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Improved estimates of growth for wild Yellowtail Kingfish (*Seriola lalandi*) off eastern-Australia using multiple data sources

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Unbiased growth functions are imperative for stock assessment and sustainable management of fisheries. We present a case-study demonstrating implications of data collection biases from fishery-dependent sampling where length-selective fishing occurs. Yellowtail Kingfish *Seriola lalandi* supports substantial fisheries around the world and is the focus of a developing aquaculture industry. Estimating growth rates in wild populations has been challenging, with uncertainties around accurate estimates of length-at-age from which to model growth. Length-at-age data are generally derived from sectioned sagittal otoliths. We generated new estimates of growth rates for Yellowtail Kingfish from south-eastern Australia by excluding data for age classes not fully recruited to the fishery based on significance tests of normality and skewness. New length-at-age estimates for young fish were generated from dive surveys around offshore Fish Aggregation Devices (FADs) to inform early growth. Otolith-derived age classes younger than 5 years old were biased in terms of faster growing individuals being sampled. Length-selective biases from fishery dependent sampling results in over-estimation of the von Bertalanffy growth function parameter L_∞ and under-estimation of the parameters K and t_0. Revised growth function parameters of $L_\infty = 133.40$ cm fork length, $K = 0.13$ year -1, and $t_0 = -1.20$ years are substantially different from those used for stock assessment. We recommend that future studies of growth rates would benefit from more fishery-independent sampling, the collection of greater numbers of larger and older fish, and regular sampling and direct aging of young-of-the year fish recruiting to offshore FADs.

KEYWORDS
bias, fishery dependent sampling, growth models, length-at-age, *Seriola lalandi*

1 Introduction

In fished species, growth represents the link between biology, the environment, and exploitation. Understanding the growth rates of exploited species is therefore fundamental to their stock assessment and ultimately sustainable management (1, 2). The most common and useful growth curve for stock assessment is the von Bertalanffy growth function (VBGF) (3–5), described by the parameters L_∞ (theoretical average maximum length), K (the growth coefficient describing how quickly L_∞ is approached), and t_0 (theoretical age at length zero). So established is the VBGF in fisheries research that leading stock assessment software packages like Stock Synthesis (6) use it as the default growth model.

Potential biases in the estimation of growth functions using length-at-age data from fishery dependent sampling have been well-described (7–9). Data collected from fisheries may be biased by the selectivity of fishing gears or management regulations including minimum legal lengths (MLLs). The result is that observed variation in length-at-age data may not be representative of the entire population. In the case of MLLs, data for smaller and younger fish may either be absent or skewed toward faster growing individuals that may attain any regulated MLL at earlier ages. Such skewed data typically results in negative biases of the estimated VBGF parameters t_0 and K, thus influencing stock assessment outcomes, and the determination of appropriate management arrangements.

Despite the widely acknowledged issues in modeling fish growth using fishery-dependent data, such modeling continues to be undertaken and used in assessment, without due consideration of potential biases resulting from length-selective fishing practices. Various methods of bias-correction have been investigated, including modeling the shape of the length-at-age probability density functions for partially selected age classes (8, 10), fixing parameters such as the VBGF parameters L_∞ and t_0 (when known) and removing data from less-than-fully sampled age classes (11). Integrating length-at-age data from various sources, that may cover different stages of the life cycle, is another way to overcome length-selective biases resulting from fishery dependent sampling (12, 13). It is clear that consideration of potential biases resulting from data collection methods is vital, as growth rate misspecification can result in adverse management advice and undermine the intent of sustainable fisheries management decisions (14).

Yellowtail Kingfish (*Seriola lalandi*, Carangidae) has a circumglobal distribution throughout temperate and subtropical oceans (15), where it supports substantial commercial and recreational fisheries as well as a growing aquaculture industry (15–17). Within their circumglobal range several broad genetic lineages have been identified, being South Africa, South Pacific, north-eastern Pacific and the north-western Pacific, with little mixing between hemispheres (18). Yellowtail Kingfish of the South Pacific, extending from Chile in the east to Australia in the west, are genetically similar (18) and those from the south-west Pacific demonstrated to be highly mobile, with tagged individuals moving throughout the waters of south-eastern Australia, offshore seamounts and New Zealand (NZ) (19). Yellowtail Kingfish are reported to have extremely fast early growth rates, one of the reasons for their potential as an aquaculture species (20). Despite their fast initial growth rates and high mobility, it is highly likely that growth rates will vary throughout the species south-western Pacific distribution due to varying temperatures and food availability (21).

Yellowtail Kingfish off south-eastern Australia are reported to attain 195 cm in length and approximately 70 kgs in weight (22) with a maximum reported age of 21 years (23). The maximum age reported from NZ waters is 29 years (24). Several studies have historically estimated growth rates of Yellowtail Kingfish in south-eastern Australia and NZ. In NZ, growth rates of Yellowtail Kingfish have been estimated using tag-recapture data (25, 26) and length-at-age data derived from sectioned otoliths and observations of small fish around offshore Fish Aggregation Devices (FADs) (24, 26, 27). Each of these studies reported Yellowtail Kingfish to grow relatively rapidly but with estimates of L_∞ substantially lower than estimated in Australia by Stewart et al. (23). These NZ studies reported similar growth estimates between areas sampled, and some evidence for differential growth between the sexes (females growing faster and to larger sizes).

In south-east Australian waters, Gillanders et al. (28) developed aging protocols for Yellowtail Kingfish and provided formative growth curves based on sectioned otoliths, tag-recapture data and cohort analysis. Growth was described using the Schnute growth function (29) for the otolith derived length-at-age data and the tag-recapture data and using the VBGF for the cohort analysis using the package MULTIFAN (30). These estimates indicated faster growth rates than for Yellowtail Kingfish in NZ. Subsequently Stewart et al. (23) published growth rates of Yellowtail Kingfish off NSW based on sectioned otoliths from a larger dataset (1,215 fish) than Gillanders et al. (28). Stewart et al. (23) reported the VBGF parameters that again indicated faster growth rates than in NZ.

The current growth function for Yellowtail Kingfish in eastern-Australia is acknowledged as having a high degree of uncertainty due in part to potential sampling biases identified by Stewart et al. (23). These uncertainties stem from the nature of the length-at-age information collected more than 25 years ago and largely from the commercial fishery (23). The fishery at the time was managed under a MLL of 60 cm total length (TL), and Stewart et al. (23) did not attempt to resolve potential biases in the distribution of lengths within age classes not fully sampled due to the fishery dependent sampling that was done. Rather, Stewart et al. (23) presented a Schnute growth function which provided a better fit to the data than the VBGF. However, fits to the length data for the most common age classes in the fishery (2–5 years old) were poor using this growth function.

Yellowtail Kingfish mortality rates and spawning potential ratios in eastern-Australia are currently estimated through length-converted catch curves (17, 31, 32) and using the growth parameters estimated in Stewart et al. (23). Clearly the growth function applied in these analyses influences the mortality estimates derived, and biases in the growth function will influence the results. The objective of the present study was therefore to estimate a more biologically realistic population growth curve for Yellowtail Kingfish off the coast of New South Wales (NSW), Australia. We aimed to achieve this through removing biases in the distribution of lengths by not fitting to data from partially sampled age classes, together with the addition of more contemporary length-at-age data derived from a recreational fisher frame donation program. These data were combined with derived length-at-age estimates of Yellowtail Kingfish less than 2 years old from monitoring of offshore FADs to more realistically model early growth. We then compared our revised estimates of growth for Yellowtail Kingfish off eastern Australia with those reported in other populations within the “South Pacific” genetic lineage.

2 Methods

Length-at-age data were obtained from several sources for analysis. Data from 1,122 Yellowtail Kingfish were obtained from the study reported by Stewart et al. (23), funded by the Fisheries

Research and Development Corporation (FRDC Project No. 97/126). These data comprised mainly fish from commercial landings during the late 1990s and early 2000s, supplemented by fish smaller than the MLL at the time (60 cm TL, ~52 cm fork length—FL) from observers onboard commercial vessels, and fish from Lord Howe Island. Many of these data were previously used to model growth of Yellowtail Kingfish in Stewart et al. (23). In addition, data from 146 Yellowtail Kingfish donated by recreational fishers to the NSW Research Angler Program (dpi.nsw.gov.au/fishing/recreational/resources/fish-tagging/researchangler) between 2012 and 2018 were included. These individuals were aged using sectioned sagittal otoliths using the same method and laboratory as those from Stewart et al. (23).

We estimated the age of small Yellowtail Kingfish observed through dive surveys around offshore FADs and reported in Figure 3 of Dempster (33). Dempster (33) estimated the average FL within schools when more than 5 fish were in the school, with sampling being generally monthly between April 1999 to April 2002. Fish length estimates by eye were validated by comparing underwater estimates with measured lengths of fish following capture (33). We therefore were able to estimate the average FL of each school sampled from Figure 3 in Dempster (33), resulting in 64 mean FL samples. Yellowtail Kingfish off eastern Australia spawn mainly during the austral summer, peaking during December (28). Spawning has been linked to maximum day length (34) that occurs around mid-December off eastern Australia, and we assumed a universal birth date for Yellowtail Kingfish of 15th December. Each monthly sample of average FL from the FADs surveys was assigned a decimal year age based on this general birthdate. We used the growth rates of Yellowtail Kingfish reported in aquaculture environments to infer whether each sample were young-of-the-year or the 1+ year cohort. Becker et al. (49) reported an average of 29.8 cm FL after 230 days following weaning onto commercially available pellets in an aquaculture facility. McKenzie et al. (26) reported a mean age of Yellowtail Kingfish around FADs in NZ estimated at just more than 1 year of age to be 28.6 cm FL. Given the abnormally fast growth rates reported for Yellowtail Kingfish in aquaculture conditions (25, 35) we considered any samples in Dempster (33) having an average FL of greater than 28 cm to be more than 12 months old. The data then separated distinctly into two groups of fish we considered as 0+ and 1+ year cohorts.

We examined the distribution of lengths within each age class for individuals where age was estimated using sectioned otoliths, and also data from fish around FADs for potential sampling bias, using the fundamental concept that lengths should be approximately normally distributed (30, 36). We tested each age class containing more than 15 data points for normality using a Shapiro–Wilk test and for skewness using a D'Agostino test of skewness. Analyses were done in R statistical software (37) using the packages *nortest* and *moments*. We used these analyses to justify excluding data in subsequent growth function fitting.

Growth was estimated by fitting the VBGF to the selected length-at-age data using the FSA (Fisheries Stock Assessment) package in R (38, 39). The model is fitted using non-linear least squares regression. Ages for the FAD-derived data were in decimal years and the age classes for the otolith-derived estimates as yearly mid-points. Growth models were initially fitted to the entire dataset, then to the datasets where partially sampled age-classes were sequentially removed, and finally to the dataset assessed as being most representative of the population.

TABLE 1 Tests for normality and skewness of length data within each age class.

Age class	*N*	*W*	*P*	Skewness	*p*-Value
FADS 1	58	**0.98**	**0.40**	**–0.205**	**0.485**
1	60	0.94	<0.005	**0.301**	**0.303**
2	545	0.92	<0.005	1.068	<0.005
3	356	0.90	<0.005	1.313	<0.005
4	106	0.97	0.008	**0.303**	**0.184**
5	42	**0.95**	**0.058**	**0.624**	**0.077**
6	29	**0.95**	**0.214**	**0.034**	**0.929**
7	26	**0.93**	**0.100**	**–0.007**	**0.100**
8	31	0.92	0.018	**0.207**	**0.586**
9	15	0.92	**0.226**	**–0.669**	**0.188**

N is number of observations, W is the Shapiro–Wilks test statistic, P is the probability of accepting the null hypothesis, skewness is the test statistic from the D'Agostino test of skewness. Numbers in bold indicate the data were normally distributed or not skewed at $p < 0.05$.

3 Results

The compiled length-at-age dataset showed no obvious increase in length variation with increasing age (Supplementary Figure S1). Data for age classes greater than 9 years were somewhat limited, comprising fewer than 15 length observations within each age class.

Only age classes 1–9 years had 15 or more observations. Otolith-derived age classes from 1 to 4 years were not normally distributed, with age classes 2 and 3 also exhibiting skewness (Table 1, Figure 1). The data derived from fish around FADs aged 1+ were normally distributed and not skewed (Table 1, Figure 1). On those bases we excluded the otolith-derived length-at-age data for age classes 1–4 from the growth curve fitting process. We retained data for older age classes as they did not exhibit skewness.

The VBGF fitted to the otolith-derived length-at-age data, comprising 201 fish from age classes 5–20 years, and 64 mean length-at-age data derived from observations of fish around FADS, produced parameter estimates with 95 % confidence intervals of $L_\infty = 133.40$ (124.50, 145.07) cm FL, $K = 0.13$ (0.11, 0.16) year^{-1}, and $t_0 = -1.20$ (-1.67, -0.83) years (Figure 2, Table 2). The VBGF provided substantially better fit (AIC = 2,033.1, RSS = 32,331.8) compared to the Schnute model (AIC = 9,535.2, RSS = 99,472.3, ΔAIC = 7,502.1).

Fitting the VBGF to the entire dataset, then consecutively removing the biased datasets and refitting the model, showed improvements in model fits as data were removed, with decreases in L_∞ and increases in K with removal of each younger age-class (Supplementary Table S1).

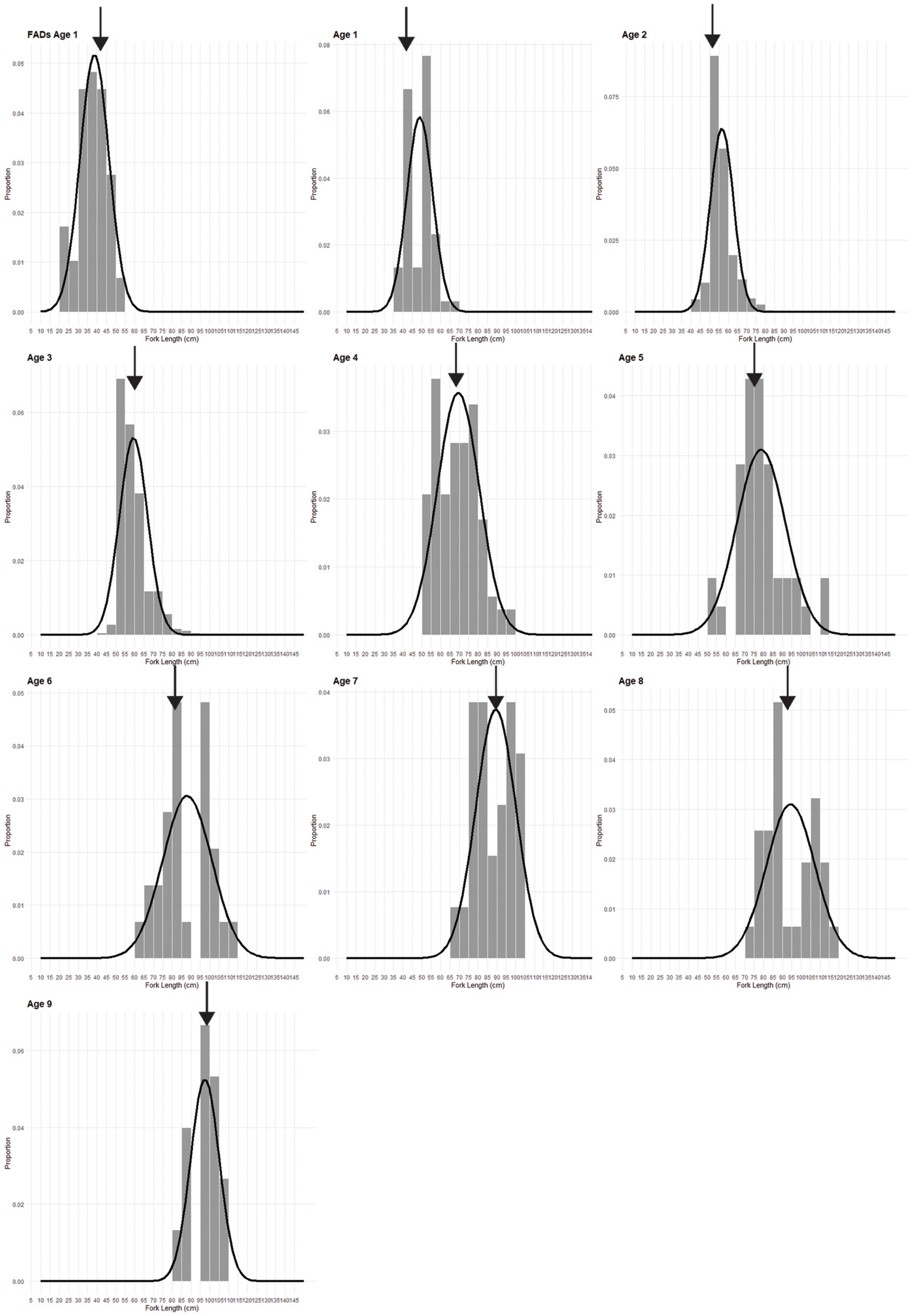

FIGURE 1
Length distributions for otolith-derived age classes 1–9 years for Yellowtail Kingfish sampled from the commercial and recreational fisher catches, and length distributions of mean lengths of fish aged 1+ observed around FADs, with normal distribution overlays. Otolith-derived age classes 1–4 showed significant departures from normality (Table 1). Arrows indicate the length estimated from the fitted growth curve.

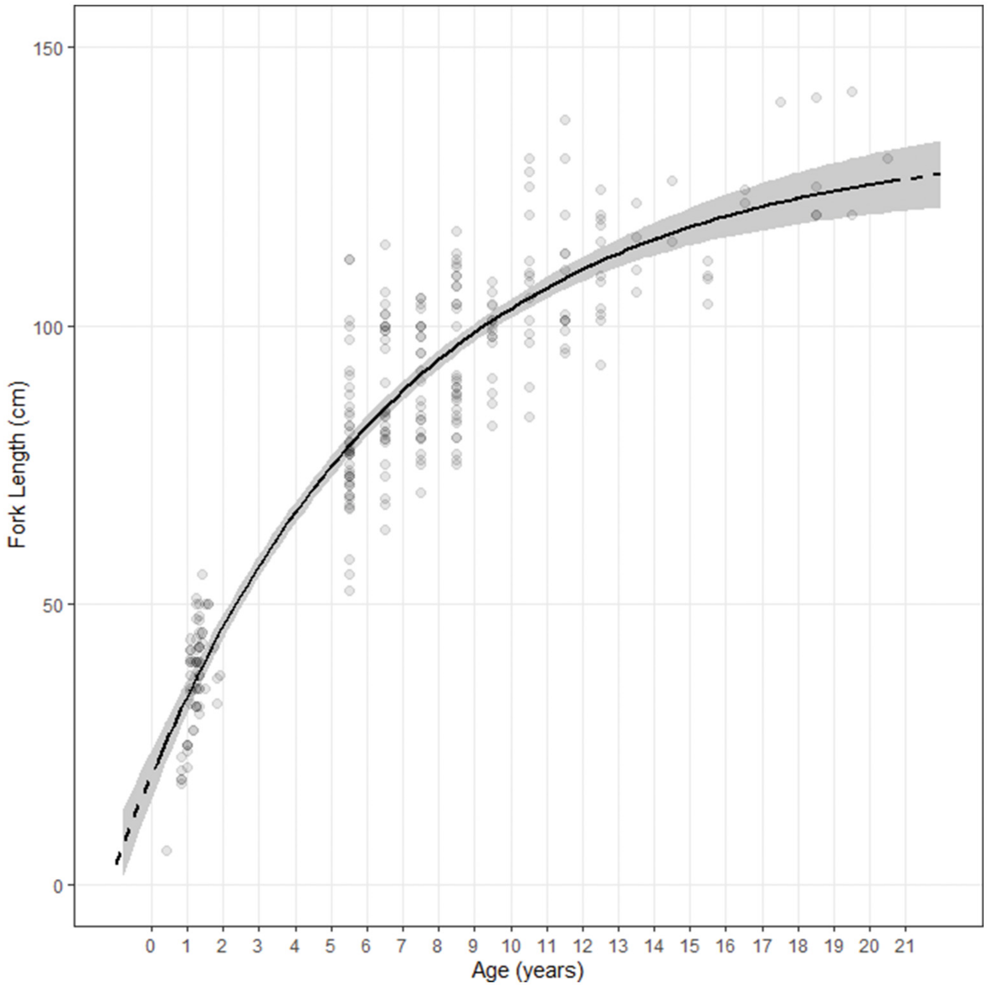

FIGURE 2
Fitted von Bertalanffy growth function to the selected length-at-age data for Yellowtail Kingfish. Shaded areas are the 95% confidence band. The dashed line shows the model fit outside the range of observed ages.

4 Discussion

The results presented here may be considered as a case-study on the implications of data collection biases when modeling growth rates of exploited species. Through detailed analysis of the distribution of lengths within each age class for the otolith-derived dataset for Yellowtail Kingfish, we demonstrated that the length distribution within age classes younger than 5 years were unlikely to be representative of the population due to non-normality and skewness. We do however acknowledge that despite the theoretical basis for expecting normally distributed lengths within an age class, that this may not always be the case due to variable growth and recruitment. Nevertheless, given that lengths within age classes 5, 6, and 7 were normally distributed provides evidence that for Yellowtail Kingfish the theoretically expected shape of length distributions for fully recruited age classes holds true. In the absence of evidence for non-normal or skewed distributions of lengths within age classes at the population scale, the approach presented here provides an objective tool for excluding age classes based on statistical analyses and removes subjectivity from the process. We therefore conclude that the predominance of samples obtained from fishery landings must consist of samples that are skewed toward faster growing individuals within those early age classes that had attained the MLL in the fishery of 60 cm TL or approximately 52 cm FL. Fitting the VBGF to such data, as done for Yellowtail Kingfish by Stewart et al. (23), and is done frequently to estimate the growth rates of exploited fish worldwide, may result in negative biases for the parameters t_0 and K and overestimates of L_∞. We suggest this may be the reason why the growth function parameters currently used for Yellowtail Kingfish in eastern-Australia (23) are markedly different from those reported in other studies of Yellowtail Kingfish globally, having by far the largest L_∞ and consequent lower values for t_0 and K (Table 2). In fact, the L_∞ derived from growth parameters estimated in Stewart et al. (23) of 184.0 cm FL and previously used in stock assessments for the species in this region (17, 32) is larger than the largest size reported for the species in south-eastern Australia of $\sim$ 172 cm FL (195 cm TL) (22). Stewart et al. (23) also reported that the Schnute growth function provided better fit to the data; however, we demonstrated that using the unbiased data resulted in the VBGF being a significantly better model for Yellowtail Kingfish.

TABLE 2 von Bertalanffy growth function parameters for Yellowtail Kingfish.

L_∞ (cm) FL	K (year^{-1})	t_0 (years)	Method	Region	Source
133.40 (124.50, 145.07)	0.13 (0.11, 0.16)	−1.20 (−1.67, −0.83)	Length-at-age Sectioned otoliths	Eastern Australia	Present study
184.0	0.054	−4.4	Length-at-age Sectioned otoliths	Eastern Australia	Stewart et al. (23)
125.2	0.19	−0.74	Length frequency data MULTIFAN	Eastern Australia	Gillanders et al. (28)
135.84	0.15	−1.23	Length-at-age Sectioned otoliths	Australia. Victoria	Green et al. (45)
140.58	0.096	−1.339	Sectioned otolith	New Zealand. Northern	McKenzie (48)
141.91	0.13	N/A	Tag-recapture data	New Zealand. Northern	McKenzie (48)
125.63	0.21	−0.99	Length-at-age Sectioned otoliths	New Zealand. Bay of Plenty. Females	Holdsworth et al. (27)
119.32	0.23	−0.98	Length-at-age Sectioned otoliths	New Zealand. Bay of Plenty. Males	Holdsworth et al. (27)
124.48	0.23	−0.89	Length-at-age Sectioned otoliths	New Zealand. East Northland. Females	Holdsworth et al. (27)
113.69	0.28	−0.79	Length-at-age Sectioned otoliths	New Zealand. East Northland. Males	Holdsworth et al. (27)
129.69	0.173	−1.07	Length-at-age Sectioned otoliths	New Zealand. Bay of Plenty/ East Cape. Females	Holdsworth et al. (24)
120.27	0.184	−1.31	Length-at-age Sectioned otoliths	New Zealand. Bay of Plenty/ East Cape. Males	Holdsworth et al. (24)
131.06	0.173	−1.26	Length-at-age Sectioned otoliths	New Zealand. Northland/Hauraki Gulf. Females	Holdsworth et al. (24)
116.4	0.247	−0.71	Length-at-age Sectioned otoliths	New Zealand. Northland/Hauraki Gulf. Males	Holdsworth et al. (24)
98.58	0.59	0.07	Length-at-age Otolith weight	Northern Chile	Ndjamba et al. (50)
106.4	0.17	−2.75	Length-at-age Whole otoliths	South Africa	Dunn (46)
110.8	0.31	−0.59	Length-at-age Sectioned vertebrae	Japan	Shiraishi et al. (47)

Values in parentheses are 95% confidence intervals.

Alternative bias correction approaches such as modeling the shape of the length-at-age probability density functions for partially selected age classes (10) are likely to produce similar results to ours by reducing biases. Nevertheless integrating data from early life-history stages, such as the estimated lengths of juvenile Yellowtail Kingfish observed around offshore FADs each month as done in the present study, is a proven method for providing fishery-independent data that better informs the growth function at young ages and small sizes to produce more biologically realistic growth models. The approach is preferable to either fixing t_0 at zero or the estimated length-at-hatching at age zero (11). Accessing length-at-age data for early life history stages is therefore crucial if using our approach of excluding fishery-dependent data for age classes not fully recruited to the fishery. In this study, the requirement to assume a common birthday of December 15 for each school of fish observed around offshore FADs, combined with likely inter-annual variation in growth rates, mean that our assigned estimates of age for these fish are somewhat uncertain. Estimating age from size for early life-history stages is much more reliable than doing so later in life and allowed us to make approximations of length-at-age for small fish around FADs which were important for estimating early growth and informing the VBGF. Importantly the length distribution of the fish observed around offshore FADs that were categorized as aged 1+ years were normally distributed and not skewed, providing strong evidence that: (i) our allocation to age classes were reasonable, and; (ii) that the fish sampled were likely representative of the population cohort. Unpublished analyses pooling all FADs fish into either the 0+ or 1+ age classes to examine potential biases from incorrect assignments showed only minor differences in growth parameters, with biases toward making the fish younger producing lower values of K and more negative t_0. Nonetheless, future surveys of the relative abundance and daily age of very young Yellowtail Kingfish around offshore FADs would be useful in quantifying interannual variability in recruitment strength and growth.

Our sensitivity analysis modeling growth using the entire dataset, then consecutively removing each otolith-derived dataset for partially sampled from ages 1 to 4 and re-fitting the growth model showed decreases in the estimated L_∞ values and increases in the estimated K values as data were removed, with increasing R^2 values (Supplementary Table S1). This result supports our assertion that the VBGF estimated for Yellowtail Kingfish off eastern-Australia presented here is likely the most biologically realistic and defensible undertaken due to integrating length-at-age data from young fish and excluding potentially biased fishery-dependent data. Indeed, our revised estimates of $L_\infty = 133.40$ cm FL, $K = 0.13$ year-1, and $t_0 = -1.20$ years are similar to the most current growth parameters estimated for Yellowtail Kingfish in NZ (24, 26) (Table 2). Mckenzie et al. (26) used a similar data integration and exclusion technique, using estimated length-at-age data for small fish observed around offshore FADs to anchor the left-hand side of the growth function, and excluding otolith-derived estimates for all age classes younger than 8 years as they were not considered to be fully recruited to their fishery, where the MLL is 75 cm TL.

There have been few published studies on the growth rates of wild Yellowtail Kingfish from populations within the other “South Pacific” genetic lineages in South Africa, the north-eastern and north-western Pacific, but those that exist consistently estimate substantially smaller values of L_∞ (Table 2). Those studies used different methods (whole otoliths, vertebrae) to estimate length-at-age and as such may not be directly comparable to other studies undertaken on “South Pacific” Yellowtail Kingfish populations, nonetheless results do provide some corroborative evidence that is consistent with the revised estimates presented here.

It is apparent that Yellowtail Kingfish are similar to their conspecifics in having fast early growth rates and moderate longevity [e.g., *Seriola dumerili* (40, 41), *Seriola dorsalis* (42), *Seriola hippos* (43)]. The majority of the published research on growth within the genus has come from aquaculture studies, with growth of individuals exhibiting substantial variability governed largely by water temperatures and food availability (44). It is likely that the strong influence of environmental conditions on growth rates, particularly during early years, will result in regional and interannual differences that may have driven some of the variability in published results on growth rates within this genus.

Despite substantial progress in the estimation of growth rates of Yellowtail Kingfish from the south-western Pacific during the past 20 years there remain some important uncertainties. The species is reported to attain 195 cm TL ($\sim$172 cm FL) (22), which if true infers that the range of L_∞ values reported may be underestimates of the average maximum size the species can achieve in this region. Importantly, none of the published studies have had large sample sizes of fish greater than 10 years old and efforts to sample sufficient numbers of larger and older fish are therefore warranted. Related to the lower level of sampling for the older and larger fish is the uncertainty around sex-related differences in growth. Some studies from the south-western Pacific have reported differences in growth rates between sexes (24, 27), whereas others have found no significant differences (23, 26). Yellowtail Kingfish mature at a relatively large size of approximately 84–95 cm FL (16, 28) and greater sampling of mature-sized fish may elucidate whether sex-related differences in growth occur. Future attempts to generate length-at-age data for growth rate estimation would therefore benefit from fishery-independent sampling to ensure sufficient representative sampling of those age classes not fully recruited to the fishery.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because the study used data from previously sampled fish that were obtained from fishers following normal practices.

Author contributions

JS: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. SS: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. JH: Methodology, Project administration, Supervision, Writing – review & editing. DB: Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frish.2026.1733032/full#supplementary-material

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