ORIGINAL ARTICLE

Fisheries



Growth and maturation of three commercially important coral reef species from American Samoa

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Received: 20 February 2020 / Accepted: 4 October 2020 / Published online: 23 October 2020 © Japanese Society of Fisheries Science 2020

Abstract

This study presents age-based life history information on three small-bodied species targeted in the American Samoan fishery: *Chlorurus japanensis* palecheek parrotfish/fuga-alosama, *Lethrinus rubrioperculatus* spotcheek emperor/fiola pa`o`omumu, and *Naso lituratus* orangespine unicornfish/ili`ilia. Age and reproductive information were derived from sagittal otoliths and gonads. Maximum observed ages were 7 years for *C. japanensis*, 10 years for *L. rubrioperculatus*, and 25 years for *N. lituratus*. Due to a limited numbers of immature samples, a proxy for size at 50% maturity (L_{50}) was derived from the relationship between asymptotic fork length (L_{∞}) and L_{50} based on data published for species from similar geographic regions and respective families. L_{50} was estimated at 20.9 cm for *C. japanensis*, 20.4 cm for *L. rubrioperculatus*, and 17.5 cm for *N. lituratus*. Derived estimates were within 1 % of the L_{50} calculated for *C. japanensis* and *N. lituratus* from the limited number of immature samples collected in this study, indicating that for regions where sampling ability is limited, derived relationships between L_{∞} and L_{50} can be used to calculate an appropriate proxy. *Naso lituratus* demonstrated a biphasic mortality schedule with a higher than expected total mortality rate in the first 7 years of life. The age-based demographic information presented here can be used for future stock assessments and ecosystem models, which should facilitate improved management.

Keywords American Samoa · Growth · Life history · Maturity

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s12562-020-01471-9) contains supplementary material, which is available to authorized users.

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Introduction

Fish are an integral part of Samoan culture (*fa*[']*asamoa*), and are utilized in both ceremonies and cultural exchanges. The cultural importance of fish in American Samoa drives much of the fishing effort (Craig et al. 1993; Carroll et al. 2012; Severance et al. 2013). Fish are also a critical source of dietary protein within Pacific communities (Bell et al. 2009; Barnett 2011). The nearshore fishery in American Samoa consists of nearly 300 species of fish from over 40 families with varying growth and maturation strategies (Pacific Islands Fisheries Science Center 2020). However, this nearshore fishery is considered data limited due to a lack of information on the life history of a majority of its targeted fish species. Thus, the management of this fishery has been hindered by limited data on fish growth and maturity.

The objective of this study was to provide estimates of growth, life span, and size at maturity for three targeted species from different families within American Samoa: fugaalosama/palecheek parrotfish *Chlorurus japanensis* (Bloch 1789), fiola pa`o`omumu/spotcheek emperor *Lethrinus*

rubrioperculatus (Sato 1978), and ili`ilia/orangespine unicornfish Naso lituratus (Forster 1801). These species were selected in collaboration with the Division of Marine and Wildlife Resources (DMWR) based on information required by the local fishery management agency. Each of the selected species ranks within the top three in terms of biomass of total catch for each of their respective families: C. japanensis, second in terms of biomass within the Scaridae (22% of family catch); L. rubrioperculatus, second in terms of biomass within the Lethrinidae (38% of family catch); and N. lituratus, third in terms of biomass within the Acanthuridae (7% of family catch) (Pacific Islands Fisheries Science Center 2020). All three species are commonly targeted by commercial and subsistence fisheries throughout the Indo-Pacific region (Gillett and Moy 2006; Houk et al. 2012; Taylor et al. 2014a, b). The majority of L. rubrioperculatus are captured using hook and line, while both N. lituratus and C. *japanensis* are caught almost exclusively by spear within American Samoa. Age-based life history information has been relatively well studied for all three families in recent decades (Choat and Axe 1996; Choat and Robertson 2002; Ebisawa and Ozawa 2009; Trianni 2011; Taylor et al. 2014b, 2017; Andrews et al. 2016). The resultant age-based information including that on growth, mortality, and maturity facilitates stock assessments and management strategies for different regions of the Indo-Pacific (Newman et al. 2016).

Chlorurus japanensis

Chlorurus japanensis is one of the most abundant parrotfish species within American Samoa, and is the second highest landed parrotfish species by mass (Page 1998). Parrotfishes (Labridae: subfamily Scarinae) are microphages that feed on endolithic microbial resources on and within the reef surface (Clements et al. 2017). Parrotfishes are common members of reef fish assemblages, with most species exhibiting short to moderate life spans ranging from 3 to 20 years (Taylor et al. 2018c). While there has been a great deal of life history work performed on parrotfish species throughout the Pacific, *C. japanensis* is relatively scarce in many regions outside of American Samoa, and there are no demographic data on this species.

Naso lituratus

Naso lituratus is a highly targeted species throughout the Indo-Pacific, and consistently ranks among the most targeted species in nearshore fisheries including those of American Samoa (Gillett and Moy 2006; Houk et al. 2012; Taylor et al. 2014b). Unicornfish (genus *Naso*, family Acanthuridae) have been shown to have moderate to long life spans (14–52 years) throughout the Pacific (Choat and Axe 1996; Choat and Robertson 2002; DeMartini et al. 2014; Taylor

et al. 2014b; Andrews et al. 2016). However, most of these studies were focused on *Naso unicornis*, and relatively little demographic information has been published for *N. litura-tus*. Maximum age estimates have been published for *N. lituratus* from three different regions: Pohnpei (14 years), Guam (13 years), and the Great Barrier Reef (39 years) (Choat and Robertson 2002; Taylor et al. 2014b). Based on published data from Guam, *N. lituratus* is thought to mature at a very small size (<16 cm), with females maturing before males (Taylor et al. 2014b).

Lethrinus rubrioperculatus

Lethrinus rubrioperculatus (family Lethrinidae) is a mesopredator that preys on small fish and invertebrates and is commonly targeted by commercial and subsistence fisheries throughout its broad Indo-Pacific range (Carpenter and Allen 1989). Previous work on L. rubrioperculatus from the Marianas and Japan estimated the age of the studied fish at 8 years and 13 years, respectively (Ebisawa 1997; Ebisawa and Ozawa 2009; Trianni 2011). Lethrinids are generally considered protogynous hermaphrodites (transitioning from female to male after initial maturation as females) (Young and Martin 1982). Size at maturity of L. rubrioperculatus from both the Marianas and Japan has been calculated to be around 22 cm (Ebisawa 1997; Trianni 2011). Local demographic information from American Samoa suggested that Lethrinus xanthochilus, a larger emperor fish, has a maximum age of 16 years (Taylor et al. 2018b). Life span has been positively linked to body size for emperor fish; therefore, we expect L. rubrioperculatus to have a lower maximum age than the larger bodied L. xanthochilus (Taylor et al. 2017).

The age, growth, and size at maturity information from this study will help to facilitate future management of these commercially and culturally important species within American Samoa. The derived age and growth information can also be used for future stock assessments to help inform managers about the status of this fishery.

Materials and methods

Study area and sample protocol

To analyze growth and reproductive life history of the three target species, *C. japanensis*, *L. rubrioperculatus*, and *N. lituratus*, staff from DMWR purchased samples opportunistically from vendors and participating fishermen on the island of Tutuila, American Samoa (14.3°S, 170.7°W) between April and August 2019. Each fish was measured to the nearest centimeter for fork length (FL) and its total weight determined (accuracy of 10 g). Each fish was

assigned a unique alphanumeric code that linked its physical specimens (otoliths and gonads) to the following associated data: body length, weight, gonad weight, sex, and sampling date. Paired otoliths (sagittae) were removed from each fish, cleaned with ethanol and stored dry in individually labeled vials. Gonads were extracted and weighed to the nearest milligram and sex determined macroscopically. Cross sections of fresh gonad lobes from the mid-section were removed and stored in histological cassettes in a 10% buffered formalin solution.

Age and growth determination

Otoliths were weighed to the nearest 0.1 mg. Otolith weight was compared to age using a linear regression to determine if otolith weight was a good indicator of age for each of the species. One otolith from each fish was selected at random and attached to a slide using Crystalbond 509, a thermoplastic glue, so that the primordium was just inside the edge of the slide and the sulcal ridge was perpendicular to the slide edge. The otolith was then sanded down until flush with the edge of the slide using a 600-grit diamond lapping wheel with continuous water flow. The otolith was removed with heat, and the newly sanded surface reattached to the slide. A second sanding of the otolith was undertaken to produce a thin (~200–250 μ m) transverse section encompassing the core material, and the section covered with Crystalbond 509 to improve clarity.

Using reflected and transmitted light, annuli were identified by stereomicroscope as alternating translucent and opaque bands, which were counted along a consistent axis on the face of the sections to estimate the age in years. Annual periodicity of otolith bands has been well documented in all three families, and validated for *L. rubrioperculatus* and *N. lituratus* (Ebisawa and Ozawa 2009; Taylor et al. 2014b). Annuli of each specimen were counted on three separate occasions, and the age was determined when at least two counts agreed. If three counts differed by one presumed annulus, the middle count was used to determine age. Repetitive count patterns falling outside the above criteria never occurred. The index of average percent error (IAPE) was calculated as an indicator of the precision between readings for each species (Campana 2001).

The length and weight of each species was fitted using a power function represented by $W = aL^b$, where weight (W) can be estimated given the length (L) and the two parameters *a* and *b* (Schneider et al. 2000).

Sex-specific and combined size-at-age data were fitted with the von Bertalanffy growth function (VBGF) to estimate growth parameters using the least squares estimation. The VBGF is represented by: $L_t = L_{\infty}[1 - e^{-K(t-t_0)}]$, where L_t is the mean FL (cm) at age t (years), L_{∞} is the mean asymptotic FL, K is the growth coefficient describing the curvature towards L_{∞} , and t_0 is the theoretical age at which the FL is equal to zero. Growth was compared between the sexes using a likelihood ratio test (Kimura 1980).

Since the samples were collected from the fishery and no recently settled fish were collected, the fitted VBGF growth curve was constrained to the following inferred sizes at settlement: *C. japanensis*, 2.5 cm (Bellwood and Choat 1989); *L. rubrioperculatus*, 3.0 cm (Nakamura et al. 2010); and *N. lituratus*, 5.0 cm (Planes et al. 2002). These sizes are based on those of similar species, and were approximated to fit the correct type of length measurement. The selected sizes represent the best estimates of size at age 0, when fish recruit from the larval life phase to the reef and begin a more rapid phase of growth and development.

Maturity

Fixed sections of gonad material were histologically processed at Hawaii Diagnostic Laboratories in Honolulu, Hawaii. Samples were imbedded in paraffin wax, sectioned transversely at 6 μ m and stained with hematoxylin and eosin (Sullivan-Brown et al. 2011). Slides were assessed under a compound microscope with transmitted light to determine sex and level of reproductive development following the standardized terminology of Brown-Peterson et al. (2011). Females were classified as immature, developing, spawning capable, actively spawning, regressing, and regenerating. Males were classified as either immature or mature based on the presence/absence of spermatozoa.

Since the sampling was based on commercial catch, very few immature specimens were collected. Due to the lack of immature fish in the samples, size at 50% maturity (L_{50}) was estimated by fitting a curve (least squares estimation) to the relationship between asymptotic FL (L_{∞}) and L_{50} for species from the same family and similar locations from the published literature.

For female *C. japanensis* and male *N. lituratus* (species for which there were seven and six immature samples, respectively), L_{50} was also estimated, using the FSA package in R (Ogle et al. 2019; R Core Team 2019), by logistic regression analysis and fitting the FL as the explanatory variable to the stage of maturity (immature 0, mature 1) as the binomial response variable. The regression was fitted using a binomial generalized linear model. Confidence intervals for size at maturity were derived by bootstrap resampling (1000 iterations).

Mortality

Total mortality (Z) was calculated based on age distributions using an age-based catch curve for each species. The natural logarithm of the number of fish per age class was plotted against the corresponding age, where Z represents the absolute value of the slope of the descending limb of the fitted line. If zero values arose for the different age classes, they were omitted from the catch curve analysis.

Naso lituratus demonstrated a two-phase mortality schedule, with higher mortality rates in the earlier stages of life. A biphasic mortality schedule has also been described for *N. unicornis* from multiple regions across the Pacific (Taylor et al. 2019). Breakpoint analysis was used to calculate the optimal age at which the mortality schedules shift. Two independent lines were fitted on either side of the breakpoint and mortality was modeled using a segmented analysis.

Results

A total of 79 *C. japanensis*, 116 *L. rubrioperculatus*, and 184 *N. lituratus* samples were measured, weighed and dissected within the 5-month sampling period. Specimens of *C. japanensis* ranged from 19.2 cm to 29.6 cm FL (mean \pm SD = 24.8 \pm 3 cm), *L. rubrioperculatus* ranged from 19.9 cm to 32.5 cm FL (25.9 \pm 3 cm), and those of *N. lituratus* from 15.3 cm to 28.1 cm FL (21.5 \pm 2 cm). Length frequency distributions for the three species are displayed in Fig. 1. Males of each species had a larger average length than females, especially in *L. rubrioperculatus*, where the males were on average 4 cm larger than the females (males 28.5 \pm 2 cm, females 24.7 \pm 3 cm). The weight-length relationships for each species are as follows: $W_{kg} = 1.793 \times 10^{-5} (FL_{cm})^{2.951} (r^2 = 0.947)$ for *C. japanensis*, $W_{kg} = 2.217 \times 10^{-5} (FL_{cm})^{2.951} (r^2 = 0.931)$ for *L. rubrioperculatus*, and $W_{kg} = 4.582 \times 10^{-5} (FL_{cm})^{2.793} (r^2 = 0.75)$ for *N. lituratus* (Table 1).

Age determination and growth

The maximum observed ages were 7 years for *C. japanensis*, 10 years for *L. rubrioperculatus*, and 25 years for *N. lituratus*. IAPE values comparing first and second otolith reads were 1.8, 2.9, and 2.0 for *C. japanensis*, *L. rubrioperculatus*, and *N. lituratus*, respectively. Previously published otolith-based age data demonstrated that opaque zones were

fully deposited during the period of the lowest sea surface temperatures in American Samoa, between August and September (Taylor et al. 2018b). All three species deposited clearly defined annuli signified as opaque and translucent bands characteristic of otolith patterns previously identified for their respective families (Fig. 2) (Grandcourt et al. 2010; Taylor et al. 2014b; DeMartini et al. 2017).

Otolith weight was a strong predictor of age for all three species (*p*-value < 0.005), with the relationship best explained by a linear equation for *C. japanensis* and *L. rubrioperculatus* and a standard quadratic equation for *N. lituratus* (Fig. 3). The relationship between otolith weight and age did not differ substantially between the sexes for the three species.

The likelihood ratio test (Kimura 1980) demonstrated that growth profiles for C. japanensis ($\chi^2 = 23.1$) and L. *rubrioperculatus* ($\chi^2 = 21.7$) were significantly different (p-value < 0.001) between males and females (Fig. 4a, b). There was no significant difference in growth between males and females for N. lituratus ($\chi^2 = 6.0$, p-value = 0.112) (Fig. 4c). N. lituratus demonstrated a more rapid initial growth phase than the other two species, reaching a maximum size before 3 years of age. Von Bertalanffy growth parameter values L_{∞} and K for the combined sexes of each species were as follows: C. japanensis, $L_{\infty} = 28.1$ cm and K = 0.82 year⁻¹; L. rubrioperculatus, $L_{\infty} = 28.5$ cm and K = 0.65 year⁻¹; and N. lituratus, $L_{\infty} = 24.3$ cm and K = 0.77 year⁻¹. Sex-specific VBGF parameters and confidence intervals (CI) are presented in Table 1. Sex-specific maximum ages were 5 and 7 years for female and male C. japanensis, respectively; 10 years for both male and female L. rubrioperculatus; and 25 and 16 years for female and male N. lituratus, respectively.

Maturity

Sexual identity and female maturation profiles were characterized using histological sections of gonads from 74 *C. japanensis* (39 females), 105 *L. rubrioperculatus* (69 females), and 182 *N. lituratus* (51 females). The sample data set included very few immature specimens, i.e., only seven



Fig. 1 Sex-specific length-frequency distributions for females (*black bars*) and males (*gray bars*) of **a** *Chlorurus japanensis*, **b** *Lethrinus rubrioperculatus*, and **c** *Naso lituratus*

	Chlorurus japanensis			Lethrinus rubrioperculatus			Naso lituratus		
	Males	Females	Sexes com- bined	Males	Females	Sexes com- bined	Males	Females	Sexes com- bined
L_{∞} (cm)	28.7 (27.5– 30.0)	27.1 (25.5– 28.9)	28.1 (26.9–29.3)	29.1 (28.1– 30.5)	27.3 (26.5– 28.2)	28.5 (27.8– 29.2)	24.6 (23.8– 25.4)	23.4 (22.0–24.9)	24.3 (23.6– 25.0)
K (year ⁻¹)	0.88 (0.74– 1.07)	0.84 (0.68– 1.07)	0.82 (0.71– 0.97)	0.71 (0.50– 1.19)	0.74 (0.65– 0.84)	0.65 (0.58– 0.73)	0.76 (0.68– 0.86)	0.83 (0.68– 1.07)	0.77 (0.70– 0.86)
t_0 (year)	- 0.10	- 0.12	- 0.11	- 0.15	- 0.16	- 0.17	- 0.30	- 0.29	- 0.30
n (aged)	35	43	78	42	71	114	132	51	183
LWa	-	-	$1.79E^{-5} \\ (1.0E^{-5} - 2.8E^{-5})$	-	-	$2.22E^{-5} \\ (9.2E^{-6} - 4.5E^{-5})$	-	-	4.58E ⁻⁵ (2.2E ⁻⁵ - 9.5E ⁻⁵)
LWb	-	_	3.069 (2.9–3.2)	-	_	2.951 (2.7–3.2)	_	_	2.79
$L_{50} ({\rm cm})$	-	20.8/21.0 ^a (18.9– 21.9)			21.2 ^a		17.7 (16.3– 18.3)		17.5 ^a
L ₉₅ (cm)	-	23.2 (21.1– 24.7)	_				19.2 (17.8– 19.9)		
Z (year ⁻¹)	-	-	0.58 (0.50– 0.66)	-	-	0.62 (0.41– 0.83)	-	-	0.79 ^b (0.66– 0.91)

Associated 95% confidence intervals are presented in parentheses, where appropriate

b

 L_{∞} Asymptotic fork length; K growth coefficient; t_0 hypothetical age when length equals zero; n (aged) number of specimens used in age analysis; LWa, LWb parameters for length–weight relationship; L_{50} length at 50% sexual maturity; L_{95} length at 95% sexual maturity; Z instantaneous total mortality estimated from the catch curve

1.0 mm

 ${}^{a}L_{50}$ was derived from the published literature based on the relationship between L_{∞} and L_{50}

^bZ was estimated for the younger portion of the biphasic mortality schedule for *N. lituratus*

Fig. 2 Photomicrographs of transverse otolith sections for **a** *Chlorurus japanensis*, **b** *Lethrinus rubrioperculatus*, and **c** *Naso lituratus*. Annual increments (opaque bands) are denoted by *white marks*



immature female *C. japanensis*, zero immature specimens for *L. rubrioperculatus*, and six male *N. lituratus*. Therefore, length at maturation (L_{50}) was estimated by assessing the relationship between L_{∞} and L_{50} for species from the same family and similar locations from the published literature (Fig. 5; Online Resource Table S1). Data points from the published literature were fitted to several simple models to derive the best fit; for *L. rubrioperculatus* and *N. lituratus* the best fit was a linear regression, while for *C. japanensis* a quadratic polynomial regression fitted the data the best.

1.0 mm



Fig. 3 Sex-specific relationships between sagittal otolith weight and annual age (represented by number of annuli) for **a** *Chlorurus japanensis*, **b** *Lethrinus rubrioperculatus*, and **c** *Naso lituratus*. Equations are as follows: *C. japanensis*, age=216.10(ot.wt.)

- 0.4913 (r^2 =0.8471); *L. rubrioperculatus*, age=70.11(ot.wt.) - 0.8455 (r^2 =0.9014), *N. lituratus*: age=72,587(ot.wt.)² - 213.23(ot.wt.)+1.4786 (r^2 =0.9236); where ot.wt. is otolith weight



Fig. 4 Sex-specific and combined von Bertalanffy growth curves for **a** *Chlorurus japanensis*, **b** *Lethrinus rubrioperculatus*, and **c** *Naso lituratus*. The *solid line* represents the combined best fit curve for both sexes for each species. See Table 1 for parameter estimates



Fig.5 Size at 50% maturity (L_{50}) interpolations based on published life history information for **a** *Chlorurus japanensis*, **b** *Lethrinus rubrioperculatus*, and **c** *Naso lituratus. Gray dots* represent data

points from the literature, and the *black diamonds* represent the estimated L_{50} for each species based on the calculated asymptotic fork length (L_{∞}) fitted to the trend line

Nineteen different data points for 14 species from four locations were used to calculate the L_{50} for *C. japanensis* (Choat and Robertson 2002; Hamilton et al. 2008; Taylor et al. 2014a, 2018a; Taylor and Cruz 2017; Taylor and Pardee 2017), which was estimated at 20.9 cm. For *L. rubrioperculatus*, ten data points for six species from six locations (Ebisawa 1997; Ebisawa and Ozawa 2009; Trianni 2011; Taylor et al. 2017, 2018b) were used, and L_{50} was estimated at 20.4 cm. The fewest data points, only four for two species from three locations (Taylor et al. 2014b; Andrews et al. 2016) were used for *N. lituratus*, for which the estimated L_{50} was 17.5 cm.

Length at maturity (L_{50}) was also modeled for *C. japanensis* using the seven immature samples, and for male *N. lituratus* using the six immature male samples. Length at maturity was estimated as 20.8 cm (18.9–21.9 cm 95%)

CI) and 17.7 cm (16.3–18.3 cm 95% CI) for *C. japanensis* and male *N. lituratus*, respectively (Fig. 6). Both calculated values were within 1 % of the L_{50} derived from the literature.

Mortality

Based on catch at age frequency, all three species fully entered the fishery at 2 years of age. Catch curves estimated values of Z as 0.58 year⁻¹ for *C. japanensis*, and 0.62 year⁻¹ for *L. rubrioperculatus* (Fig. 7a, b).

Naso lituratus showed a two-phase mortality schedule, where the breakpoint occurred at 7 years (Fig. 7c). Z was estimated at 0.79 year^{-1} for the first 7 years, and 0.18 year^{-1} for the later part of the life span. The mortality rate prior to the breakpoint was 4.4 times higher than the rate after the breakpoint.

Discussion

This study provides a demographic baseline for future stock assessments and management of three targeted species in American Samoa that differ in their growth, maximum age, maturity, and mortality rates. *Chlorurus japanensis*, *L*.



Fig. 6 Size at maturity for **a** female *Chlorurus japanensis* and **b** male *Naso lituratus*, where *1* indicates mature and 0 indicates immature. The *dotted line* indicates L_{50}

rubrioperculatus, and *N. lituratus* represent various trophic levels and ecosystem niches, and are targeted using different fishing methods. All three species fall within the top three of landings in terms of biomass per respective family (*C. japanensis*, 22%; *L. rubrioperculatus*, 38%; and *N. lituratus*, 7%).

Due to few specimens of smaller individuals, size at maturity was interpolated based on the relationship between L_{∞} and L_{50} for similar species in the primary literature. The interpolated L_{50} is used as an informative proxy rather than a means of definitively deriving L_{50} when immature samples are absent. However, the calculated estimates for L_{50} for C. japanensis and N. lituratus were within 1 % of the interpolated L_{50} from the primary literature, indicating that for regions where the ability to sample is limited, the relationship between L_{∞} and L_{50} can be used to calculate an appropriate proxy. Derivations of life history parameters such as L_{50} and K from L_{∞} reported in published growth studies for other regions have been used to produce the necessary input data for data-limited stock assessments, e.g., spawning potential ratio (Prince et al. 2015; Nadon and Ault 2016). However, care should be taken when selecting published life history data because growth parameters from other regions or time periods could include shifts in productivity and life history strategies of fish (Prince et al. 2015).

Size at maturity for *L. rubrioperculatus* from Japan and the Marianas was estimated at around 22 cm (Ebisawa 1997; Trianni 2011). The interpolated size at maturity for *L. rubrioperculatus* from American Samoa was estimated in the present study at 20.4 cm. Only two samples were below this size, so more sampling of smaller size classes would help to validate the interpolated L_{50} .

Maturity of male *N. lituratus* was calculated to correspond with a size of 17.7 cm, which is 0.2 cm larger than the L_{50} interpolated from the literature. There were no immature females in the dataset, and out of the five female samples smaller than 18 cm all were mature. Life history data from Guam indicated that female *N. lituratus* mature earlier than males, at around 14–15 cm (Taylor et al. 2014b), but the only



Fig. 7 Age-based catch curve for a *Chlorurus japanensis*, b *Lethrinus rubrioperculatus*, and c *Naso lituratus. Bars* represent samples in each age class. The *solid line* represents the fitted regression catch

curve used to calculate total mortality (Z), and the *dotted lines* define the 95% confidence envelope

female specimen below 16 cm was a mature female. More sampling in the smaller size classes is needed to determine the size at maturity of female *N. lituratus*.

In data-poor fisheries, life history proxies are often used from similar species or from the same species from different regions (Bejarano et al. 2013; Nadon et al. 2015). However, a warmer sea-surface temperature (SST) has been found to be a significant factor in determining life span, with warmer waters yielding populations of shorter lived fish (Munch and Salinas 2009; Taylor et al. 2019). This was evident in the life spans of L. rubrioperculatus from three different areas. The oldest recorded age for L. rubrioperculatus, 13 years, was for fish from an area of Japan with a lower SST than that of American Samoa (Ebisawa and Ozawa 2009). In contrast, fish from the Marianas, an area with a similar SST to Samoa, had a similar maximum age, 8 years, to those from American Samoa (Trianni 2011). Without accounting for demographic changes due to SST, fishery stock assessment models could lead to over- or underestimation of exploitation, mortality, and yield (Taylor et al. 2019).

There can also be growth variations within populations which are often not accounted for in data-limited stock assessments. Natural mortality is often assumed constant across time. However, *N. lituratus* showed a biphasic mortality schedule, which results in the atypical combination of high mortality and long life span, similar to that of *N. unicornis* (Taylor et al. 2019). If only maximum age were used to produce a natural mortality estimate, early phase high mortality would not be taken into account. This would make a species appear more vulnerable to fishing than it likely is.

The species selected for the present study represent highly valued components of the nearshore coral reef fishery in American Samoa. Even data-limited stock assessments require basic life history information for the production of useful management regimes. Our results provide important estimates of population-level biological traits that can be used for stock assessments and fishery management in the region.

Acknowledgments We would like to thank the team at DMWR in American Samoa for collecting and processing the fish samples in a short amount of time, and Dr. Eva Schemmel for additional assistance on gonad histology staging. This project was made possible by support from the Nature Conservancy under cooperative agreement award no. NA16NOS4820106 from the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Conservation Program (CRCP), US Department of Commerce. The statements, findings, conclusions, and recommendations reported in this article are those of the authors and do not necessarily reflect the views of NOAA, NOAA CRCP, or the US Department of Commerce. All the experiments complied with the current laws of American Samoa and the United States of America. We thank the three anonymous reviewers for their constructive comments on the manuscript.

Author contribution All the authors contributed to the study conception and design. Data generation was performed by D. O. and S. F.

Material preparation and analysis were performed by C. P. and B. T. The first draft of the manuscript was written by C. P., and all the authors commented on previous versions of the manuscript. All the authors read and approved the final manuscript.

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