

ARTICLE

Markedly Similar Growth and Longevity of Green Jobfish *Aprion virescens* over an Expansive Geographic Range between the Hawaiian Archipelago and the Eastern Indian Ocean

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Abstract

The Green Jobfish *Aprion virescens* supports important commercial, recreational, and subsistence fisheries throughout its Indo-Pacific range. Concerns with previous estimates of age and growth from fish in Hawaii, along with evidence of variability in these parameters from locations outside the Pacific Ocean, limits their reliability as input parameters for assessments of this species, particularly in Hawaii. Previously validated aging criterion were applied to fish collected from within the Hawaiian Archipelago (main Hawaiian Islands and Northwestern Hawaiian Islands) and the eastern Indian Ocean to provide length-at-age, growth, and longevity information for stock assessment and management purposes as well as to further examine spatial variability across its range. The Bayesian information criterion was used as a measure of goodness of fit for von Bertalanffy models with different covariates to explore the influence of sex and location on growth. No divergence in growth trajectories was identified between sexes, and growth parameter estimates were not different within the Hawaiian Archipelago or between Hawaii and the eastern Indian Ocean. Empirical natural mortality estimates revealed that mortality was also very similar between sexes and among locations due to the similarity in maximum ages and growth parameter estimates. Considering there was dissimilarity in age and growth parameters between the current study and those published for this species from the Coral Sea and the western and central Indian Ocean, further investigation of potential clines in relation to latitude, and subsequently water temperature, need to be determined.

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Received October 9, 2020; accepted March 8, 2021

Eteline snappers (family Lutjanidae) are important to commercial, recreational, and subsistence fisheries throughout their range (Newman et al. 2016). The Green Jobfish *Aprion virescens* (known locally in Hawaii as uku) is a large-bodied, reef-associated lutjanid with a tropical Indo-Pacific distribution ranging from east Africa, Mauritius, and the Red Sea to Indonesia, southern Japan, the Ogasawara Islands, Australia, Micronesia, the Hawaiian Archipelago (main Hawaiian Islands [MHI] and Northwestern Hawaiian Islands [NWHI]), and the Tuamotu Archipelago (Mundy 2005). They occupy shallow-water reefs and insular shelves and extend down steep slopes to at least 180 m (Lieske and Myers 1994; Pyle et al. 2016). This wide distribution, coupled with a wide habitat range (Haight et al. 1993b; Meyer et al. 2007), results in their large contribution to a variety of fisheries, including shallow-water trolling, spearfishing, and deepwater handline gears (Haight et al. 1993a, 1993b).

In the MHI, Green Jobfish accounted for the second largest estimated commercial total reported poundage landed and was the third most valuable nonpelagic species from 2014 to 2018 (WPacFIN, Hawaii Department of Land and Natural Resources). This species is also important to local subsistence and recreational fisheries because they can be caught from shore, small boats, and kayaks. A commercial fishery also operated in the NWHI prior to the 2011 establishment of the Papahānaumokuākea Marine National Monument, after which all fishing, commercial and recreational, in the area was prohibited. Comparatively, the MHI supported higher effort levels relative to the NWHI, particularly when weather conditions or management measures prevent targeting of the more lucrative “Deep 7” bottom fish species (mix of six deepwater snappers [family Lutjanidae] and one grouper [family Epinephelidae] under federal management in Hawaii). The MHI Green Jobfish landings are highest during aggregated spawning in the boreal summer but are still caught throughout the year (Ralston and Kawamoto 1988; Haight et al. 1993a, 1993b; O'Malley et al. 2016). The NWHI fishery was and the MHI fishery is currently managed collaboratively by the state of Hawaii, National Oceanic and Atmospheric Administration (NOAA) Fisheries, and the Western Pacific Fishery Management Council using a minimum-size restriction (unlawful to sell or spear fish <0.45 kg; HAR 13-95) and annual catch limits. The MHI also have several areas closed to fishing with bottom handline gear (i.e., trolling for Green Jobfish can still take place in these areas).

In the eastern Indian Ocean (EIO), the Green Jobfish is found in relatively lower abundances along the continental shelf of northwestern Australia compared with the nearby offshore reefs and atolls of Rowley Shoals, Scott Reef, and Seringapatam Reef. Despite this species representing a very small portion of the commercial catches along the

continental shelf of northwestern Australia (Newman et al. 2020), it is considered a prized target species for recreational fishers, particularly spearfishers. The commercial catches of demersal teleosts in these subtropical and tropical waters typically comprise more than 60 retained species predominantly belonging to the Lutjanidae, Epinephelidae, and Lethrinidae families (Newman et al. 2016). Considering that it is logistically infeasible and cost prohibitive to undertake biological assessments of all species, indicator species are used to assess the risk to sustainability of all species susceptible to exploitation within the fisheries resource (Newman et al. 2018). As such, opportunities to collect information on the life history characteristics of data-poor species should be undertaken where practical to assess their specific inherent vulnerability and to compare these traits with those of the indicator species to ensure such an approach is appropriate (e.g., Wakefield et al. 2020).

Despite the subsistence and economic value of Green Jobfish to Hawaii and Western Australia fisheries, reliable age and growth information is not available for quantitative stock assessments for either location. Previously, Ralston and Kawamoto (1988) estimated the von Bertalanffy growth parameters for this species in Hawaii by utilizing commercial catch length frequency data to estimate L_{∞} and a growth performance equation to estimate K , which, in turn, was used to estimate natural mortality (M). However, they state that the results were highly dependent on a variety of assumptions and too much emphasis on specific parameter estimates was “unwise.” An improved understanding of growth and longevity would provide important information on the inherent vulnerability and potential impacts of fishing on this species. To address the lack of length-at-age information and associated life history parameters, O'Malley et al. (2016) developed and validated an aging criteria for Green Jobfish. The purpose of this current study was to apply this nascent criteria to otoliths collected throughout the Hawaiian Archipelago and the EIO. The resulting length-at-age information was used to estimate growth rates and natural mortality and to test for variations in these parameters between sexes and locations within the Hawaiian Archipelago (MHI versus NWHI) and between the Hawaiian Archipelago and the EIO. This age-based life history information provides a unique opportunity to examine differences in growth and mortality between two geographically similar areas that have experienced different fishing histories (i.e., MHI and NWHI).

METHODS

Sampling.—Green Jobfish otoliths were collected by NOAA Fisheries throughout the Hawaiian Archipelago (Figure 1) from 2007 to 2016 from a variety of different

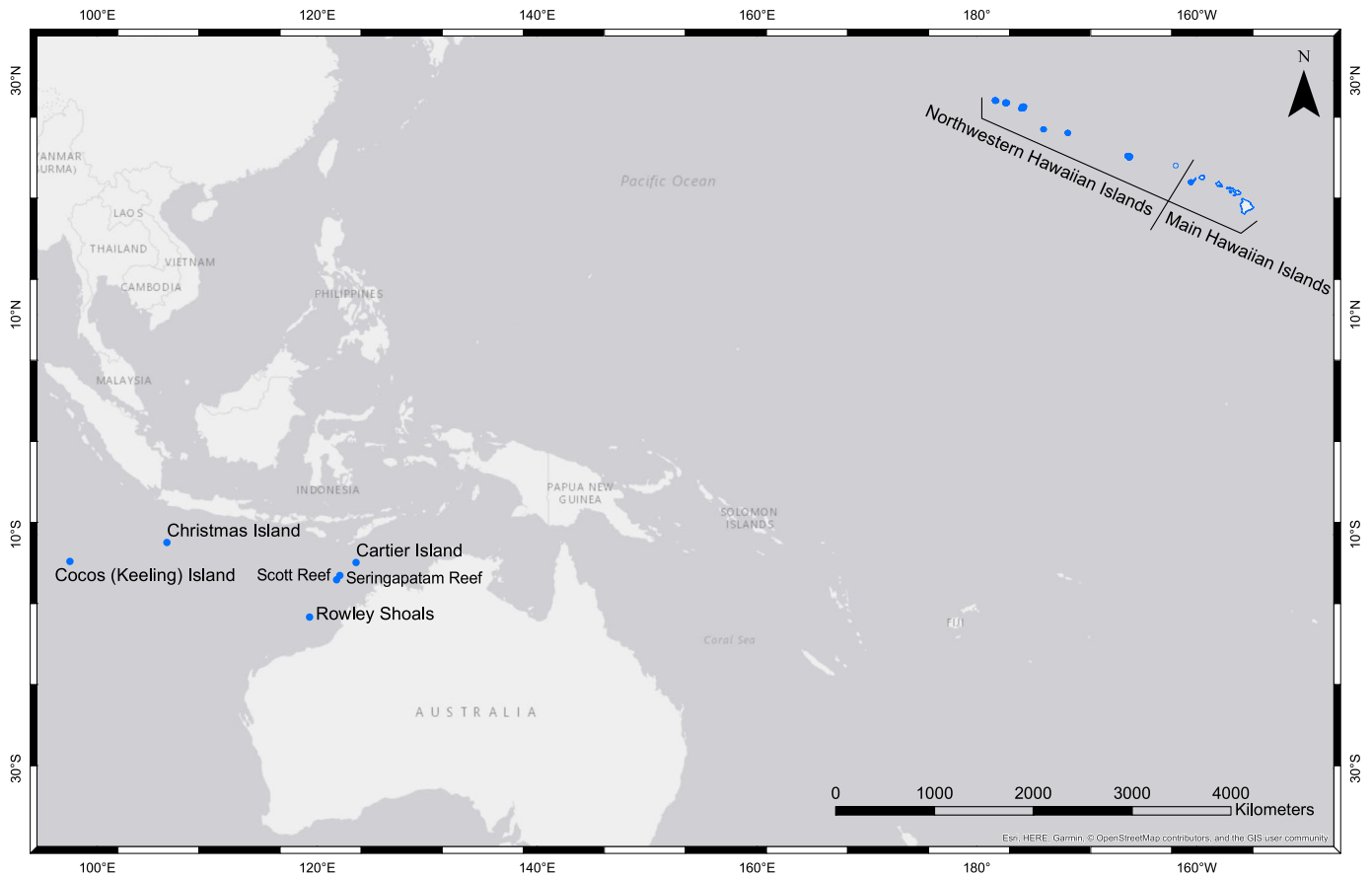


FIGURE 1. Map of the Green Jobfish sampling locations in the Hawaiian Archipelago (main Hawaiian Islands and the Northwestern Hawaiian Islands) and the eastern Indian Ocean (Western Australia, Scott Reef, Seringapatam Reef, Rowley Shoals, Cartier Island, Christmas Island, and Cocos [Keeling] Island).

sources, including (1) research trips on federal research vessels, (2) purchases from commercial fishermen, and (3) donations by local recreation or subsistence fishermen. Juvenile and adult fish from all sources were captured via both trolling and handlining from the reef edge to 200 m. Larval fish were captured using a Cobb trawl during research surveys in the Hawaii Archipelago. Samples of Green Jobfish from the EIO (Figure 1) were collected by the Government of Western Australia during scientific surveys at offshore atolls (i.e., Scott and Seringapatam reefs, Rowley Shoals, Cartier Island) off the northwestern coast of Australia and from two Indian Ocean Territories (i.e., Christmas Island and Cocos [Keeling] Islands) from 1996 to 2009. At these locations, fish were captured on reef habitats from lagoons, insular shelves, or steep slopes using hook and line, hydraulic droplines, or demersal long lines at depths ranging from 3 to 200 m. Whole fish were measured for fork length (FL) to the nearest centimeter, and the sex of each fish was determined by macroscopic examination of the gonads. The sex of fish that were

difficult to determine was classified as “unknown.” Sagittal otoliths were extracted, cleaned, and stored dry in vials.

Otolith preparation and aging criteria.—Thin sections of juvenile and adult Green Jobfish otoliths were prepared by first mounting the whole otolith to a glass slide by using a thermal adhesive; the primordium was aligned with the short edge of the slide and the sulcus acusticus was aligned perpendicular to the long edge of the slide. The otolith was ground transversely and perpendicular to the sulcus to within close proximity of the primordium by using 1,600-grit diamond-coated lap on a grinding wheel. The otolith was removed from the slide edge and remounted with the previously ground section facing downward, and then it was ground to a thickness of 130–250 μm .

Whole otoliths from larval fish were immersed in immersion oil and examined using a compound microscope (400 \times magnification) to count daily rings. The number of days were divided by 365 to get a decimal age for

each larval fish. Aging of sectioned Green Jobfish otoliths followed the previously established aging criterion that identified the first annual mark using daily growth increments and validated annual growth zones (i.e., deposition of one opaque and one translucent zone per year) using bomb radiocarbon and edge increment techniques (O'Malley et al. 2016). When applied to a reference collection of Green Jobfish otoliths, this criterion resulted in between-reader aging precision that was within the acceptable ranges for deepwater snappers (O'Malley et al. 2016; Wakefield et al. 2017). Final annual age estimates were converted to decimal age using the peak-spawning month, timing of opaque zone formation, and month of capture:

$$\text{Age}_d = \text{age}_c + \frac{\text{month}_c - \text{month}_p}{12},$$

where Age_d = decimal age, age_c = estimated age-class, month_c = month of capture, and month_p = month of peak spawning (June) (Everson et al. 1989).

Growth trajectories.—Growth of Green Jobfish was described using the von Bertalanffy growth function (VBGF; von Bertalanffy 1938) fitted to the FL-at-age data by using nonlinear least-squares regression with constant residual variance:

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)} \right],$$

where L_t = the predicted mean FL at age t (in years), L_∞ = the asymptotic length (FL in centimeters), K = the growth coefficient (per year), t = estimated age (in decimal years), and t_0 = the theoretical age (in years) at which fish would have zero length. Confidence limits were determined by bootstrapping where 1,000 sets of parameters were derived by random resampling with replacement. Allowing the VBGF to estimate t_0 resulted in large negative values in some of the data sets lacking small fish (<20 cm FL). The exception was the MHI pooled-sexes data set, which contained 7 presettlement fish of unknown sex ranging from 1.3 to 2.9 cm FL and 10 to 25 d old as well as 13 postsettlement (small or young) fish of unknown sex ranging from 9.4 to 30.4 cm FL and 93 to 486 d old (Table S1 in the Supplement available separately online). Fitting the unconstrained VBGF to the MHI pooled-sexes data set resulted in realistic t_0 and L_0 estimates: -0.16 and 3.90 cm, respectively. Therefore, rather than using an uninformed t_0 value of 0, t_0 was fixed at -0.16 when fitting the constrained VBGF to all other data sets. Informed values of t_0 overcome some of the biases inherent in constrained growth models when small fish are lacking (Berumen 2005; Pardo et al. 2013).

To investigate the effects of sex and location on growth, these factors were added as covariates to an

informed constrained ($t_0 = -0.16$) Kimura's (2008) extended VBGF (EVB). The advantage of this approach is that all data can be used to estimate multiple effects, some of which may have relatively small samples sizes (Kimura 2008). In this general fixed-effects nonlinear model, K and L_∞ are modeled as functions of the covariates (β):

$$\begin{pmatrix} L_{\infty i} \\ K_i \end{pmatrix} = \begin{pmatrix} \beta_{0L} + x_{i1}\beta_{1L} + x_{i2}\beta_{2L} \\ \beta_{0K} + x_{i1}\beta_{1K} + x_{i2}\beta_{2K} \end{pmatrix},$$

where x_{i1} = the sex (female or male) dummy variable (either 0 or 1) and x_{i2} = the location (MHI versus NWHI or Hawaiian Archipelago versus EIO) dummy variable for the i th fish.

Models with no effects (i.e., sex only, location only, and with sex and location) were compared using the Akaike information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002) and the Bayesian information criterion (BIC). The AIC_c difference (ΔAIC_c) was calculated for each model by comparing it to the model with the smallest AIC_c . The ΔAIC_c values between 0 and 2 are thought to empirically support model selection, while values between 4 and 7 lend less support to selection (Burnham and Anderson 2002). Akaike weights (w_i) were estimated to determine the probability of choosing the correct model from a set of R models using the ΔAIC_c from each model:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)}.$$

The BIC was also used because of its ability to overcome AIC dependence on low heterogeneity between data sets by assigning a higher penalty for complexity (Brewer et al. 2016). The BIC difference (ΔBIC) was also calculated for each model by comparing with the model with the smallest BIC.

To specifically examine differences in growth between the MHI and the NWHI, these data were evaluated in a stepwise fashion by first removing EIO data. If no differences were found, step two was combining MHI and NWHI data sets into a Hawaiian Archipelago data set and then comparing that to the EIO data set. Statistical analyses were conducted in the statistical software environment R version 3.5.1 (R Core Team 2018) with the `nl` function in the `stats` package.

Natural mortality.—In each region, sex-specific M was estimated indirectly using two methods that leverage empirical relationships between M and specific life history parameters. The first was the Then et al. (2015) maximum-age-based estimator, which is an updated version of Hoenig's (1983) equation:

$$M = 4.899t_{\max}^{-0.916},$$

where t_{\max} = maximum observed age. The second indirect method was the Then et al. (2015) growth-parameter-based estimator, which is an updated version of the modified Pauly (1980) estimator (Pauly_{nls-T}):

$$M = 4.118K^{0.73}L_{\infty}^{-0.33},$$

where K and L_{∞} are the region-specific (i.e., MHI, NWHI, Hawaiian Archipelago, and EIO) VBGF parameter estimates. These two methods were recommended by Then et al. (2015) over other indirect M estimators.

RESULTS

Sample Sizes, Length and Age Ranges, and Maximums

A total of 450 Green Jobfish otoliths were collected and aged from the Hawaiian Archipelago (MHI = 139, NWHI = 248) and EIO (63) (Pacific Islands Fisheries Science Center 2020) (Table 1). Sizes ranged from 1.3 to 93.5 cm FL, and ages ranged from 10 d to 32 years.

Qualitative comparisons between sexes indicated that maximum estimated ages were similar for Hawaiian Archipelago males and females, but females obtained a larger maximum size (Table 1). In the EIO, the oldest male was 5 years younger than the oldest female, and females attained a larger maximum size (Table 1).

Spatial qualitative comparisons indicated that the NWHI maximum estimated age was 5 years older, and the maximum size 2.1 cm smaller, relative to the MHI (Table 1). The EIO maximum age was the same as the Hawaiian Archipelago, and the maximum size was 4 cm larger.

Growth Trajectories and Spatial Comparisons

All Green Jobfish growth curves indicated relatively fast growth for the first 8 years before reaching their asymptote (Figure 2; Table 1). According to the AIC_c estimates, the best fit of the EVB model to the length at age of Hawaiian Archipelago Green Jobfish supported the model with factors for only sex (Table 2). The w_i indicated there was a 60% chance that this was the best model describing the data given the other models considered. The next best-fit model (no effects) had a ΔAIC_c of 2.24 and a 20% probability of being the correct model. The ΔAIC_c for all remaining models were ≤ 4.43 . However, the BIC values indicated the reverse, with the no-effects model having the lowest BIC value and the sex-only covariate being the second-best model at 5.59 higher (Table 2). The differences between Hawaiian Archipelago male and female K and L_{∞} estimates were minimal (0.04 and 0.02, respectively; Table 2), and the sex- and location-specific bootstrap estimates of K and L_{∞} were all overlapping (Figure 3).

Because Green Jobfish growth rates indicated no significant differences between the MHI and NWHI but some evidence of possible sex-specific differences, data were pooled into a sex-specific Hawaiian Archipelago data set and compared with sex-specific growth of EIO fish. According to the AIC_c estimates, the best fit of the EVB model to the length-at-age data supported the model with factors for sex and location (Table 2). The w_i indicated there was a 77% chance that this was the best model describing the data given the other models considered. The next best-fit model (location) had a ΔAIC_c of 3.76 and a 12% probability of being the correct model. The ΔAIC_c values for the remaining models indicated little support for the remaining models (4.0 for sex only and 7.99 for no covariates). However, similar to the within

TABLE 1. Green Jobfish pooled (male, female, and unknown) and sex-specific size range, mean size, age range, mean age, constrained ($t_0 = -0.16$) von Bertalanffy growth model parameter estimates (K and L_{∞}), sample size (n), and maximum-age-based natural mortality estimate (M) from the main Hawaiian Islands (MHI), the Northwestern Hawaiian Islands (NWHI), the Hawaiian Archipelago (HI = MHI and NWHI pooled), and the eastern Indian Ocean (EIO).

Location	Sex	FL range (cm)	Mean FL (cm)	Age range (years)	Mean age (years)	K	L_{∞}	n	M
MHI	Pooled	1.3–89.5	56.0	0.03–27	8	0.31	72.78	139	0.24
	Male	37.4–80.0	61.0	3–21	8	0.33	72.53	65	0.30
	Female	26.7–89.5	62.6	1–27	10	0.29	73.26	74	0.24
NWHI	Pooled	46.8–87.4	68.19	2–32	13	0.34	71.65	248	0.20
	Male	46.8–80.4	67.35	2–32	11	0.35	71.92	124	0.20
	Female	53.3–87.4	69.03	3–31	14	0.30	71.90	124	0.21
HI	Pooled	1.3–89.5	63.29	0.03–32	11	0.33	72.02	387	0.20
	Male	37.4–80.4	65.15	2–32	10	0.34	72.16	189	0.20
	Female	26.7–89.5	66.61	1–31	12	0.30	72.18	198	0.21
EIO	Pooled	40.2–93.5	60.3	3–32	10	0.28	72.19	63	0.20
	Male	40.2–85.7	57.62	3–32	9	0.31	70.85	31	0.20
	Female	40.3–93.5	62.82	3–27	12	0.25	73.54	32	0.24

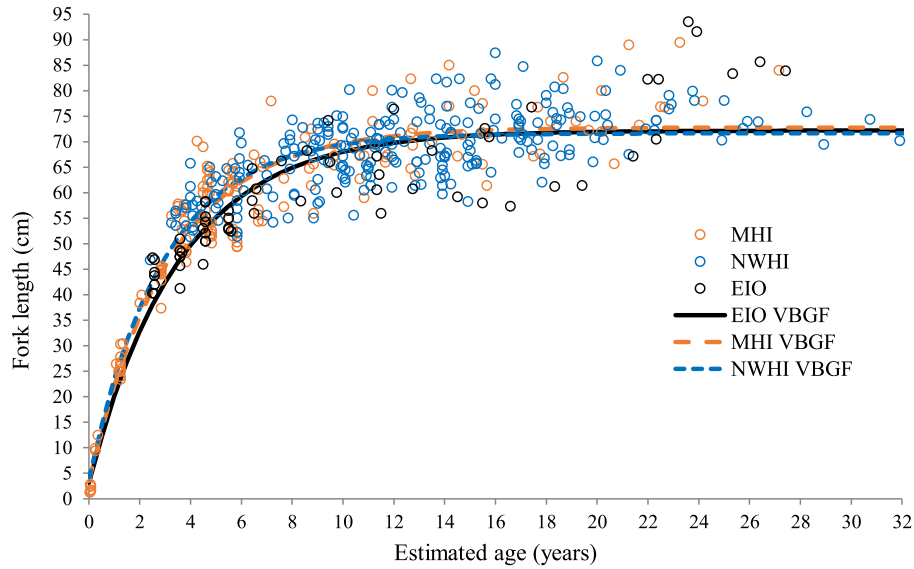


FIGURE 2. Von Bertalanffy growth curve (t_0 fixed to -0.16) with sexes pooled fitted to length-at-age data for Green Jobfish from the main Hawaiian Islands (MHI), the Northwestern Hawaiian Islands (NWHI), and eastern Indian Ocean (EIO).

TABLE 2. Comparisons of extended von Bertalanffy growth function models fitted to length-at-age data for Hawaiian Archipelago and eastern Indian Ocean Green Jobfish. Models with no covariates and with sex, location, and sex and location as covariates were compared by using the Akaike information criterion corrected for small sample sizes (AIC_c), differences in AIC_c between models (ΔAIC_c), Akaike weights, the Bayesian information criterion (BIC), and differences in BIC between models (ΔBIC). Location abbreviations are defined in Table 1.

Data set	Effects	df	AIC_c	ΔAIC_c	Akaike weight	BIC	ΔBIC
HI	None	3	2,467.64	2.24	0.20	2,479.45	0.00
	Sex (male, female)	5	2,465.40	0.00	0.60	2,485.04	5.59
	Location (MHI, NWHI)	5	2,469.83	4.43	0.07	2,489.47	10.02
	Sex, location	7	2,468.44	3.04	0.13	2,495.86	16.41
All	None	3	2,913.11	7.99	0.01	2,925.39	0.00
	Sex (male, female)	5	2,909.12	4.00	0.10	2,929.53	4.14
	Location (HI, EIO)	5	2,908.88	3.76	0.12	2,929.29	3.90
	Sex, location	7	2,905.12	0.00	0.77	2,933.63	8.24

Hawaiian Archipelago analysis, the model with the lowest BIC value had no effects. This model was separated by 3.90 from the second candidate model, which contained location as the only covariate. The differences between the models with the smallest and largest growth parameters was small ($K=0.09$, $L_\infty = 2.69$; Table 1). The Hawaiian Archipelago and EIO sex- and location-specific bootstrap estimates of K and L_∞ were overlapping, except for EIO females and Hawaiian Archipelago males (Figure 4).

Natural Mortality

The NWHI and EIO male Green Jobfish had a greater t_{max} than females, resulting in relatively lower estimates of M when using the updated Hoenig estimator, whereas MHI females had a greater t_{max} than males, which resulted in their lower estimate of M (Table 1). The

pooled-sex t_{max} (Table 1) did not differ greatly between areas; therefore, unsurprisingly, the indirect estimates of M using the updated Hoenig estimator were similar: pooled-sex MHI = 0.24, NWHI = 0.20, Hawaiian Archipelago = 0.20, and EIO = 0.20. The updated version of the modified Pauly (1980) estimator ($Pauly_{nls-T}$) provided similar estimates to the t_{max} estimator: pooled-sex MHI = 0.20, NWHI = 0.22, Hawaiian Archipelago = 0.21, and EIO = 0.19.

DISCUSSION

The population characteristics and age-based demography of tropical snappers are poorly understood, yet what is known indicates that they can vary considerably. This is the first study that compares the sex-specific population

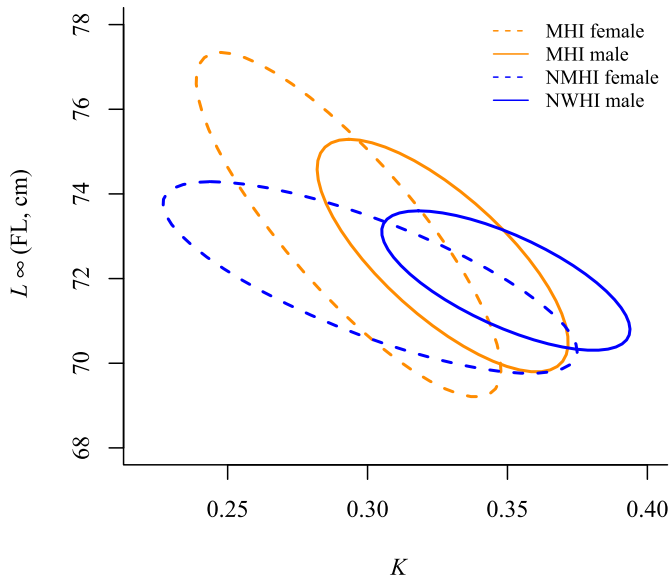


FIGURE 3. Green Jobfish von Bertalanffy growth parameter (K and L_{∞}) bootstrap ellipses for main Hawaiian Islands females ($n=74$) and males ($n=65$) and Northwestern Hawaiian Islands females ($n=124$) and males ($n=124$).

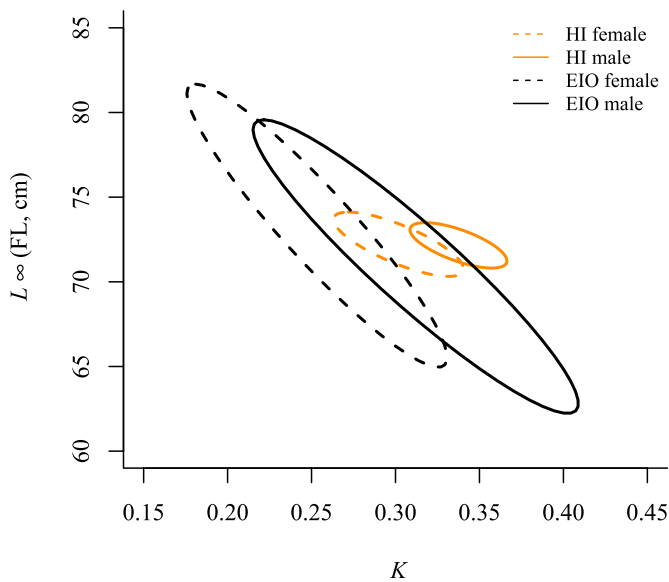


FIGURE 4. Green Jobfish von Bertalanffy growth parameter (K and L_{∞}) bootstrap ellipses for Hawaiian Archipelago females ($n=198$) and males ($n=189$) and eastern Indian Ocean females ($n=32$) and males ($n=31$).

characteristics and age and growth of Green Jobfish from the Hawaiian Archipelago and the EIO using nascent and standardized otolith preparation and aging techniques. The results will inform stock assessments and management measures, while furthering our understanding of these species.

Green Jobfish display sexual dimorphism, with females obtaining a greater maximum size than males regardless of location. Despite this, there was no sex-specific difference in maximum age. Within the Hawaiian Archipelago, the slightly larger maximum and mean ages and mean size in the NWHI relative to the MHI may be due to the historic lack of a recreational or subsistence fishery in the NWHI and the area being closed to all fishing since 2011. Relative to the EIO, the mean size was larger in the Hawaiian Archipelago, but the maximum size was smaller. Caution is advised with the conclusions drawn here because the otoliths were not collected in a truly random manner, and the resulting maximum and mean size and age information may not be representative of the populations. However, the collection of numerous larger individuals lends confidence to maximum ages in the early 30s.

The AIC_c and the BIC selected different growth models as the most informative. The AIC_c -based approach indicated that covariates affected the von Bertalanffy growth parameter estimates in the within Hawaiian Archipelago analysis (sex) and in the Hawaiian Archipelago and EIO analysis (sex and location), whereas the BIC indicated that the inclusion of covariates did not improve model fits in either analysis. The decision to use an AIC_c or BIC approach to select the most appropriate growth model, and therefore determine if factors affect Green Jobfish growth, is difficult (Brewer et al. 2016; Dziak et al. 2020). The AIC_c assigns a greater penalty for complexity than BIC when sample sizes are very small (generally, when n/k is less than 40, where k = the number of fitted parameters in the most complex model [Symonds and Moussalli 2011]); however, the BIC penalty is greater than that of the AIC_c when heterogeneity is large (Brewer et al. 2016). The choice between the AIC_c or BIC approach is a matter of sensitivity versus specificity (Dziak et al. 2020). In this study, the BIC-based approach was selected because (1) there is a large amount of heterogeneity in the data and (2) all of the models for within the Hawaiian Archipelago EVB and two out of three of the models in the Hawaiian Archipelago–EIO EVB had $\Delta AIC_c < 5$, indicating that multiple models were plausible and should be considered despite small differences in the growth parameter estimates. When the BIC penalty was applied to the more complex sex models, it likely overwhelmed the influence of the marginal differences in growth parameter estimates between the data sets that the AIC_c interpreted as influential. Based on our data, the BIC-selected final models indicate that Green Jobfish do not exhibit variation in growth between sexes nor are there any differences in growth within or between the Hawaiian Archipelago and the EIO. The small differences in the estimated VBGF parameters support the modelling results that growth is not sex- or location-specific.

Latitude (and the associated effect of temperature) is known to influence fish growth (Conover and Present 1990; Stocks et al. 2014), particularly within the lutjanids (Williams et al. 2007; Cappo et al. 2013; Williams et al. 2017). Green Jobfish growth and maximum age varies among populations in the Coral Sea ($K=0.85$, $L_{\infty}=62.3$ cm, and maximum age = 16 years [Heupel et al. 2010]), the western Indian Ocean (Mauritius and the Seychelles) ($K=0.13$, $L_{\infty}=79.0$ cm, and maximum age = 19 years [Pilling et al. 2000]), and the central Indian Ocean (Chagos Archipelago) ($K=0.16$, $L_{\infty}=77.9$ cm, and maximum age = 23 years [Pilling and Mees 2000]). Why growth is similar among the MHI, the NWHI, and the EIO but dissimilar to any of these other locations (the Great Barrier Reef, Mauritius–Seychelles, and the Chagos Archipelago) is hard to explain. Typically, it is difficult to compare growth estimates between constrained and unconstrained growth models, but the other Green Jobfish studies used constrained growth models ($t_0=0$). This study also used constrained growth models yet with a different informed $t_0=-0.16$. It is unlikely that a different t_0 is the reason for the observed growth variability between locations since a post hoc analysis with $t_0=0$ resulted in only a 0.02 and 0.25 cm difference in K and L_{∞} , respectively. Perhaps the radically different growth estimates and maximum ages may be due to differences in fishing pressure or different sampling designs (Chang et al. 2019; Goodyear 2019) among locations. It also may be related to the otolith preparation methods and aging criteria used (Newman et al. 2015, 2016, 2017).

Then et al. (2015), based on cross validation prediction error, model residual patterns, model parsimony, and biological considerations, found that the updated version of the Hoenig (1983) M estimator performed better than other commonly used estimators. They recommended using this estimator or the modified Pauly estimator. This study found that both methods produced similar M estimates among locations. The inconsistent sex-specific differences in M that were estimated using the updated Hoenig estimator were driven by differences in t_{max} . Pilling and Mees (2000) estimated Chagos Archipelago Green Jobfish M using the Pauly (1980) empirical formula and found a similar value as this study's pooled-sex value (0.22). The updated version of the Hoenig (1983) estimator provided similar M estimates as those using a multinomial age-based catch curve analysis of two lutjanids with similar t_{max} from unfished areas of the Samoa Archipelago and Mariana Archipelago (O'Malley et al. 2019), lending further support for this estimator for snappers that exhibit a similar longevity and its use in subsequent related stock assessments.

In conclusion, Green Jobfish in both the EIO and Hawaiian Archipelago exhibited long life spans, moderately slow growth, and low rates of natural mortality.

These traits are similar to many shallow-water lutjanids (e.g., Malabar Snapper *Lutjanus malabaricus*, Five-lined Snapper *L. quinquelineatus*, Emperor Snapper *L. sebae*), indicating a similar exploitation risk profile (Newman et al. 1996; Newman 2002; Newman and Dunk 2002). These age-based life history characteristics are different than for their deepwater congeners that are generally longer lived, have slower growth, and show lower rates of natural mortality, resulting in a very different exploitation vulnerability (Newman et al. 2016). The length-at-age and growth information generated by this research was an important component of enabling the change in the MHI Green Jobfish stock assessment approach. A 2017 stock assessment used a length-based mortality model with life history parameters (K and L_{∞}) estimated from a data-poor approach to obtain the spawning potential ratio (Nadon 2017). The 2020 approach used an integrated statistical catch-at-age model (Nadon et al. 2020). While both assessment approaches reached the same conclusion on stock status, the catch-at-age model was able to integrate multiple data sets (including the explicit use of this length-at-age information), and therefore, it is considered an improvement in the scientific information available for sustainable management of this species.

ACKNOWLEDGMENTS

We sincerely thank the commercial and recreational fishers who provided the Green Jobfish otoliths. Funding for sample collection in the Hawaiian Archipelago was provided by NOAA Improve a Stock Assessment, the U.S. Fishermen Disaster Release funds, and NOAA Cooperative Research Funds. Logistic support for the collection of samples from northwestern Australia was provided by the Department of Primary Industries and Regional Development, Government of Western Australia. We thank B. Richard for creating the map and E. Reed, R. Nichols, and E. Schemmel, as well as two anonymous reviewers and the journal editor, for thoughtful reviews and input. There is no conflict of interest declared in this article.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.