



Abstract—Growth of roosterfish (*Nematistius pectoralis*) was estimated by analyzing daily growth increments of sagittal otoliths collected from individuals captured in El Golfo Dulce, Costa Rica during 2013–2014 and in southern Baja California Sur, Mexico during 2010–2015. Isometric growth was observed for all individuals and no significant differences were observed in the length–weight relationships between sexes or locations. Age estimates ranged from 18 d (0.05 years) to 545 d (1.5 years), although 26% of otoliths (57–133 cm) were not legible because narrow daily growth increments were difficult to differentiate in older fish. Individual growth parameters indicate that roosterfish grow at a rapid rate during the first year of life, reaching sizes of around 60–70 cm in fork length. Although future field validation is necessary, the results of our study provide insight into the life history of this valuable resource of the eastern Pacific Ocean.

Age, growth, and length–weight relationship of roosterfish (*Nematistius pectoralis*) in the eastern Pacific Ocean

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A game fish that inhabits the neritic waters of the subtropical and tropical eastern Pacific Ocean (Eschmeyer et al., 1983), the roosterfish (*Nematistius pectoralis*) is the only species in the genus *Nematistius* (family Nematistiidae). The most notable external feature of this species is the presence of 7 elongated dorsal spines, which give rise to its common name (Rosenblatt and Bell, 1976) and allows it to be easily distinguished from other species (Niem, 1995).

The roosterfish is a coastal species that has been found to occur in the Pacific Ocean from San Clemente, Southern California to San Lorenzo Island, Peru, including the Gulf of California and the Galapagos Islands (Love et al., 2005). Results from work to date indicate that roosterfish reside primarily in warm (23–31°C), shallow waters where they may spend up to 90% of their time between the sea surface and a depth of 12 m (Sepulveda et al., 2015). All age classes are considered neritic; juveniles are often found along the shoreline and larger individuals are

commonly associated with both the surf line and complex near shore habitats (i.e., reefs and sand bars) (Niem, 1995; Sepulveda et al., 2015).

Roosterfish can attain sizes up to 191 cm in total length and more than 51.7 kg (Robertson and Allen, 2015). They are active predators that have been reported to feed in shallow waters (i.e., depths of 3–4 m) on schooling fish species, such as species of mojarra (i.e., Pacific spotfin mojarra [*Eucinostomus dowii*] and graceful mojarra [*E. gracilis*]), and species of anchovy (i.e., sharpnose anchovy [*Anchoa ischana*] and *Anchoa* spp.) (Hobson, 1968; Rodríguez-Romero et al., 2009).

The roosterfish is a very important resource for sportfishing industries, especially for those that operate at destinations favored by ecotourists, such as Baja California Sur, mainland Mexico, and the coast of Central America. Roosterfish contribute significantly to the local economy because it is a common target of inshore anglers; in fact, this species is sought out among anglers around the

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world (Eschmeyer et al., 1983). To a lesser degree, the roosterfish also supports small-scale artisanal fisheries along the coast of Baja California Sur and Central America; however, because of its limited market value, it is not typically the primary target of such fishing operations (Lindner, 1947; Niem, 1995).

Despite the ecological and economic importance of roosterfish, very few scientific studies have focused on this species and basic biological parameters remain largely unknown. In particular, questions pertaining to age and growth, natural mortality, longevity, and reproductive biology remain unanswered. These parameters are essential for fisheries management and form the basis for most stock assessment models (Goldman, 2005). This information is also essential for understanding other biological and population traits such as productivity, yield per recruit, predator and prey dynamics, and habitat requirements (DeVries and Frie, 1996; Campana, 2001; Robinson and Motta, 2002).

Given the importance of this species to regional fisheries off the coast of Baja California Sur and Central America, we estimated age and growth in our study by counting presumed daily growth increments (DGIs) within the sagittal otolith. The results of our study provide the first estimates of growth for this species and allow intraspecific comparisons of growth between 2 geographically distinct locations along the range of the roosterfish in the eastern Pacific Ocean.

Materials and methods

Collection details

From 2010 through 2015, roosterfish specimens were obtained from the sportfishing fleet in Cabo San Lucas and La Paz, Baja California Sur, Mexico. Similarly, from 2013 through 2014, specimens were collected from commercial and recreational fleets that operated out of the Golfo Dulce, Costa Rica. Each specimen was measured to determine fork length (FL) to the nearest 0.1 cm and weighed to the nearest 0.01 kg. Sex was determined by visual inspection of the gonads, and, when possible, sagittal otolith pairs were removed, cleaned, and stored dry.

Length–weight relationships

Length–weight relationships (LWRs) were estimated by using the allometric equation:

$$W = aFL^b,$$

where W = the weight; and

a and b = the intercept and the slope of the regression line, respectively (Ricker, 1975).

As with previous works, we assumed that, when b was equal to 3, the relationship was considered to be isometric (Sangun et al., 2007). Similarly, b values $\neq 3$ were associated with allometric growth (Froese, 2006). Estimates of LWRs were calculated independently for

both sex (males and females) and location (Baja California Sur and Golfo Dulce) and compared by using a Student's t -test (Zar, 2010). A Student's t -test was also used to evaluate whether b values were significantly different from the null hypothesis for isometric growth ($H_0: b=3$) (Sangun et al., 2007; Zar, 2010).

Preparation and analysis of otoliths

Preparation of otoliths followed closely the protocol described by Secor et al., 1992. Briefly, the right otolith of each specimen was embedded in crystal polyester resin and allowed to harden and dry for a 24-h period. We created transverse sections (0.6 mm) through each otolith that included the core (Fig. 1) by using an IsoMet Low Speed Saw¹ (model 11-1280-160; Buehler, Lake Bluff, IL) equipped with a diamond wafering blade (series 15HC, Buehler). Because otolith increments (e.g., daily or annual) of many perciform fish species are not deposited in the sagittal plane, the transverse or the frontal planes typically are used for assessing DGIs (Secor et al., 1992).

Most otoliths need some form of preparation before their microstructure can be accurately determined; therefore, a polishing procedure was used to remove material, expose the core region, and reveal the presumed DGIs (Secor et al., 1992). To clearly define DGIs and facilitate readings, transversal sections were mounted on histological slides with Cytoseal mounting medium (Thermo Fisher Scientific, Waltham, MA) and hand polished with a series of micrometric sandpaper of decreasing grit size (15–3 μm , Diamond Lapping Film disc; Buehler). For finishing, sections were polished with 0.3- μm MicroPolish alumina (Buehler) and 0.3- μm MicroCloth micrometric sandpaper (Buehler).

Two readers independently counted presumed DGIs of prepared otolith sections without prior knowledge of fish length and weight. Readers counted DGIs on transverse sections by using a microscope with transmitted light (40–100 \times). Daily growth increments were counted from the core toward the dorsal edge of the otolith along the same transect (Fig. 1).

The consistency or concordance of counts between readers was estimated by using a coefficient of variation (CV) (Chang, 1982):

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^R (X_{ij} - X_j)^2 / (R-1)}}{X_j}, \quad (1)$$

where CV_j = the age precision estimate for the j th fish;
 X_{ij} = the i th age determination of the j th fish;
 X_j = the mean age estimate of the j th fish; and
 R = the number of times each fish was aged.

Lengths at age derived from otolith readings were used to estimate the 3 parameters of the standard von Bertalanffy growth model:

¹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

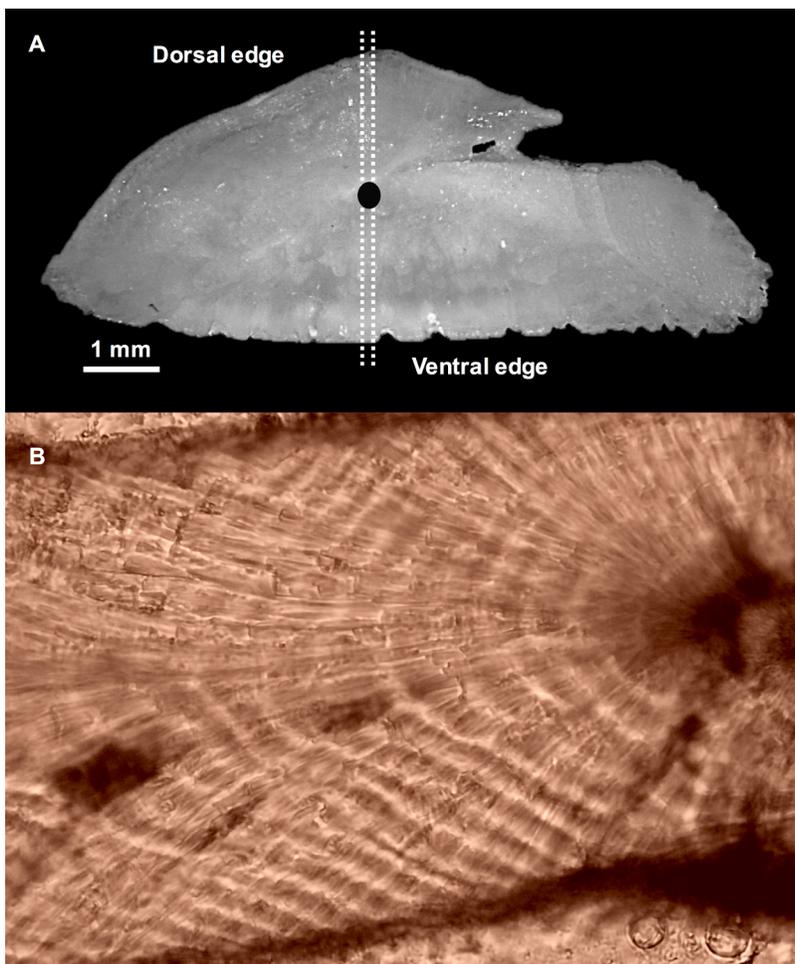


Figure 1

(A) Right sagitta of a 63.5-cm-FL roosterfish (*Nematistius pectoralis*) captured in Baja California Sur, Mexico, in 2014. Dotted white lines represent a transverse section through the core, which is indicated by the black circle. (B) Sagitta showing daily growth increments (that consists of two rings: gray and white) from a 5.2-cm-FL roosterfish (18 d in age) captured in Baja California Sur in 2014.

$$L_t = L_\infty [1 - e^{-k(t-t_0)}], \tag{2}$$

where L_t = length (FL in centimeters) at age t ;
 L_∞ = average maximum length;
 k = the individual growth coefficient;
 t_0 = the hypothetical age when the length is equal to 0; and
 t = age.

A power function was also tested; however, because our results were similar to those of the von Bertalanffy growth model, only results from the von Bertalanffy growth model were included for consistency and comparison with other growth studies.

Growth parameters were estimated independently

for both study areas (Baja California Sur and Costa Rica), and an analysis of the residual sum of squares was used to evaluate the possible differences in parameters between the 2 locations (Ratkowsky, 1983).

Parameters for both the LWR and von Bertalanffy growth model were estimated by using nonlinear least squares by means of an iterative process with the Gauss-Newton algorithm (Bates and Watts, 1988), which allows estimation of nonlinear model parameters without needing to transform the data into a linear function. Statistical analyses were performed with R statistical software, vers. 3.2.3 (R Core Team, 2015). Significance was determined by using a t -test with an alpha level of 0.05.

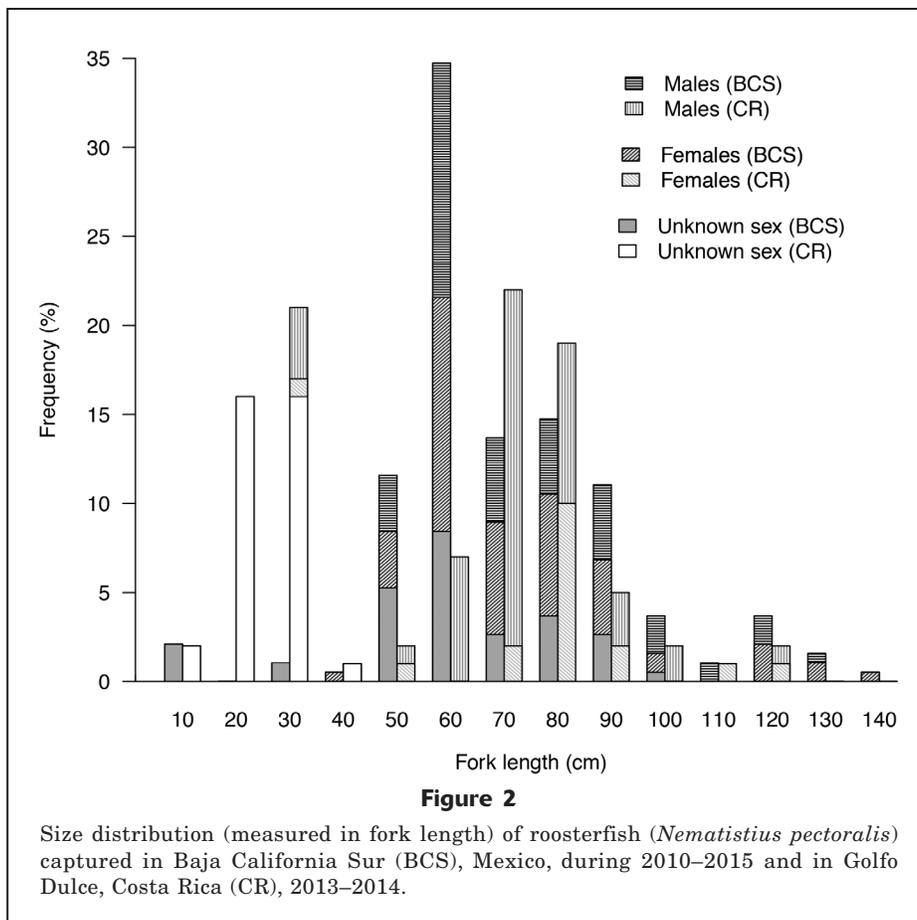
Results

During the sampling period, 290 roosterfish (190 specimens from Baja California Sur and 100 specimens from Costa Rica) were measured and weighed. Specimens from Baja California Sur (66 males, 74 females, and 50 fish of unknown sex) ranged from 5.2 to 133.0 cm FL and from 0.01 to 25.87 kg in weight. Specimens from Costa Rica (47 males, 18 females, and 35 fish of unknown sex) ranged from 8.3 to 116.0 cm FL and 0.01 to 17.80 kg (Fig. 2).

The estimated parameters of the LWR by area and sex are provided in Table 1. Comparisons of growth parameters (values of the exponent b) revealed that all LWRs were not significantly different from a value

of 3 (Student’s t -test: $P > 0.05$) and indicated that roosterfish growth is isometric (Table 1). Given the finding of isometric growth for both location and sex, the length and weight data were pooled into one representative LWR for this study (Fig. 3, Table 1).

For age estimation, 182 pairs of sagittal otoliths were collected and processed, 103 pairs from fish collected in Baja California Sur (5.2–120.0 cm FL) and 79 pairs from fish collected in Costa Rica (13.5–116.0 cm FL). Of these pairs, 130 pairs or 71.5% (Baja California Sur=68 and Costa Rica=62) were readable and used in the age estimation analyses. The remaining 52 otolith pairs (Baja California Sur=35 and Costa Rica=17) were discarded for one or more of the following reasons: the otoliths were broken, crosscuts did not include the core,

**Table 1**

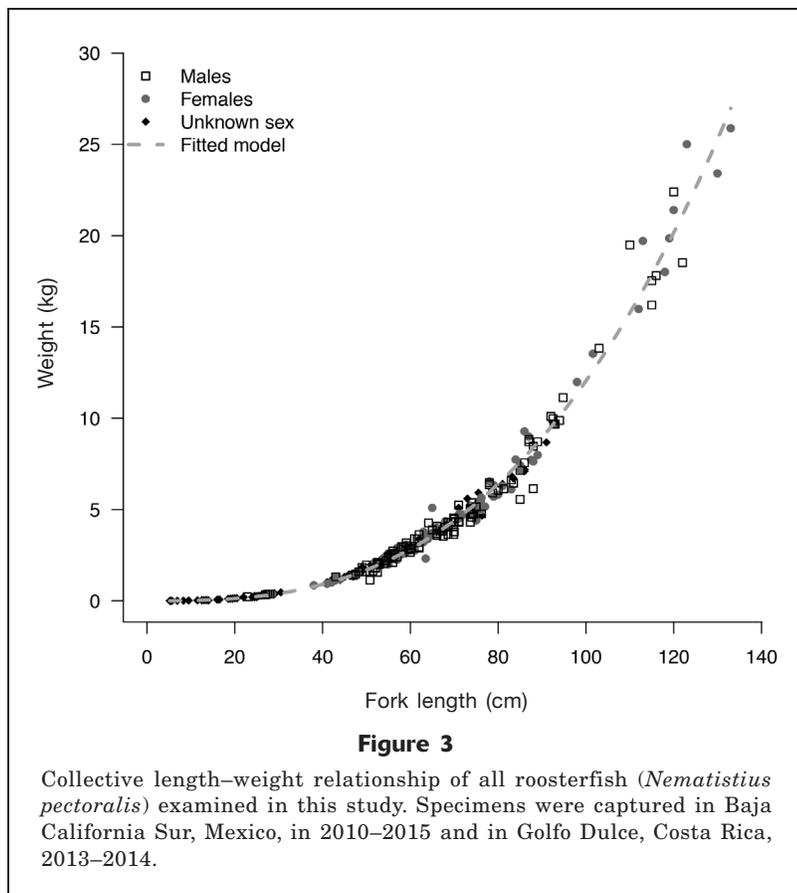
Parameters (a and b) of the length–weight relationship of roosterfish (*Nematistius pectoralis*) captured from 2 locations, Baja California Sur (BCS), Mexico, during 2010–2015 and Costa Rica (CR) during 2013–2014, by area and sex, and Student's t -test results for the testing of isometric growth.

Area	Sex	a	b	t	P
BCS	Males	2.4×10^{-5}	2.84	-0.18	0.85
BCS	Females	2.8×10^{-5}	2.81	-0.25	0.80
BCS	Sexes combined	2.7×10^{-5}	2.82	-0.25	0.79
CR	Males	2.7×10^{-5}	2.81	-0.48	0.62
CR	Females	2.8×10^{-5}	2.81	-0.50	0.62
CR	Sexes combined	2.7×10^{-5}	2.81	-0.60	0.54
Combined	Sexes combined	2.6×10^{-5}	2.82	-0.29	0.76

sections were overpolished, and otolith sections were illegible because of increasingly narrow widths of DGIs in older fish.

The estimated ages of the fish assessed from Baja California Sur ranged from 18 d (0.05 years, 5.2 cm FL) to 548 d (1.49 years, 86 cm FL). The range of age estimates from Costa Rica was 32 d (0.08 years, 13.5 cm FL) to 448 d (1.22 years, 78.7 cm FL).

In most cases, it was possible to count DGIs from sagittal otoliths of fish <57 cm FL (the size reached at an age of approximately 1 year). The agreement between the estimated ages assigned independently by the 2 readers revealed a CV of 9.02%, indicating a high consistency. The average CV for different size classes increased from 5.9 for fish with 18–100 DGIs to 6.8 for fish with 101–199 DGIs and 9.5 for fish with 200–



549 DGIs. Reader confidence was reduced for samples from fish that ranged from 57 to 86 cm FL, primarily because of the narrowing and softening of DGI edges. Similarly, for roosterfish >86 cm FL, DGIs were not easily differentiated and, therefore, these fish were not included in the age-estimation portion of our study. Annual growth marks were not observed in sagittal otoliths or in cross sections.

The estimated parameters of the von Bertalanffy growth model are given by area in Table 2. The analysis of residual sums of squares did not reveal significant differences in growth parameters between Baja California Sur and Costa Rica ($P>0.05$). Therefore, the data for both locations was combined into a single growth model (Fig. 4). Estimates of growth parameters indicate that roosterfish grow rapidly during the first year of life, attaining a size of approximately 60–70 cm FL within the first year (40% of L_{∞}).

Discussion

Our study provides the first estimates of age and growth for the roosterfish, a species that supports a substantial recreational fishery throughout the eastern Pacific Ocean. The growth estimates presented here indicate that roosterfish grow at a rapid rate and

that they may reach up to 60–70 cm FL (40% of L_{∞}) during the first year of life. Accelerated growth in the first year of life has been reported for other warm-water pelagic species, such as the cobia (*Rachycentron canadum*; Franks et al., 1999), dolphinfish (*Coryphaena hippurus*; Schwenke and Buckel, 2008), blue marlin (*Makaira nigricans*; Prince et al., 1991), and sailfish (*Istiophorus platypterus*; Alvarado-Castillo and Félix-Uraga, 1996). As hypothesized previously, rapid early growth is likely advantageous for survival because it is linked to swimming speed, foraging success, and predation (Prince et al., 1991). Although field validation is necessary, our work provides an initial hypothesis regarding the growth of this valuable eastern Pacific Ocean species and increases scientific knowledge of this poorly known species.

Samples of roosterfish were obtained primarily from recreational fisheries that operate seasonally throughout Baja California Sur and Central America. Because roosterfish are typically released in most of these recreational fisheries, acquisition of samples was challenging; specimens from smaller size classes (<50 cm FL) proved to be especially difficult to obtain. In addition, because larger individuals are particularly prized in the catch-and-release fisheries, guides and captains rarely harvest specimens >100 cm FL, a tendency that further inhibited the collection of larger individuals for our study.

Length-weight relationships

The estimated b values (Table 1) were within the normal, expected range for fish ($b=2.5-3.5$) (Froese, 2006). Bagenal and Tesch (1978) suggested that when the

Table 2

Parameter values from the von Bertalanffy growth model for roosterfish (*Nematistius pectoralis*) captured in Baja California Sur (BCS), Mexico, and Golfo Dulce, Costa Rica (CR), during 2010–2015: average maximum length (L_{∞}), measured as fork length in centimeters, individual growth coefficient (k), and the hypothetical age when the length is equal to 0 (t_0), measured in years.

Area	L_{∞}	k	t_0
BCS	166.90	0.48	-0.02
CR	171.72	0.47	-0.08
Areas combined	163.77	0.47	-0.08

value of b is between 2.8 and 3.2, growth is considered to be isometric (i.e., growth of all body parts is consistent and proportional throughout development). Based on t -test results, estimated b values were not significantly different from 3 (Table 1), indicating that isometric growth for roosterfish is independent of location and sex.

Because we did not identify differences in the LWR, samples were pooled and collectively presented (see Froese, 2006). A similar b value was reported by González-Sansón et al. (2014) for roosterfish caught in a coastal lagoon off Barra de Navidad, Jalisco, Mexico. However, the González-Sansón et al. (2014) study was based on a limited sample size and size range of fish ($b=2.92$, $n=8$; 7.5–29.3 cm in total length). Values of the exponent b can be influenced by statistical procedure and sample size (Bolger and Connolly, 1989), as well as by variations associated with size range, maturation, sex, and time of year (Cone, 1989). Because the spawning dynamics of this species (i.e., season and time of year) remain unknown and we were unable to obtain samples from exceptionally large individuals, it is possible that differences in LWR exist for larger, mature roosterfish.

Age and growth

The sagittal otolith is the preferred hard structure for estimating age in fish because deposition occurs continuously throughout life, a scenario that enhances age estimation when compared with the use of other hard structures (Campana and Thorrold, 2001). Otoliths are also preferred for age estimation because the structures are not lost or shed (as they are with scales) or reabsorbed (as with bones and spines) (Ramírez-Peréz et al., 2011). Sectioned and polished otoliths from individuals <57 cm FL provided visible DGIs that were readily distinguishable. However, in otoliths from larger individuals (>57 cm FL), it was difficult to differentiate between recent outer edge DGIs, thus causing increased uncertainty in age estimates. Campana (1999) reported that calcium, oxygen, and carbon dominate the elemental composition of the otolith and that these elements form the calcium carbonate matrix of the otolith. An excess of calcium carbonate in sagittal otoliths may hinder ridge quantification to varying degrees (Hill et al., 1989).

In cross sections, DGIs were counted from the core to the dorsal edge of the otolith. The path of visual counts were not always in a straight line from the core to the outer edge of a sagitta. The optimal reading path that provided the best visual clarity of DGIs typically followed a somewhat circuitous route that shifted from one area of the sagitta to another (Uchiyama et al., 1986).

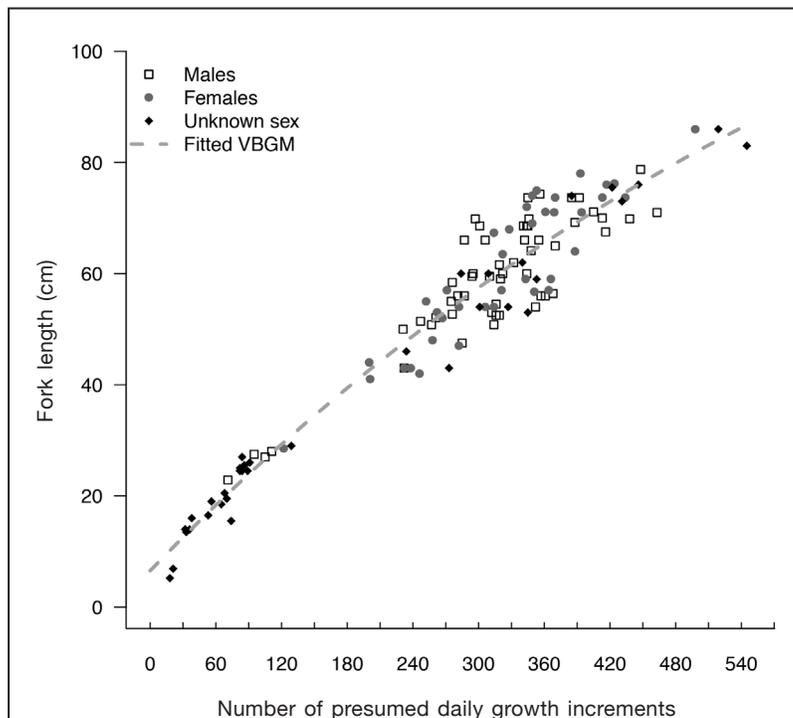


Figure 4

The combined (sex and location) von Bertalanffy growth model (VBGM) of roosterfish (*Nematistius pectoralis*) captured in Baja California Sur, Mexico, in 2010–2015 and in Golfo Dulce, Costa Rica, 2013–2014.

The precision of age estimates for the 2 readers of this study was high (CV=9.02%) and aligns with CV values from other studies in which counts of annual marks were used (Prince et al., 1991; DeMartini et al., 2007). Campana (2001) proposed that there is no a priori value of CV that can be assigned as a target level for studies of age because it is highly influenced by the species and the nature of the hard structure itself. In addition, the consistency between readings often decreases as fish age increases because growth marks are closer together in older fish (Steward et al., 2009).

We found that the precision of DGI counts decreased with increasing age (18–548 d) and FL (5.2–86.0 cm). Prince et al. (1991) suggested that estimating the age of large or old fish by using DGI counts may result in an underestimation of age and an overestimation of the growth rate. Because it was not possible to count DGIs precisely in roosterfish >86 cm FL (1.5 years old), it is recommended that otolith DGIs be used only for individuals of ages less than 1 year (the age reached at a size of approximately 66 cm FL).

Although it was not possible to detect annual marks on the otoliths of roosterfish in our study, a previous study had focused on assessing the potential use of dorsal spines for aging this species (Chávez-Arellano, 2016). Chávez-Arellano (2016) analyzed roosterfish between 14 and 133 cm FL and found a similar average length (70.61 cm FL) for year-1 individuals. However,

robust comparisons between these studies are not possible because the work of Chávez-Arellano (2016) was not focused on age determination; he assessed only dorsal spine suitability for aging purposes. Despite differences in our study and that of Chávez-Arellano (2016), both works support the hypothesis of rapid growth in this species, especially in the first year of life. As has been reported for others species like the dolphinfish, additional structures (e.g., scales) may prove useful in future age assessments of the roosterfish (Schwenke and Buckel, 2008).

Although field validation is necessary to confirm the proposed growth hypothesis for roosterfish, the inclusion of small size classes (5 cm FL) and a large size range provides support for the use of DGIs for age estimation. Oxenford and Hunte (1983) assumed DGIs for dolphinfish, and Uchiyama et al. (1986) subsequently validated those values with both hatchery-reared and fish caught in the wild. For some species, DGIs have been validated by experiments with fish reared in captivity, otolith marking, radiochemical dating, or various other techniques (Prince et al., 1991; Campana, 2001). Ideally, validation experiments should include the period during which the initial growth ring is formed and should evaluate the regularity of growth-ring formation during all life stages (e.g., spawning, migration, and periods of starvation) because all of these factors may influence the regularity of deposition rates (Uchiyama et al., 1986).

Values of L_{∞} estimated from the von Bertalanffy growth equation were greater than the length of the largest roosterfish sampled in our study (133 cm FL) and slightly lower than the maximum length recorded by Robertson and Allen (2015). This difference likely occurred because the estimated parameters were based only on the initial phases of growth for roosterfish (up to 1.49 years).

The relatively rapid growth rate that we report here is similar for both regions (Baja California Sur and Costa Rica), despite differences in oceanographic conditions (e.g., annual sea-surface temperature) or potential prey sources and availability. These similarities may be due to the lack of larger individuals in this study (e.g., readability of fish >86 cm FL), a scenario that may have masked potential ontogenetic differences. It may also be that roosterfish from the 2 regions have deposition rates that differ from each other. If ring formation occurs at a rate that is less than one ring per day, it may be that this study underestimates the actual age of the fish surveyed. Regardless, this work presents the first data supporting a growth hypothesis for this species, and future investigations should focus on the use of field validation techniques.

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