

Growth stanzas in an Epinephelidae-Lutjanidae complex: considerations to length-weight relationships

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Abstract: Growth stanzas or abrupt changes in growth rates are present throughout the life span of fish. Identifying growth stanzas will help to adequately described growth taking into account that fishes are indeterminate growers. In this study, we used length-weight (L-W) relationships to analyze the growth stanzas in the Grouper-Snapper complex of Southern Gulf of Mexico. For this, the type of sexuality, sex and different sexual maturity phase were considered in the analyses of three species of gonochoric Snappers (Lutjanidae) and six species of protogynous hermaphrodite Groupers (Epinephelidae). Welch ANOVA tests were carried out to determine the existence of differences in length and weight between juveniles and adults per sex. According to the observed differences, L-W relationship parameters (a and b), standard error (SE b) and coefficients of determination (R^2) were calculated for all species separately by sex and sexual maturity phase. Snappers' juvenile-females b -value ranged from 2.44-2.77, juvenile-males from 2.16-2.94, adult-females from 2.63-2.80 and adult-males from 2.63-2.98. Groupers' b -value ranged for juvenile-females 2.66-3.20, adult-females from 2.73-3.31 and for adult-males 2.93-3.29. For each relationship b -value was t -tested (t -Student) to explore differences from the allometric coefficient ($b=3$), which indicated changes in body form. Hypothesis test, for regression slopes (b) between Snappers' juvenile-females vs. adult-females and juvenile-males vs. adult-males and Groupers' juvenile-females vs. adult-females and adult-females vs. adult-males, indicated different growth stanzas related to gonadal development for Snappers, and to gonadal development and sex change in Groupers. The identification of growth stanzas is crucial to avoid an overestimation or misleading growth rate which is used in fisheries management to establish some target reference points, such as maximum sustainable yield or yield-per-recruit. Rev. Biol. Trop. 63 (1): 175-187. Epub 2015 March 01.

Key words: growth stanzas, length-weight relationships, Grouper-Snapper complex, Gulf of Mexico.

Length-weight (L-W) relationships are used to assess biomass of fish populations (Keller, & Kerstetter, 2013), as indicators of fish condition (Dubey et al., 2012), to compare life histories of certain species among regions (Pauly, 1993) or to allow the conversion of growth-in-length equations to growth-in-weight for use in stock assessment models (Moutopoulos, & Stergiou, 2002). Even though L-W relationships are commonly and widely used, there is no single regression that will

adequately describe growth of a fish, because growth rate change throughout their life span. These growth rate variations may be reflected as abrupt changes in growth rate known as growth stanzas (Ricker, 1979; Froese, 2006; Katsanevakis et al., 2007). Growth stanzas could be observed in juvenile stage (pre-maturity) and/or after they reach sexual maturity (post-maturity). Pre-maturity growth models should consider that all surplus energy is devoted to somatic growth (the growth rate should



be higher) whereas to describe post-maturity, it must be considered that some or all of the extra energy is channeled to gonadal development (Lester, Shuter, & Abrams, 2004).

The status of most reef fish stocks is unknown in the Southeastern United States and Mexico. Reef fishes must be conservatively managed because their communities comprise slow-growing and late maturing fish such as Groupers and Snappers (Coleman, Koenig, Eklund, & Grimes, 1999). Groupers and Snappers are top predators and play a vital ecological role in the trophodynamics of tropical environments. They face different threats to their populations such as nursery habitat destruction, juvenile extraction, and spawning aggregations exploitation. In Southern Gulf of Mexico, for the reef fishery of the Yucatan Peninsula continental shelf (Campeche Bank), nine species of the Grouper-Snapper complex (SAFMC, 2013) are the most economically important and represent almost 94% of the total number of specimens captured (Brulé, Noh-Quiñones, Sánchez-Crespo, Colás-Marrufo, & Pérez-Díaz, 2009), generating more than USD\$19 million in annual revenue (SAGARPA, 2012). Of these, three species from the Lutjanidae family (Snappers), are gonochoric: *Lutjanus campechanus* (Poey 1860), *Lutjanus synagris* (Linnaeus 1758) and *Ocyurus chrysurus* (Bloch 1791) whereas the other six species from the Epinephelidae family (Groupers), are protogynous hermaphrodites: *Epinephelus morio* (Valenciennes 1828), *Epinephelus guttatus* (Linnaeus 1758), *Mycteroperca bonaci* (Poey 1860), *Mycteroperca microlepis* (Goode and Bean 1880), *Mycteroperca tigris* (Valenciennes 1833) and *Mycteroperca venenosa* (Linnaeus 1758). Worldwide, *E. morio*, *M. bonaci* and *M. venenosa* populations are considered as nearly threatened (IUCN, 2013), *E. guttatus*, *M. microlepis*, *M. tigris* as vulnerable with declining populations (Morris, Callum, & Hawkins, 2000) and *L. campechanus* as overfished in recovery (NOAA, 2011). For Southern Gulf of Mexico, *E. morio* populations are considered overexploited (Burgos, & Defeo, 2004) and its fishery in danger of collapse (Burgos,

& Pérez-Pérez, 2006). The other species have neither stock assessments nor L-W relationship records for their populations.

Few growth studies take into consideration the presence of growth stanzas to calculate L-W relationships, which may lead to a growth rate overestimation if juveniles are not separated from adults or to a misleading growth rate if relationships are calculated with joined sexes (Froese, 2006). This study aimed to analyze the presence of growth stanzas, by the use of L-W relationships, in nine species of the Grouper-Snapper complex from the Campeche Bank. We considered the type of sexuality (gonochoric and hermaphrodites), sex (females and males) and different sexual maturity phases (juveniles and sexually mature adults), and expected to provide a realistic growth scheme for each species, which may be useful for fisheries management.

METHODS AND MATERIALS

Collection site and field sampling: Specimens were collected on the Yucatan Peninsula continental shelf from 1999 to 2009, through monthly catches on a yearly basis, through a tropical sequential fishery by the artisanal (using hook and line) and technified fishing fleets (using automated long lines). Groupers were measured for total (TL cm) and standard length (SL cm) except for *E. guttatus* (only TL) and weighed for total (TW g) and gutted weight (GW g). Due to their fork tail, Snappers were measured for total (TL cm), standard (SL cm) and fork length (FL cm) except for *L. campechanus* (only TL and SL), and weighed for total (TW g) and gutted weight (GW g). For all species fresh gonad weight (gW g) was recorded and gonadosomatic index ($IG=100x[gW/GW]$) was calculated.

Gonadal analysis: Type of sexuality, sex and gonadal developmental phase were determined for each specimen by microscopic examination of gonadal structure. Hermaphroditism was defined following the criteria established by Sadovy and Shapiro (1987)

and Sadovy de Mitcheson and Liu (2008), and sex and gonad developmental stage following Brown-Peterson, Wyanski, Saborido-Rey, Macewicz & Lowerre-Barbieri (2011).

Groupers analyzed in this study, are protogynic hermaphrodites (specimens undergo a sexual transition from a functional female to a functional male) (Shapiro, 1987) therefore, no juvenile-males were registered while Snappers are gonochoric species with female and males-juveniles. Considering group sample variances were unequal, Welch (Welch, 1951) ANOVA (means are weighted by the reciprocal of the group mean variances) independent tests were performed to know if there were differences in mean length (TL, FL, SL) and weight (TW, GW), regardless the magnitude, between sex and gonad developmental phase.

Following the procedure established by Ricker (1973) with the proposed modifications by Froese (2006), L-W relationships were calculated by sex and gonad developmental phase, for each species, using the equation $W=aL^b$ where W is total weight of the fish in grams, L is total length of the fish to the nearest centimeter, a the intercept and b the slope following a double-logarithmic least square linear regression. It was taken into account that L-W b -value according to Carlander (1969) (as cited in Keller & Kerstetter, 2013) should fall between the expected range for $b=2.5-3.5$ in fishes. The b -value for each relationship was afterwards t -tested (t -Student) to explore significant statistically differences from the allometric coefficient $b=3$ (Cinco, 1982) using the equation $t=(b-3)/sb$ (Sokal, & Rohlf, 1995) where t is t -student value, b is the slope and sb is the slope standard error. According to Froese (2006) b -value indicates changes in body form or condition: If $b=3$ individuals in the sample have the same form as large specimens, if $b>3$ specimens increased in height or width more than in length and if $b<3$ specimens become more elongated. Finally, hypothesis tests of differences between regression line slopes (b -value) were performed according to Zar (1999) among gonochoric Snappers' female-juveniles vs. female-adults and male-juveniles

vs. male-adults and for protogynous hermaphrodites Groupers' juvenile-females vs. adult-females and adult-females vs. adult-males. Statistically significant differences in b -value between regression slopes in each species were considered as different growth stanzas. All statistical analyses were performed using MATLAB R2012b (The MathWorks, Inc.).

RESULTS

A total of 12 114 specimens of nine different species were sampled: *Lutjanus campechanus* (N=914), *Lutjanus synagris* (N=1 022), *Ocyurus chrysurus* (N=1 431), *Epinephelus guttatus* (N=1 522), *Epinephelus morio* (N=2 328), *Mycteroperca bonaci* (N=739), *Mycteroperca microlepis* (N=1 083), *Mycteroperca tigris* (N=519) and *Mycteroperca venenosa* (N=2 556). Gonochoric Snappers' juvenile-females ranged in total length (TL) from 13.5-49.9cm, juvenile-males from 14.0-58.5cm, adult-females ranged from 18.5-61.6cm and adult-males from 17.7-81.6cm. Protogynous hermaphrodite Groupers' juvenile-females ranged from 1.9 to 61.0cm, adult-females from 25.6-123.5cm and adult-males from 29.0-124.5cm (TL). Mean gonadosomatic index percent (IG%) varied for Snappers: *L. campechanus* females (max-min monthly mean values \pm SE: 1.02 \pm 8.80-0.20 \pm 0.09%) and males (0.24 \pm 0.40-0.09 \pm 0.03%) for *L. synagris* females (3.00 \pm 0.18-0.50 \pm 0.03%) and males (0.90 \pm 0.13-0.20 \pm 0.02%) and for *O. chrysurus* females (2.30 \pm 0.13-0.50 \pm 0.03%) and males (3.30 \pm 0.23-0.50 \pm 0.03%). For Groupers mean IG% varied for *E. guttatus* females (max-min values \pm SE: 10.57 \pm 0.71%-0.12 \pm 0.01%) and males (0.95 \pm 0.04-0.10 \pm 0.01%), *E. morio* females (2.14 \pm 0.21-0.07 \pm 0.02%) and males (0.29 \pm 0.08-0.14 \pm 0.01%), *M. bonaci* females (2.2 \pm 0.27-0.6 \pm 0.01%) and males (0.22 \pm 0.03-0.11 \pm 0.03%), *M. microlepis* females (3.40 \pm 0.23-0.40 \pm 0.03%) and males (0.36 \pm 0.11-0.06 \pm 0.01%), *M. tigris* females (3.47 \pm 0.31-0.15 \pm 0.02%) and males (1.36 \pm 0.14-0.10 \pm 0.01%) and *M. venenosa* females (8.70 \pm 0.55-0.15 \pm 0.03) and males

($5.83 \pm 0.40 - 0.05 \pm 0.03\%$). For all species, IG% was higher in females than in males (except for *O. chrysurus*) even though females of all species tend to be smaller in size and weight.

Welch ANOVA tests showed significant statistical differences ($p < 0.05$) for all Snappers and Groupers species in TL, FL, SL, TW and GW (Table 1) between sex (females and males) and gonad developmental phase (juveniles and adults). Therefore, length-weight relationships were calculated separately for juveniles and for mature individuals per sex in Snappers and for juvenile-females, adult-females and adult-males in Groupers (Table 2). Linear regressions were significant for all species (females/males, juveniles/adults) ($p < 0.05$) and coefficients of determination ranged from 0.96-0.99 indicating a strong relationship between variables. Length-weight b -values for Snappers and Groupers fell between the expected 2.5-3.5 range for b . Snappers' b -values varied from 2.3 to 2.7 for juvenile-females, from 2.1 to 2.9 for juvenile-males, from 2.6 to 2.8 for adult-females and from 2.6 to 2.9 for adult-males. For Groupers, b -values ranged from 2.6 to 3.2 for juvenile-females, from 2.7 to 3.3 for adult-females and from 2.9 to 3.2 for adult-males (Table 2).

The t -test (t -Student) to explore differences from the allometric coefficient $b=3$ acknowledge differences for Snappers: in juvenile-females for the three species ($b < 3$), in adult-females only for *L. campechanus* ($b < 3$), in juvenile-males for *L. synagris* and *O. chrysurus* ($b < 3$) and in adult-males for the three species ($b < 3$). *Lutjanus campechanus* juvenile-females and adult-females displayed the same b -value ($b < 3$) showing that specimens conserve an elongated body as they grow and mature sexually, whereas juvenile-males ($b = 3$) change their uniform body shape to an elongated one as they reach sexual maturity ($b < 3$). On the contrary, *L. synagris* and *O. chrysurus* displayed changes from an elongated body shape as juvenile-females ($b < 3$), to a more uniform body shape ($b = 3$) as adult-females. For both species juvenile-males and adult-males conserve the same elongated body shape ($b < 3$)

as they grow and mature (Table 3). Differences from $b=3$ for Groupers were registered: in juvenile-females of *E. morio* ($b > 3$), *M. bonaci* ($b > 3$), *M. microlepis* ($b > 3$) and *M. tigris* ($b < 3$), in adult-females for all species ($b < 3$ or $b > 3$) except for *M. tigris* ($b = 3$) and in adult-males only for *E. morio* ($b > 3$) and *M. venenosa* ($b < 3$). *Epinephelus morio* displayed the same body shape becoming gradually thicker with size ($b > 3$). For *E. guttatus* juvenile-females' uniformity in body shape ($b = 3$) change to an elongated form as they reach adulthood (adult-females $b < 3$) and then change back to a more uniform body shape as adult-males ($b = 3$). For *M. bonaci* and *M. microlepis* juvenile-females ($b > 3$) and adult-females ($b > 3$) continuously increase in height or width more than in length, whereas through sex change, this tendency ceases and adult-males display a more uniform body shape ($b = 3$). *Mycteroperca tigris* exhibits changes from an elongated form in juvenile-females ($b < 3$) to a uniform body shape as adult-females and adult-males ($b = 3$). *Mycteroperca venenosa* show a uniform body shape ($b = 3$) in juvenile-females, changing to an elongated form in adult-females ($b < 3$) that conserve as adult-males ($b < 3$) (Table 3).

Hypothesis tests on differences between regression lines slopes were performed in order to observe possible growth stanzas. Growth stanzas were accounted for Snappers' *L. campechanus* and *L. synagris* from juvenile-females to adult-females and for the three species (including *O. chrysurus*) from juvenile-males to adult-males. For Groupers growth stanzas could be identified in *E. morio*, *M. bonaci* and *M. microlepis* from juvenile-females to adult-females and for *E. guttatus*, *E. morio*, *M. microlepis* and *M. tigris* from adult-females to adult-males (Table 4).

DISCUSSION

Growth stanzas are characterized by some kind of crisis or discontinuity in development (Ricker, 1979) described by changes in growth rate. Since fishes are indeterminate growers, growth models should be carried out in

TABLE 1
 Welch ANOVA results for gonochoric Snappers (Lutjanidae) and protogynous hermaphrodite Groupers (Epinephelidae)
 from Southern Gulf of Mexico captured from 1999 to 2009

	TL			FL			SL			TW			GW			
	SS	d.f.	P	SS	d.f.	P	SS	d.f.	P	SS	d.f.	P	SS	d.f.	P	
Lutjanidae																
<i>L. campechanus</i>	163.7	3	52.4	0.0	103.8	3	49.7	0.0	1 033 956.9	3	104.9	0.0	919 516.0	3	81.0	0.0
<i>L. synagris</i>	55.5	3	115.3	0.0	44.7	3	113.5	0.0	22 522.9	3	137.5	0.0	19 337.4	3	135.0	0.0
<i>O. chrysurus</i>	220.6	3	357.7	0.0	133.1	3	329.7	0.0	62 195.9	3	585.4	0.0	51 421.5	3	563.1	0.0
Epinephelidae																
<i>E. guttatus</i>	42.6	2	192.6	0.0	788.7	2	639.4	0.0	142 470.7	2	173.4	0.0	125 009.2	2	178.3	0.0
<i>E. morio</i>	901.0	2	748.9	0.0	3 810.2	2	1 960.8	0.0	7 206 584.2	2	347.5	0.0	6 598 284.5	2	350.4	0.0
<i>M. bonaci</i>	4 723.1	2	1 763.1	0.0	9 418.2	2	10 224.9	0.0	322 716 114.2	2	1 533.3	0.0	563 619 213.1	2	1 532.4	0.0
<i>M. microlepis</i>	10 973.1	2	11 652.3	0.0	94.0	2	108.0	0.0	537 245.3	2	57.7	0.0	89 393 585.5	2	1 521.4	0.0
<i>M. tigris</i>	103.6	2	113.1	0.0	89.0	2	100.2	0.0	1 448 996.1	2	54.0	0.0	1 342 851.2	2	54.3	0.0
<i>M. venenosa</i>	103.6	2	109.7	0.0												

Total length (TL), standard length (SL), fork length (FL), total weight (TW) and gutted weight (GW). Source of variation: Sex and gonad developmental stage, for Lutjanidae: juvenile-females, juvenile-males, adult-females and adult-males whereas for Epinephelidae: juvenile-females, adult-females and adult-males, SS=Sum of squares, d.f.=degrees of freedom, F=F ratio and P=probability value. All analyses displayed significant statistical differences ($p < 0.05$). Species are listed in alphabetical order.



TABLE 2
Estimated parameters of length-weight relationships ($W=aTL^b$), in g and cm) by sex and gonad developmental phase for nine species of Grouper-Snapper complex from Southern Gulf of Mexico captured from 1999 to 2009

		FEMALES									
<i>n</i>	TL	log <i>a</i>	SE(<i>a</i>)	95%CI of log <i>a</i>	<i>t</i>	<i>b</i>	SE (<i>b</i>)	95%CI of <i>b</i>	<i>t</i>	<i>R</i> ²	
Luftjanidae											
Juveniles											
	<i>L. campechanus</i>	32.0-49.9	-0.947	0.59	-2.14 to 0.25	-1.6	2.399	0.371	1.64 to 3.15	6.4	0.98
	<i>L. synagris</i>	13.5-29.0	-1.556	0.05	-1.66 to -1.45	-29.5	2.775	0.040	2.69 to 2.86	68.4	0.98
	<i>O. chrysurus</i>	15.8-26.3	-1.232	0.19	-1.61 to -0.86	-6.6	2.444	0.140	2.16 to 2.73	17.3	0.97
Adults											
	<i>L. campechanus</i>	32.5-61.6	-1.526	0.06	-1.65 to -1.41	-25.2	2.800	0.039	2.73 to 2.87	77.9	0.98
	<i>L. synagris</i>	18.5-45.9	-1.330	0.05	-1.43 to -1.23	-26.7	2.634	0.034	2.57 to 2.70	-26.7	0.98
	<i>O. chrysurus</i>	24.4-50.4	-1.714	0.04	-1.79 to -1.64	-43.6	2.795	0.025	2.74 to 2.85	107.7	0.96
Epinephelidae											
Juveniles											
	<i>E. guttatus</i>	20.5-44.5	-1.756	0.20	-2.16 to -1.34	-8.6	2.943	0.132	2.67 to 3.20	22.2	0.97
	<i>E. morio</i>	6.5-25.8	-1.928	0.05	-2.03 to -1.83	-38.0	3.077	0.020	3.01 to 3.15	82.5	0.99
	<i>M. bonaci</i>	4.8-25.0	-2.175	0.05	-2.28 to -2.07	-41.9	3.207	0.054	3.10 to 3.28	84.9	0.99
	<i>M. microlepis</i>	1.9-33.4	-2.095	0.01	-2.12 to -2.07	-178.9	3.004	0.010	3.14 to 3.19	295.1	0.99
	<i>M. tigris</i>	25.3-60.0	-1.305	0.17	-1.65 to -0.96	-7.6	2.665	0.104	2.46 to 2.87	25.5	0.97
	<i>M. venenosa</i>	27.0-61.0	-1.719	0.09	-1.89 to -1.55	-20.0	2.900	0.050	2.80 to 3.00	57.8	0.98
Adults											
	<i>E. guttatus</i>	26.2-51.3	-1.821	0.10	-2.02 to -1.61	-17.4	2.978	0.065	2.84 to 3.10	45.1	0.98
	<i>E. morio</i>	29.5-88.0	-2.406	0.03	-2.47 to -2.34	-72.5	3.319	0.019	3.28 to 3.36	174.3	0.97
	<i>M. bonaci</i>	25.6-123.5	-1.938	0.03	-1.99 to -1.88	-68.4	3.047	0.008	-3.14 to -1.63	-68.4	0.99
	<i>M. microlepis</i>	38.6-111.0	-1.909	0.01	-1.93 to -1.89	-161.5	3.004	0.008	2.99 to 3.02	362.4	0.99
	<i>M. tigris</i>	32.6-74.2	-1.475	0.19	-1.18 to -1.10	-7.7	2.737	0.111	2.52 to 2.96	24.3	0.97
	<i>M. venenosa</i>	34.0-94.0	-1.824	0.07	-1.96 to -1.68	-25.4	2.936	0.049	2.86 to 3.02	72.9	0.98

TABLE 2 (Continued)

		MALES									
	<i>n</i>	TL	log <i>a</i>	SE(<i>a</i>)	95%CI of log <i>a</i>	<i>t</i>	<i>b</i>	SE (<i>b</i>)	95%CI of <i>b</i>	<i>t</i>	<i>R</i> ²
Lutjanidae											
Juveniles											
<i>L. campechanus</i>	13	32.0-58.5	-1.782	0.45	-2.73 to -0.83	-3.97	2.942	0.281	2.35 to 3.54	10.4	0.99
<i>L. synagris</i>	58	14.0-32.5	-1.615	0.06	-1.73 to 1.50	-28.6	2.820	0.042	2.73 to 2.91	-28.6	0.99
<i>O. chrysurus</i>	16	15.9-28.4	-0.874	0.17	-1.24 to -0.50	-5.07	2.164	0.132	1.88 to 2.45	16.3	0.97
Adults											
<i>L. campechanus</i>	436	32.5-81.6	-1.858	0.06	-1.98 to -1.74	-29.7	2.987	0.036	2.91 to 3.06	80.84	0.99
<i>L. synagris</i>	443	17.7-34.7	-1.330	0.06	-1.25 to -1.02	-18.9	2.634	0.042	2.40 to 2.56	58.55	0.98
<i>O. chrysurus</i>	649	19.5-50.3	-1.633	0.04	-1.71 to -1.56	-41.3	2.739	0.026	2.69 to 2.79	104.1	0.99
Epinephelidae											
Adults											
<i>E. guttatus</i>	917	29.0-54.8	-2.158	0.08	-2.32 to -1.98	-25.1	3.194	0.052	3.09 to 3.29	60.5	0.98
<i>E. morio</i>	441	37.2-89.0	-1.777	0.09	-1.96 to -1.60	-19.3	3.040	0.050	2.94 to 3.14	57.8	0.98
<i>M. bonaci</i>	28	101.5-124.5	-2.384	0.37	-3.14 to -1.63	-6.4	3.269	0.180	2.90 to 3.64	18.0	0.97
<i>M. microlepis</i>	34	95.0-111.0	-1.838	0.83	-4.22 to -0.86	-3.0	2.978	0.046	2.50 to 4.15	8.10	0.98
<i>M. tigris</i>	242	42.5-81.2	-2.464	0.17	-2.80 to -14.3	-14.3	3.294	0.097	3.10 to 3.49	33.8	0.97
<i>M. venenosa</i>	1 287	40.0-100.0	-1.830	0.16	-2.16 to -1.50	-11.1	2.937	0.087	2.76 to 3.11	33.4	0.97

n is the sample size; TL range: maximum and minimum total length in cm; log *a* and *b* are the L-W relationship parameters; SE(*a*)=standard error of parameter *a*, SE(*b*)=standard error of parameter *b*, C.I.=minimum and maximum confidence intervals for each parameter. *t*=*t*-statistic for both parameters. *R*²=coefficient of determination. All relationships displayed *p*<0.05. Species are listed by alphabetical order.

TABLE 3

Results of *t*-test for *b*-value (slope) to acknowledge differences from the allometric coefficient *b*=3 in nine species of the Grouper Snapper complex from Southern Gulf of Mexico captured from 1999 to 2009

	FEMALES					
	<i>b</i>	SE (<i>b</i>)	SE Model	<i>d.f.</i>	<i>t</i>	<i>p</i>
Lutjanidae						
Juveniles						
<i>L. campechanus</i>	2.399	0.371	0.0814	27	5.327*	<0.0001
<i>L. synagris</i>	2.775	0.040	0.1555	107	5.743*	<0.0001
<i>O. chrysurus</i>	2.444	0.140	0.0465	37	8.482*	<0.0001
Adults						
<i>L. campechanus</i>	2.800	0.039	0.0551	434	3.872*	<0.0001
<i>L. synagris</i>	2.634	0.034	0.0756	410	1.432	0.0101
<i>O. chrysurus</i>	2.795	0.025	0.0827	725	1.767	0.0033
Epinephelidae						
Juveniles						
<i>E. guttatus</i>	2.943	0.132	0.1473	44	0.157	0.3897
<i>E. morio</i>	3.077	0.020	0.0887	286	2.913**	<0.0001
<i>M. bonaci</i>	3.207	0.054	0.0851	44	6.019**	<0.0001
<i>M. microlepis</i>	3.004	0.010	0.1162	907	21.363**	<0.0001
<i>M. tigris</i>	2.665	0.104	0.1341	59	3.840*	<0.0001
<i>M. venenosa</i>	2.900	0.050	0.0973	259	1.195	0.0044
Adults						
<i>E. guttatus</i>	2.978	0.065	0.1724	557	2.266**	<0.0001
<i>E. morio</i>	3.319	0.019	0.1270	1597	18.89**	<0.0001
<i>M. bonaci</i>	3.047	0.008	0.0747	663	3.161**	<0.0001
<i>M. microlepis</i>	3.004	0.008	0.0728	138	0.247**	0.0003
<i>M. tigris</i>	2.737	0.111	0.1341	214	0.123	0.0150
<i>M. venenosa</i>	2.936	0.049	0.1525	1006	3.711*	<0.0001
	MALES					
	<i>b</i>	SE (<i>b</i>)	SE Model	<i>d.f.</i>	<i>t</i>	<i>p</i>
Lutjanidae						
Juveniles						
<i>L. campechanus</i>	2.942	0.281	0.0486	11	1.697	0.0021
<i>L. synagris</i>	2.820	0.042	0.0535	56	3.473*	<0.0001
<i>O. chrysurus</i>	2.164	0.132	0.0714	14	6.318*	<0.0001
Adults						
<i>L. campechanus</i>	2.987	0.036	0.0519	433	6.486*	<0.0001
<i>L. synagris</i>	2.634	0.042	0.0540	441	9.066*	<0.0001
<i>O. chrysurus</i>	2.739	0.026	0.0592	647	6.574*	<0.0001
Epinephelidae						
Adults						
<i>E. guttatus</i>	3.194	0.052	0.1174	915	1.419	0.0044
<i>E. morio</i>	3.040	0.050	0.1129	439	9.067**	<0.0001
<i>M. bonaci</i>	3.269	0.180	0.0496	26	1.497	0.0011
<i>M. microlepis</i>	2.978	0.046	0.0621	32	1.965	0.0039
<i>M. tigris</i>	3.294	0.097	0.1319	240	1.905	0.0001
<i>M. venenosa</i>	2.937	0.087	0.1550	1285	4.445*	<0.0001

b-value from the L-W relationship ($W=aTL^b$), SE(*b*)=standard error of *b*, SE Model=standard error of the L-W relationship, *d.f.*=degrees of freedom, *t*=*t*-Student statistic and *p*=probability value. Asterisks denote significant statistical differences of *b*-value from *b*=3 considering **t* when *b*<3 and ***t* when *b*>3. Species are listed by alphabetical order.

TABLE 4
Hypothesis tests of regression line slopes between sexes and gonad developmental phase of nine species from the Grouper-Shapper complex of Southern Gulf of México captured from 1999 to 2009

Family	Species	SS	d.f.	MS	F	p	SS	d.f.	MS	F	p
Lutjanidae				Juvenile-females vs. adult-females					Juvenile-males vs. adult-males		
	<i>L. campechanus</i>	0.0232	1	0.0232	4.85	0.028*	0.0496	1	0.0496	8.75	0.003*
	<i>L. synagris</i>	0.0117	1	0.0117	4.86	0.027*	0.0434	1	0.0434	22.98	0.000*
	<i>O. chrysurus</i>	0.0176	1	0.0176	7.55	0.066	0.0178	1	0.0178	7.17	0.007*
Serranidae				Juvenile females vs. adult-females					Adult-females vs. adult-males		
	<i>E. guttatus</i>	0.0003	1	0.0003	0.04	0.836	0.0424	1	0.0424	6.95	0.008
	<i>E. morio</i>	0.1574	1	0.1574	41.23	0.000	0.2017	1	0.2017	40.98	0.000
	<i>M. bonaci</i>	0.0828	1	0.0828	31.46	0.000	0.0014	1	0.0014	0.93	0.335
	<i>M. microlepis</i>	0.7873	1	0.7873	139.85	0.000	2.4 (E ⁻⁷)	1	2.4 (E ⁻⁷)	7.56	0.006
	<i>M. tigris</i>	0.0018	1	0.0018	0.17	0.680	0.1489	1	0.1489	14.16	0.000
	<i>M. venenosa</i>	0.0023	1	0.0023	0.30	0.584	3.4 (E ⁻⁷)	1	3.4 (E ⁻⁷)	0.00	0.994

SS=Sum of squares, d.f.=degrees of freedom, MS= Mean squares, F=F ratio and p=probability value. Asterisks denote significant statistical differences (p<0.05). Species are listed in alphabetical order.

many different levels of detail (Craig, 1984; Enberg, Dunlop, & Jørgensen, 2008) in order to provide a realistic growth scheme for the species. Froese (2006) suggested a series of recommendations when calculating L-W relationships and noted that L-W relationship for juveniles (many of which do not have the adult body shape) should be calculated separately from adults to avoid the overall regression to be overestimated, since younger individuals (or premature) tend to grow at faster rates. Nevertheless, many of the published data for L-W relationships for different species do not separate juveniles nor females and males.

The evident difference between juveniles and adults for both sexes in gonochoric Snappers showed that growth stanzas could be observed from the juvenile phase to adults (sexually mature) if L-W relationships are obtained separately. Differences between sexes (for adults only) could also be appreciated even though we did not perform a direct comparison between adults: *L. synagris*, *L. campechanus* and *O. chrysurus* adult-females were bigger and heavier than adult-males. Trejo-Martínez (2011) and Brulé, Colás- Marrufo, Pérez-Díaz and Sámano-Zapata (2010) reported that in all three Snapper species males reach sexual maturity earlier and at smaller sizes than females. Mean gonadosomatic index was even bigger in males ($3.30 \pm 0.23 - 0.50 \pm 0.03\%$) of *Ocyurus chrysurus* than in females ($2.30 \pm 0.13 - 0.50 \pm 0.03\%$) suggesting that there is an important deviation of surplus energy canalized to reproduction in males. Reproductive investment reduces the energy necessary for somatic growth, causing a growth rate descend prior to the reproductive season (Lester et al., 2004). Therefore, L-W relationships should be calculated for these species by sex.

For hermaphrodite Groupers, growth stanzas were only observed in *E. morio*, *M. bonaci* and *M. microlepis* juvenile-females to adult-females. These results may be due to the size of the juveniles registered for *E. morio*, *M. bonaci* and *M. microlepis* (from 1.9cm to 33.4cm) in comparison to juveniles of *E. guttatus*, *M. tigris* and *M. venenosa* (20.5cm to

61.0cm). Since Groupers have slow growth rate and late sexual maturity (Coleman et al., 1999) and juveniles were characterized based on their gonadal developmental phase, sexual immature individuals could still be present at large sizes. As a result, growth stanzas could only be identified in smaller juvenile individuals (possibly below 30cm TL) that indeed display a different W-L relationship than larger juvenile specimens.

Groupers' growth stanzas from adult-females to adult-males were observed in *E. guttatus*, *E. morio*, *M. microlepis* and *M. tigris*. Gonadosomatic index for all species was up to three times higher in adult-females than in adult-males, which indicate that there is also, an important amount of energy directed to gonadal development in females. Munday, Hodges, Choat and Gus (2004) registered the existence of a sex-specific growth effect in other species of protogynic hermaphrodites, suggesting that females that become males grow faster than other females before the age of sex change. Only the largest female in a social group becomes male, suppressing sex change in subordinate females (Francis, 1992). Therefore different growth stanzas between sexes in Groupers were expected. Nevertheless, *M. bonaci* and *M. venenosa* did not register differences in L-W relationship slopes between adult females vs. males, even though *M. bonaci* displayed changes in body shape. Since *M. venenosa* maintain the same uniform shape regardless of the sex change, no growth stanzas between adult-females and adult-males could be observed.

Growth stanzas could be registered for gonochoric Snappers mainly due to gonadal development and in hermaphrodite Groupers due to gonadal development and sex change. These results corroborate that a single regression will not adequately describe the length-weight relationship of a species. It must be considered that growth rate is not constant and may change either continuously or abruptly during the fish lifetime (Katsanevakis et al., 2007) due to genetics, ontogenetic shifts in diet, differences in seasons, sexes, gonad

development or number of specimens examined (Andreu-Soler, Oliva-Paterna, & Torralva, 2006). Therefore, the identification of growth stanzas in L-W relationships is imperative not only to obtain a better knowledge of the growth process in reef fishes, but to establish an accurate growth rate used to calculate some target reference points such as maximum sustainable yield or yield-per-recruit used in fisheries management. This study demonstrates the presence of growth stanzas related to gonadal development in Groupers and Snappers and to sex change in Groupers. Therefore, we suggest that the determination of L-W relationships, at least for these families, should be done separating juveniles from adults and females from males in order to avoid an overestimation or a mistaken growth rate.

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RESUMEN

Etapas de crecimiento en un complejo Epinephelidae-Lutjanidae: consideraciones al cálculo de las relaciones peso-longitud. Distintos estados o estanzas de crecimiento descritos por cambios en el ritmo de crecimiento, se pueden observar en peces a lo largo de su vida ya que presentan crecimiento indeterminado. A través del análisis de relaciones longitud-peso (L-P), se identificaron distintas estanzas de crecimiento considerando el tipo de sexualidad, sexo y madurez sexual de individuos de tres especies de pargos (Lutjanidae) gonocóricos y seis de meros (Epinephelidae) hermafroditas protóginos. Pruebas independientes de ANOVA de Welch se aplicaron para conocer si existían diferencias estadísticas significativas en la media de la longitud y peso de juveniles, adultos, hembras y machos de pargos y en juveniles hembras, hembras y machos de meros. De acuerdo a las diferencias observadas, se procedió al cálculo de la relación L-P, parámetros a y b , error estándar (SE b) y coeficiente de determinación (R^2) por separado (juveniles, adultos, hembras y machos) para cada especie. Los valores del parámetro b para todas las especies se encontraron dentro del rango esperado de 2.5 a

3.5 para pendientes de la relación L-P en peces. Los pargos tuvieron valores de b : juveniles de hembras de 2.44-2.77, juveniles de machos 2.16-2.94, hembras adultas 2.63-2.80 y machos adultos 2.63-2.98. Los meros tuvieron un valor de b para juveniles de hembras: 2.66-3.20, adultos hembras: 2.73-3.31 y adultos de machos: 2.93-3.29. Para cada relación, el valor de b fue probado a través de una prueba de t -Student para explorar diferencias significativas del coeficiente alométrico ($b=3$), lo cual indicaría cambios en la forma del cuerpo de los individuos. Finalmente pruebas de hipótesis sobre las diferencias entre pendientes obtenidas de las relaciones L-P mostraron distintas estanzas de crecimiento relacionadas en pargos con el desarrollo gonadal y en meros con el desarrollo gonadal pero también con el cambio de sexo. A través de este estudio se pudo observar la existencia de distintas estanzas de crecimiento en especies de alta importancia comercial para el Sur del Golfo de México. Por lo tanto se recomienda la obtención de las relaciones L-P por separado según el sexo y desarrollo gonadal de cada especie, para evitar una sobre estimación o un cálculo erróneo de la tasa de crecimiento poblacional la cual se utiliza en manejo de las pesquerías para determinar algunos puntos de referencia como el criterio de máximo rendimiento sostenible o bien el criterio de rendimiento por recluta.

Palabras clave: estanzas de crecimiento, relaciones longitud-peso, complejo mero-pargo, Golfo de México.

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