\ L_{\infty} \left(1 - e^{-k_5(t-t_2)}\right) & \text{if } t > t_p \end{cases}$ $t_p = \frac{(k_5 t_2 - k_4 t_1)}{(k_5 - k_4)}$	$k_4, k_5$ = instantaneous growth rate coefficients $t_p$ = “pivotal age” $t_1, t_2$ = age intercept parameters	[35,71,72]
Generalized VBGM	$L(t) = L_{\infty} \left(1 - e^{-k_1(t-t_0)}\right)^p$	$p$ = dimensionless factor	[20]
Seasonal VBGM	$L(t) = L_{\infty} \left\{ 1 - e^{-k_1(t-t_0) - \left(\frac{c}{2\pi}\right) [\sin 2\pi(t-t_s) - \sin 2\pi(t_0-t_s)]} \right\}$	$c$ = amplitude of oscillations ranging between 0 and 1 $t_s$ = the summer point or when growth rate is maximized, ranging between 0 and 1	[41,73]

Table 3. Cont.

Model Name	Model Equation	Parameter Description	Reference(s)
Schnute	$L(t) = \left[ t^\rho + \delta^\rho - t^\rho \frac{1 - e^{-\lambda(\tau - \tau_1)}}{1 - e^{-\lambda(\tau_2 - \tau_1)}} \right]^{\frac{1}{\rho}}$ $L_\infty = \left[ \frac{e^{\lambda\tau_2\delta\rho} - e^{\lambda\tau_1\delta\rho}}{e^{\lambda\tau_2} - e^{\lambda\tau_1}} \right]^{\frac{1}{\rho}}$	$\tau_1$ = lowest age in the dataset $\tau_2$ = highest age in the dataset $\rho$ = an incremental relative growth rate (incremental time constant) $\lambda$ = relative growth rate (time constant) $t$ = size at age $\tau_1$ $\delta$ = size at age $\tau_2$	[21,74]
Richards	$L(t) = L_\infty \left( 1 - \delta e^{-k_6(t-t_4)} \right)^{\frac{1}{\delta}} \text{ where } \delta \neq 0$	$\delta$ = a shape parameter, and the sigmoidal Gompertz function $k_6$ = relative growth parameter	[35,75,76]
Schnute–Richards	$L(t) = L_\infty \left( 1 + \delta e^{-k_7 t^\nu} \right)^{\frac{1}{\gamma}}$	$\nu, \delta, Y$ = dimensionless parameters $k_7$ = units $\text{yr}^{-\nu}$	[21,26]
Power	$L(t) = a_0 + a_1 t^b$	$a_0$ = y-intercept or the mean length at age 0 $a_1, b$ = parameters that describe the shape of the curve but have no biological interpretation	[26,27,76]

The data were divided into two classes based on the number of models evaluated: (i) those studies that only used one growth model (a priori) and (ii) those that evaluated multiple models. We further divided the multiple-model studies based on what model was found to be best fit: (i) those that found the VBGM (or a variation of VBGM) to be best-fit and (ii) those that found a model other than the VBGM to be best-fit.

We summarized the data and analyzed spatial and temporal trends in the use of growth models and model selection criterion in the peer-reviewed literature. We also considered whether the evaluation of multiple growth models and model selection has been especially beneficial in finding better fitting growth models for certain families (or species), and how the approach to growth modeling changes as a function of a species' maximum age, system (marine or fresh), or diet by subsetting and summarizing the data. We performed an ANOVA to test the significance ( $p < 0.05$ ) of the maximum age of the study species and the range of ages used in model fitting on the number of models evaluated and the model ultimately chosen. We standardized the range of data used for model fitting by dividing the maximum age observed in the study by the reported maximum age on FishBase. In some cases, studies observed individuals that were older than the maximum age reported in FishBase; therefore, the standardized range was capped at 1 to indicate that data from the full range of ages were present for model fitting. We performed Pearson's Chi-squared to test for significant relationships ( $p < 0.05$ ) between our other covariates and the number of models evaluated and the model ultimately chosen by studies.

#### 4.2. Stock Assessments

In addition to our search of peer-reviewed literature and in order to evaluate trends in the use of growth models, model fit, and model selection among stock assessments in the United States, we searched the most recent stock assessments and compiled a dataset for species managed by NOAA regional FMCs. We recorded information from the following FMCs: Gulf of Mexico, Pacific, North Pacific, South Atlantic, and the Mid-Atlantic. We recorded the year of the assessment, the species being assessed, the location of the stock assessment, the growth model(s) evaluated, and whether or not the assessment fit separate models for male and females. Once again, from FishBase [63], we added the following species-specific information to the data: the adult diet, the maximum age, the system (e.g., fresh or marine), and the family. We searched for stock assessments that were conducted in freshwater systems but were unable to find any, although we recognize that they have been done. All data and statistical analyses were performed in the open-source software R [77].



**Author Contributions:** Conceptualization, S.A.F. and S.R.M.; methodology, S.A.F. and S.R.M.; formal analysis, S.A.F.; writing—original draft preparation, S.A.F.; writing—review and editing, S.A.F. and S.R.M.; visualization, S.A.F. and S.R.M. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Acknowledgments:** We would like to thank Richard Shaw and Robert Rohli for their help as committee members, Josh Raabe for his useful comments on the initial draft of the manuscript, and Jim Bence for his helpful comments on stock assessment.

**Conflicts of Interest:** The authors declare no conflict of interest.

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