



Linking temporal changes in the demographic structure and individual growth to the decline in the population of a tropical fish



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ABSTRACT

The exceptional biodiversity and productivity of tropical coastal lagoons can only be preserved by identifying the causes for the decline in the populations living in these vulnerable ecosystems. The Terminos lagoon in Mexico provided an opportunity for studying this issue as some of its fish populations, in particular the Silver Perch (*Bairdiella chrysoura*), have declined significantly since the 1980s. Fish sampling campaigns carried out over the whole lagoon area in 1979–81 and again in 2006–2011 revealed the mechanisms which may have been responsible for this decline. Based on biometrical data for 295 juveniles and adults from the two periods and on somatic growth derived from 173 otoliths, a study of the temporal changes in the demographic structure and life history traits (individual growth and body condition) made it possible to distinguish the causes of the decline in the *B. chrysoura* population. Growth models for the lagoon in 1980–1981 and 2006–2011 showed no significant change in the growth parameters of the population over the last 30 years with a logistic model giving an accurate estimate ($R^2 = 0.66$) of the size-at-age for both periods. The decline in the *B. chrysoura* population could not be explained by an overall decrease in individual size and condition in the lagoon, the average standard length (SL) and Fulton index (FI) having increased slightly since 1980–1981 (4.6 mm and 0.02 for juveniles and 5.42 mm and 0.07 for adults). However, the size structure of the population in the lagoon has changed, with a significant shift in the size distribution of juveniles with a marked reduction in the proportion of juveniles ≤ 60 mm in the captures (90.9% fewer than in 1980–1981). As the otolith growth rate of fish during the first 4 months also decreased significantly between the two sampling periods (–15%), it is suggested that the main reason for the decline in the abundance and biomass of *B. chrysoura* within this system may be that its habitats are less suitable for fish growth and survival in the initial months after settlement. Environmental conditions in the lagoon appear to allow compensatory growth of the individuals that survive this early demographic bottleneck. The key for the conservation of *B. chrysoura* probably lies in the identification and restoration of the habitats required by its larvae and juveniles.

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1. Introduction

Identifying the factors and mechanisms that cause global biodiversity loss and local demographic fluctuations of species is a primary challenge for conservation biology, especially in tropical lagoons and estuaries (Hutchings and Baum, 2005; Lotze et al.,

2006; Halpern et al., 2008). Due to their location at the land–sea interface, these habitats are among the most productive but also the most vulnerable ecosystems in the world (Costanza et al., 1997; Rochette et al., 2010; Layman et al., 2011). During the last century, their environmental conditions have been significantly modified by the combined effects of local human activity and climate change (Costanza et al., 1997). The changes observed in their biological communities (Jackson et al., 2001; Lotze and Worm, 2009) require a better understanding of the factors driving demographic responses to environmental changes.

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There are many reasons for fluctuations or decline of fish populations, with complex interactions between external and internal drivers (Fonseca and Cabral, 2007). However, life history traits have a determining effect on the three main components of individual fitness, i.e. survival, growth and reproduction (Hutchings, 1993; Violle et al., 2007), and can be used to predict the vulnerability status of individual species (Chessman, 2013) and differences in demographic trajectories between species (Sirot et al., 2015). Therefore, evaluating variations in life history traits and linking their temporal changes to population dynamics is essential for understanding demographic responses of fish to environmental perturbations (Winemiller, 2005).

This study evaluated the changes in the population structure (size distribution) and the life history traits (growth and body condition) of a tropical fish species, the American Silver Perch *Bairdiella chrysoura* (Lacépède, 1802), with a declining population in a very large tropical lagoon (Laguna de Terminos, Mexico). This lagoon, the third largest in the world, is of great biological, ecological and economic importance (Ramos-Miranda et al., 2005b). However, intensification of human activities within its catchment area and in the nearby marine coastal zone has caused major environmental changes in the lagoon since the 1980s (Ramos-Miranda et al., 2005a, 2005b; Villéger et al., 2010; Sirot et al., 2015), resulting in a significant decrease in both global fish abundance (−41%) and biomass (−58%) (Sirot et al., 2015). *Bairdiella chrysoura* is illustrative of this community collapse as this fish species was listed as one of the most abundant and widely distributed of the Gulf of Mexico in the 1980s (Chao and Musick, 1977), and has since suffered a decline of ~90% in both its abundance and biomass within the lagoon (Sirot et al., 2015).

Despite a short life-span (<6 years) and a small maximum size (250 mm total length) (Waggy et al., 2006), *B. chrysoura* is of commercial and recreational importance in the Gulf of Mexico (Ayala-Pérez et al., 2006) and is a key component of local coastal ecosystems as the normal prey for several large estuarine predators (Luczkovich et al., 2000; Heupel and Hueter, 2002; Blewett et al., 2006; Grammer et al., 2009). Knowledge of the mechanisms responsible for its recent decline is required so that appropriate conservation actions can be taken. In order to identify these mechanisms in the Terminos lagoon, the changes since 1980–1981 in both its demographic structure (size of cohorts and percentage of juveniles vs. adults) and life history traits (somatic growth rate and body condition) were studied. Growth rate and body condition are generally included in studies assessing demographic fluctuations of fish where there are environmental perturbations (Ashfield et al., 1998; Amara et al., 2007) as they are considered proxies for individual fitness, in particular in early life stages (Houde, 1987; Cushing, 1990; Smith and Shima, 2011). Establishing the relationships between the growth rate and body condition on the one hand with changes in the population structure on the other in the light of the environmental changes observed in the Terminos lagoon since 1980–1981 should provide a better understanding of the ongoing processes leading to the decline of this fish in this ecosystem.

2. Materials and methods

2.1. Study area

The Terminos Lagoon (90°00' – 90°20' W 18°25' – 19°00' N) is the largest estuarine system along the coast of Mexico. Located in the southwest part of the Gulf of Mexico (Fig. 1), it communicates with the sea through two wide channels, located at either end of Carmen Island, the Puerto Real outlet to the east and the Carmen outlet to the west. The lagoon is shallow (mean depth = 2.5 ± 1.0 m) and the water temperature is high throughout the year

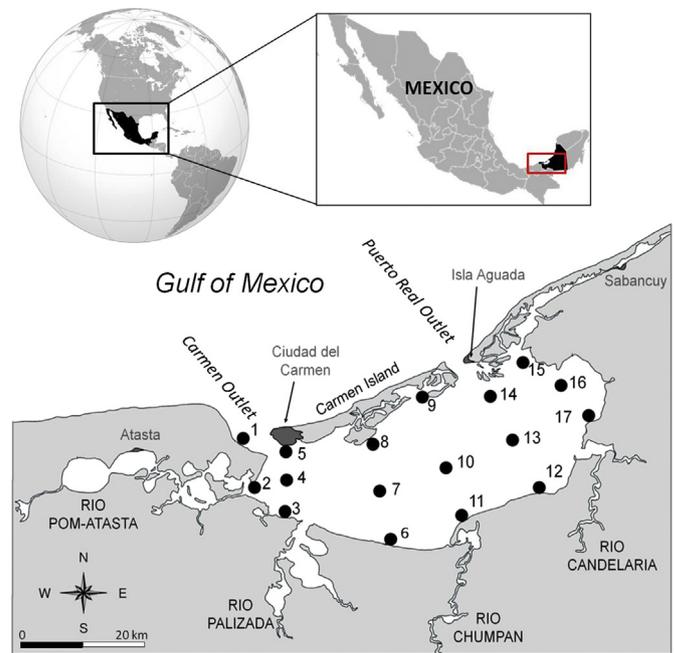


Fig. 1. Study area (Southern Gulf of Mexico) with the 17 sampling sites (black spots) in the Terminos lagoon and the main cities (dark gray).

(mean = 27.8 ± 2.7 °C), with a minimum of 20 °C and a maximum of over 32 °C (Villéger, 2008). Freshwater inputs to the lagoon originate mainly from three rivers located on its southern edge (Rio Palizada in the west and Rio Chumpan and Rio Candelaria in the east). As the water in the lagoon generally circulates from east to west, the southwestern part of the lagoon tends to have brackish water while the salinity of water in the northwestern part is close to marine levels (Carvalho et al., 2009; Villéger et al., 2010). The tropical climate in the area has three distinct seasons: a dry season from February to May and a wet season from June to September with the 'nortes' season, characterized by strong winter storms coming from the north which bring rain and low temperatures, from October to January (Yañez-Arancibia and Day Jr., 1982). As a result, the water salinity in the lagoon also varies throughout the year, with the highest levels in the dry season and the lowest levels during the rainy season.

2.2. Temporal changes in demographic structure and body condition

To compare the demographic structure and the body sizes and condition of juveniles and adults of *B. chrysoura* in 1980–1981 and 2010–2011, fish were collected throughout the year in 1980–1981 and in 2010–2011, by monthly sampling at 17 fixed stations distributed over the whole lagoon area (Fig. 1). The same method was used for all sampling dates and stations. A 5 m long shrimp trawl net with 2.5 m mouth and 19 mm mesh was towed for 12 min at a speed of 2.5 knots (i.e. 4.6 km/h), giving a sampled area of 2000 m². All the individuals captured during the two annual sampling campaigns (Table 1) were measured (standard length, SL, and total length, TL, in mm), weighed (total weight, W, in mg). Their individual body condition was evaluated using the Fulton index (FI, Ricker, 1975), defined as:

$$FI = \frac{W}{SL^3} \times 100$$

Table 1
Total abundance and biomass of *B. chrysoura* in the samples for each period and number of individuals sub-sampled for the demographic and condition studies (1), and the age and growth estimation (2). Past period (1980–1981) and present period (2010–2011).

Period	Total biomass	Total abundance	Number of individuals		Mean size SL \pm standard deviation (mm)		Mean weight \pm standard deviation (g)	
			(1)	(2)	(1)	(2)	(1)	(2)
Past period	21,098	904	216	52	92.4 \pm 26.0	84.3 \pm 36.5	20.0 \pm 15.5	14.6 \pm 14.3
Present period	2014	79	79	121	98.4 \pm 25.2	101.3 \pm 23.9	25.5 \pm 21.1	27.4 \pm 17.4

where W is the total weight (mg) and SL the standard length (mm).

The fish were then classified into 20 mm size classes and, as proposed by Chavance (1984), the size limit for distinguishing juveniles from adults was 100 mm SL. The size distributions in the whole population and for each physiological stage were compared between the two periods using Kolmogorov–Smirnov tests, and the relative proportions of juveniles (≤ 100 mm SL) and adults (> 100 mm SL) within the population were compared using a Chi-square test. The temporal changes in the average SL and FI were also estimated for the whole population, for the juveniles and for the adults, using separate Welch's t-tests. This test compares the mean of two groups with unequal variance and, where there are large numbers of individuals in each group (> 30) as in this case, it is robust to non-normality of the data (Zar, 1999).

2.3. Temporal changes in growth

The ages of a total of 173 individuals were estimated (Table 1) using the seasonal marks in their otoliths. Sub-samples were taken of the fish collected during the 1980–1981 and 2010–2011 sampling campaigns to give the best picture of the variability in individual growth or age within the lagoon area. For each month in each period, they covered the entire geographical area colonized by the species and included a minimum of 1 and a maximum of 4 individuals per size class collected at each station. 52 otoliths were collected for 1980–1981 and 79 for 2010–2011. As accurate identification of the timing for the seasonal mark deposition requires otolith samples for all months, 42 extra otoliths from an additional sampling campaign conducted in the lagoon in 2006, were added to the 2010–2011 sub-samples, giving a total of 121 otoliths. The seasonal mark deposition was only validated on present otoliths (2006 and 2010–2011) as their edges were more reliable due to their short storage duration. However, this information was also observed on past otoliths (1980–1981) to check that the timing of mark deposition had not changed.

Of the two largest otoliths (sagittae), only the right sagitta was extracted, cleaned in ultrapure water, and embedded in polyester resin (Sody 33, ESCIL® France). Transverse sections (500 μ m thick including the otolith core) were cut using a low speed, rotary saw (ISOMET, Buehler®). Each section was then mounted on a microscope slide using thermoplastic resin (Crystalbond 509®) and both faces of the section were ground and polished down to the core using 1200 grit sandpaper followed by aqueous aluminum powder (3 μ m and 1 μ m) on polishing cloths. Finally, each section was etched with 5% EDTA for 5 min, rinsed with tap water and stained with Toluidine Blue for 5 min to increase the contrast between the translucent and opaque (growth) marks. The final stained section containing the core was observed using a stereomicroscope (Olympus SZX12) under reflected light coupled to a color video camera (C5 Jenoptik) connected to an image acquisition system (ProgRes CapturePro 2.5, Jenoptik). The otolith interpretation (growth mark identification) was undertaken by two independent readers with no prior information on fish size or date of capture. For each otolith, the number of stained marks was recorded along the major axis (Fig. 2). The total length of this axis (from the core to the

edge) and the distance between two successive growth marks along it were measured using a specific R script (available on demand).

The annual timing of growth mark deposition for 2006–2011 otoliths was verified by estimating the timing in two ways. For each month, (1) the frequency of otoliths with a stained edge was counted, and (2) the relative marginal distance (RMD) was calculated using the formula:

$$RMD = \frac{AMD}{D_{(n, n-1)}} \quad (1)$$

where AMD is the absolute marginal distance between the last interpreted growth mark and the otolith edge and $D_{(n, n-1)}$ is the distance between the last two growth marks.

The growth marks were then counted for both sampling periods and converted into ages (in months) based on the timing of their deposition, the month of capture for each individual and the theoretical date of birth of *B. chrysoura* in the area. As *B. chrysoura* has two main spawning periods in the Terminos lagoon, one between February and July and the other in November (Chavance, 1984), May 1st and November 1st were taken as the birth dates for this study. For each individual, the most likely date of birth was chosen depending on the appearance of the otolith edge (stained or not), which indicated the time of year (based on the previous timing verification step).

2.3.1. Comparison of population growth parameters between periods

Size-at-age relationships in the population for the two periods were compared using a two-step process. First, the best of five possible growth functions for each case was selected: the Von Bertalanffy function, the linear, logistic and power models and the Gompertz model (Diouf et al., 2009; Mercier et al., 2011) (Appendix A). Models were fitted to the size-at-age data of the corresponding period using the Nelder-Mead optimization algorithm with residual sum of squares (RSS) as the criterion. The RSS is directly related to the likelihood provided that residuals are normal and homoscedastic (verified) (Burnham and Anderson, 2002). Model fits were compared using the corrected Akaike information criterion (AICc) (Burnham and Anderson, 2002):

$$AICc = n \log \left(\frac{RSS}{n} \right) + 2p \left(\frac{n}{n-p-1} \right) \quad (2)$$

where n is the sample size, p is the number of fitted parameters in the model (plus one for the estimated variance) and RSS is the residual sum of squares.

The lowest value of AICc indicates the best model of those tested. We additionally used R^2 -values that compare the fit of non-linear regression models with that of a linear intercept-only model (Kvålseth, 1985), as indicators of the proportion of the total variation in fish length that is explained by fish age. Once the best model had been selected, a general comparison of the growth curves for both periods was performed using an analysis of the residual sum of squares, ARSS (Chen et al., 1992).

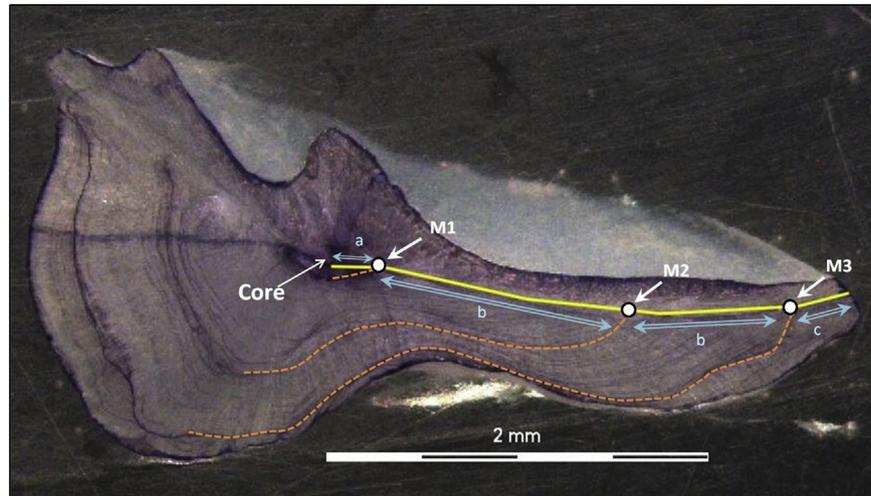


Fig. 2. Transverse section of the right otolith (sagitta) of *Bairdiella chrysoura* observed under reflected light after etching and staining with Toluidine blue. M1, M2 and M3 (white spots) respectively show the positions of the first, second and third opaque marks (orange dotted lines) along the axis (the yellow plain line) used for growth increment measurements. The double arrow (a) is the distance between the core and the first opaque mark (M1, here considered as a settlement mark) and represents the width of the first growth increment; the double arrows (b) indicate the distance between successive opaque marks (M1, M2, M3) and represent the widths of the successive growth increments used to estimate the age of the fish and the double arrow (c) indicates the distance between the last opaque mark (here M3) and the edge of the otolith and represents the absolute marginal distance (AMD) used to calculate the relative marginal distance (RMD). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3.2. Comparison of individual growth between periods

To complement the results of the length-at-age modeling, changes in growth between periods were also determined using otolith growth increment measurements. As these increments are laid down throughout the entire life of individuals without resorption (Campana and Neilson, 1985) and their width reflects the somatic growth rate (Campana, 1990), measurements of these increments gave a clear picture of detailed temporal changes in the growth rate during the whole lifespan of *B. chrysoura*, including the early life stages which were not found (SL < 20 mm) or only in small numbers (SL 20–60 mm) among the samples for both periods. Differences in individual lifetime growth patterns between periods were studied by comparing the width between successive growth marks in the otoliths separately using a Welch's t-test (if there were fewer than 30 individuals in each group or if the normality of the data could not be rejected using a Shapiro test) or a Mann–Whitney test (if there were more than 30 individuals in each group or the data was non-normal) with a Bonferroni correction. The same procedure was applied to test whether the birth date (May or November, Chavance, 1984) had an effect on the growth rate at any stage of the fish life-cycle. As only a few fish reached an age equivalent to 6, 7, 8 or 9 marks, comparisons were only carried out for marks 1 to 5 or 6 depending on the period.

All statistical analyses were performed using the R software (R Development Core Team, 2014) taking $\alpha < 0.05$ as indicating statistical significance.

3. Results

3.1. Temporal changes in demographic structure and body condition

Despite the 91% decrease in abundance (90% in biomass) that occurred between the two sampling periods (Table 1), there has been no significant change in the overall population structure of *B. chrysoura* in the Terminos lagoon (Fig. 3), with similar general distribution of sizes (Kolmogorov–Smirnov = 0.15, $p = 0.107$) and close relative proportions of juveniles (≤ 100 mm SL) and adults (> 100 mm SL) in the population (Chi-square test = 0.05, $df = 1$,

$p = 0.82$). Juveniles and adults represented 59% and 41%, respectively, of individuals caught in 2010–11, against 57% and 43% in 1980–1981. However, a separate assessment of the biometrical data for the adults and juveniles showed a significant change (Kolmogorov–Smirnov = 0.2639, $p = 0.02$) in the size distribution of juveniles since 1980–1981, with the disappearance of size classes below 60 mm SL (Fig. 3). This resulted in less variable but slightly greater individual sizes of juveniles (Welch's t-test = 2.19, $df = 134.19$, $p = 0.03$) captured in 2010–2011 (SL = 79.42 ± 9.98 mm) compared with those captured in 1980–81 (SL = 74.73 ± 17.31 mm). However, because no significant change was found in the average individual size of the adults (average SL = 118.18 ± 10.49 mm in 1980–1981 and 123.61 ± 14.86 mm in 2010–2011, Welch's t-

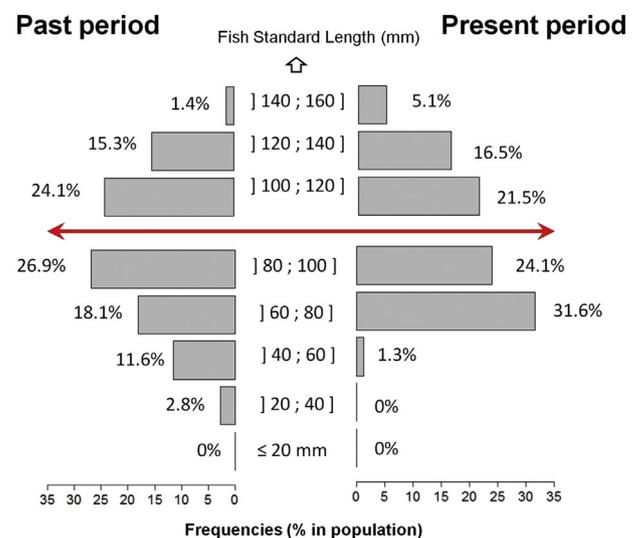


Fig. 3. 1980–1981 (past period) and 2010–2011 (present period) distributions of size classes (standard length in mm) in the population of *B. chrysoura* in the Terminos lagoon. The theoretical size at first sexual maturity (100 mm, Chavance, 1984) is indicated by the double red arrow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

test = 1.95, $df = 46.30$, $p = 0.06$) or in their size distribution between the two periods (Kolmogoriv–Smirnov = 0.2689, $p = 0.06$), the slight increase in average body size found for the whole population between 1980–1981 (SL = 92.43 ± 26.06 mm) and 2010–2011 (SL = 98.44 ± 25.19 mm) was not significant (Welch's t-test = 1.79, $df = 143.09$, $p = 0.07$). Similarly, there was no significant change in the average individual body condition in the lagoon population (Welch's t-test = 1.06, $df = 123.83$, $p = 0.28$) between 1980–1981 (FI = 2.11 ± 0.26) and 2010–2011 (FI = 2.15 ± 0.31), with similar average Fulton Indexes for the two periods for both juveniles (2.08 ± 0.26 in 1980–1981 and 2.10 ± 0.29 in 2010–2011, Welch's t-test = 0.25, $df = 70.37$, $p = 0.79$) and adults (2.15 ± 0.26 in 1980–1981 and 2.22 ± 0.33 in 2010–2011, Welch's test = 1.11, $df = 53.46$, $p = 0.27$).

3.2. Temporal changes in growth

The estimated ages were based on the otolith measurements for the same size classes in 1980–1981 (SL = 27–138 mm) and in 2006/2010–2011 (SL = 32–143 mm), but the ages differed slightly in the two periods (from 2 to 36 months and 2 to 49 months, respectively).

3.2.1. Timing of growth mark deposition

When successful (in 74% of the otoliths analyzed), staining with Toluidine blue showed the otolith seasonal increments in *B. chrysoura* as a narrow chromophilic opaque band (always colored in deep blue and hereafter called the 'growth mark') followed by a wide translucent band punctuated by a few thin chromophilic lines (Fig. 2). The otolith core was very chromophilic and therefore easily localizable and the first growth mark (i.e. that closest to the core) was always the most heavily stained.

Otoliths with opaque (stained) edges were found throughout the year, but their frequency varied seasonally, with two peaks, one in February and one in June–July (Fig. 4A). The intra-annual change in the relative marginal distance (RMD) also had two minima, in February and in June–July. This clearly suggested the deposition of two opaque marks per year in the otoliths of *B. chrysoura*, one in February and one in June–July. Despite the lower number of otoliths with interpretable edges for 1980–1981 (32), observation of the opaque edges and RMD estimates for this period matched this pattern of mark deposition (Fig. 4B), suggesting that the timing of otolith growth had remained constant in the lagoon over the last 30 years (Fig. 4C).

3.2.2. Growth modeling and comparison of population growth parameters between periods

Irrespective of the period, the standard (SL) and total (TL) lengths of *B. chrysoura* were strongly linked ($R^2 = 0.99$) by the linear relationship:

$$TL(mm) = 1.21 \times SL(mm) - 0.84 \quad (3)$$

Therefore, only the age-at-SL relationship was studied for the two periods. According to AICc, the logistic and the Gompertz models were the most relevant, for both sampling periods (Table 2). The estimated asymptotic lengths (SL_{∞}) predicted by these models were very similar for the two periods (125.03 mm in 1980–1981 and 112.08 mm for the present period for the logistic model, 131.69 mm in 1980–1981 and 113.59 mm for the present period for the Gompertz model). No significant change of the growth pattern was observed between periods irrespective of the models considered (Logistic: $F_{3,118} = 0.94$, $p = 0.42$; Gompertz: $F_{3,118} = 1.18$ and $p = 0.31$). Therefore, the data were pooled to infer a common growth curve of *B. chrysoura* in the lagoon for the two

periods. This confirmed the accuracy of the logistic model for growth prediction in this population (its AICc was at minimum less than 2 points the AICc of the next best model, i.e. the Gompertz one). The final equation obtained for the two periods pooled was (Fig. 5):

$$SL(mm) = \frac{113.91}{1 + \exp(-0.22 \times \text{age(months)} + 1.61)}, R^2 = 0.66 \quad (4)$$

3.2.3. Comparison of individual growth between periods

The otolith radius (OR) was strongly correlated with the fish standard length irrespective of the period (SL = $42.16 \times OR - 17.13$; $R^2 = 0.94$), confirming that the otolith growth rate could be used as a valid proxy of somatic growth for *B. chrysoura*. Therefore, a comparison of the widths of the successive otolith marks indicated differences in the growth histories of individuals between the two periods.

The date when the fish were born (May or November) had no significant effect on the otolith growth rate in 1980–1981 or in 2006–2011 (Table 3). The shape of the first mark, nearest to the core, was very consistent. Furthermore, the growth increment associated with this first mark and its variability were consistently lower than for the following increments (tests between the 1st and the 2nd, 3rd, 4th and 5th increments: range of Welch's t-tests = 11–36, range of $df = 57$ –117.42, $p < 2.2 \times 10^{-16}$, $p_{adjusted} < 1.1 \times 10^{-15}$, test between 1st and 6th increment: Mann–Whitney test = 519, $p = 3.6 \times 10^{-9}$, $p_{adjusted} < 1.8 \times 10^{-8}$, $p_{adjusted}$ being the *p* value adjusted by the Bonferroni correction for five tests, Fig. 6). This increment did not differ between the two sampling periods (Welch's t-test = 0.24, $df = 63$, $p = 0.81$, $p_{adjusted} = 1$). Therefore, this first mark was considered as a settlement mark and was not included in the count of seasonal marks for age estimation. The width of the second increment showed that growth was significantly different between the periods (Welch's t-test = 3.70, $df = 43$, $p = 0.005$, $p_{adjusted} = 0.025$) with a lower average width for the present period (0.92 ± 0.20 mm) than for 1980–1981 (1.09 ± 0.21 mm) (Fig. 6). As *B. chrysoura* are born in the lagoon either in May or in November and the first opaque marks would be laid down either in July or February respectively, individuals were only three to four months old when their first seasonal mark was deposited. The decrease in growth, therefore, happened after the larval stage (i.e. after the settlement mark) and before the fourth month of life. No other temporal change in increment widths was observed in the fish analyzed (range of Mann–Whitney tests = 102–688, range of $p = 0.03$ –0.23, range of $p_{adjusted} = 0.15$ –1).

4. Discussion

The significant decline observed for both the abundance and biomass of *B. chrysoura* between the sampling campaigns of 1980–1981 and 2010–2011 confirmed the recent decline in population reported for the species in the Terminos lagoon (Ramos-Miranda et al., 2005b; Sirot et al., 2015). Surprisingly, however, we showed very little change in the population structure or life history traits of the species in the lagoon, apart from a decrease in the proportion of juveniles under 60 mm SL in the captures, coupled with a reduction in individual growth rate during the few first months of life after settlement. These observations were only possible by a detailed study of the otolith growth patterns.

So far as we are aware, only one study has estimated age by reading the otolith seasonal growth marks for this species (Grammer et al., 2009) and our study provides the first

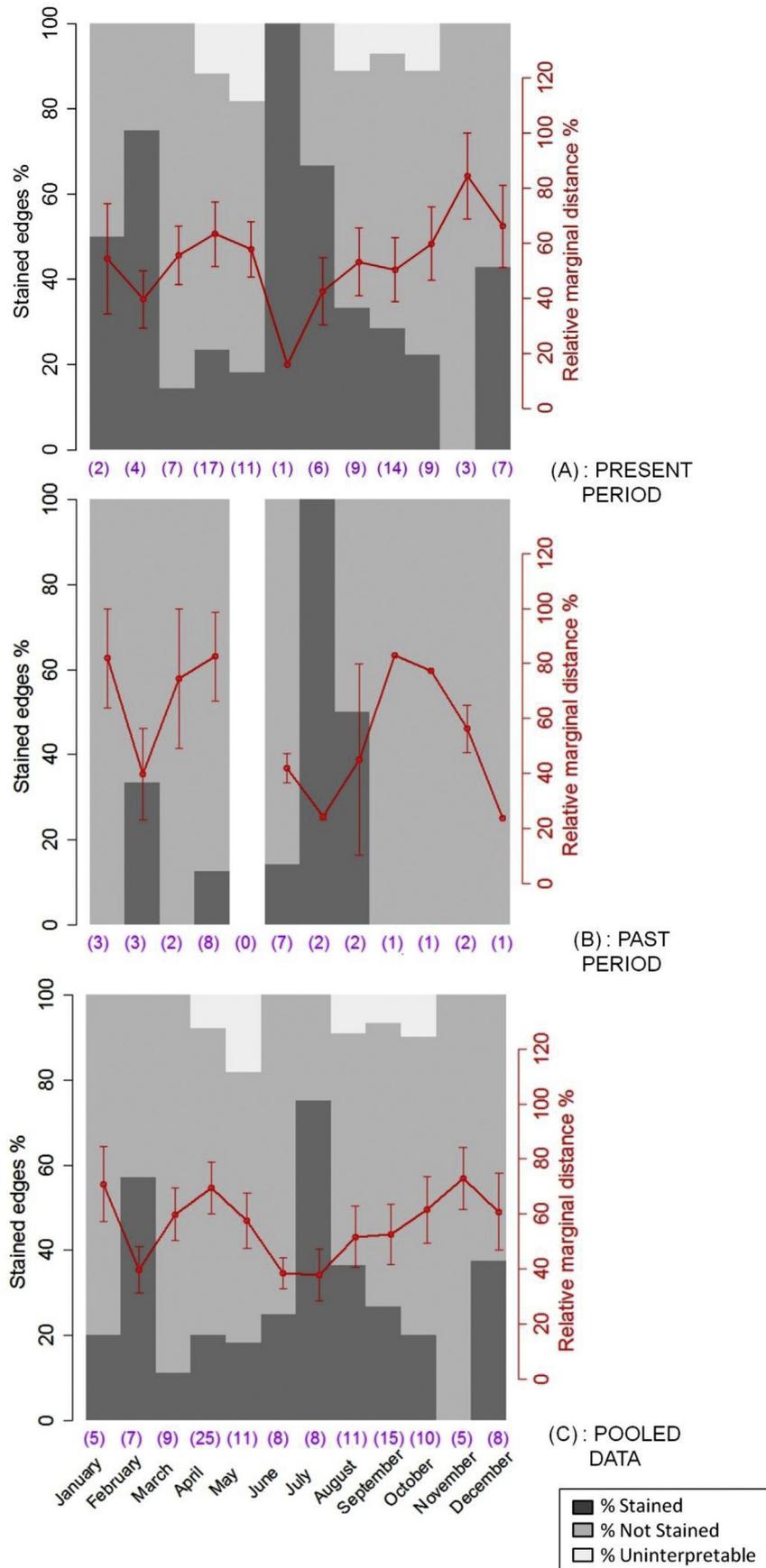


Fig. 4. Monthly variations of the percentage of opaque (stained) edges and the Relative Marginal Distance (RMD, mean \pm standard error) in the otoliths of *B. chrysoura* analyzed for 2006–2011 (A, present), 1980–1981 (B, past), and both periods pooled (C, pooled).

Table 2
Fitting results for growth models and parameter estimates: model parameters (p1, p2, p3), normality and homoscedasticity test (*p*values), coefficient of determination (R²), second order information criterion (AICc) and the delta AICc. Past period (1980–1981) and present period (2006–2011). For each period, the best model (minimizing the AICc) and its parameters are indicated in bold.

Period	Model	p1	p2	p3	Normality test	Homoscedasticity test	R ²	AICc	Delta AICc
Past period	Linear	33.67	3.41	NA	0.06	1.00	0.74	199.23	7.66
Past period	Power	19.85	0.56	NA	0.07	1.00	0.76	195.02	3.45
Past period	Gompertz	131.69	0.12	5.85	0.30	0.90	0.80	192.66	1.09
Past period	Von Bertalanffy	141.72	0.07	0.00	0.33	0.81	0.78	195.16	3.59
Past period	Logistic	125.03	0.19	1.61	0.44	0.94	0.81	191.57	0
Present period	Linear	66.52	1.54	NA	0.02	1.00	0.31	543.33	26.52
Present period	Power	39.20	0.31	NA	0.00	0.73	0.41	529.29	12.48
Present period	Gompertz	113.59	0.16	4.50	0.17	0.75	0.49	518.53	1.72
Present period	Von Bertalanffy	116.03	0.11	0.00	0.28	0.76	0.47	521.11	4.30
Present period	Logistic	112.08	0.22	1.57	0.46	0.80	0.50	516.81	0
Present + past period	Linear	53.74	2.10	NA	0.13	1.00	0.47	747.42	50.12
Present + past period	Power	30.93	0.39	NA	0.15	0.81	0.57	723.56	26.26
Present + past period	Gompertz	115.88	0.16	4.83	0.06	0.65	0.65	700.76	3.46
Present + past period	Von Bertalanffy	120.04	0.10	0.00	0.29	0.73	0.63	706.64	9.34
Present + past period	Logistic	113.91	0.22	1.61	0.14	0.71	0.66	697.30	0

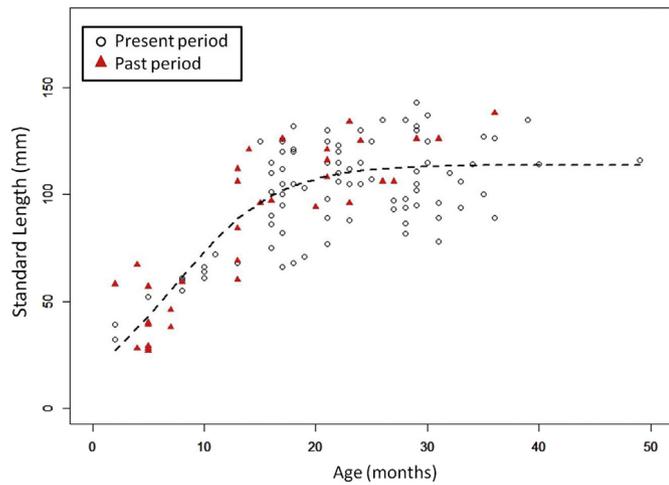


Fig. 5. Size at age recorded for *B. chrysoura* in 1980–1981 (past) and 2006–2011 (present). As the growth curves did not differ significantly between periods, only the curve obtained for the whole dataset (two periods pooled) is represented (logistic function, dotted line) on the graph.

measurements of the seasonal timing of the otolith growth increment deposit in *B. chrysoura* in the tropics. Two periods of seasonal growth mark formation were recorded in Terminos, the first in February and the second in July, corresponding to the beginning of the dry and the wet season respectively (Ramos-Miranda et al., 2005a). Measurements in the Mississippi sound (north of the Gulf of Mexico) for the same species reported only one single growth mark per year, deposited in April, linked by the authors to the spawning season (Grammer et al., 2009). This difference may be attributed to geographical climatic variations as the Terminos lagoon is located in the tropics while the Mississippi sound is in a sub-tropical area. Climatic differences between the two sites could also explain the differences in spawning periods, spawning occurring twice a year in Terminos (between February and July, and in November, Chavance, 1984) against only once a year in the Mississippi sound (mid-March to June, Grammer et al., 2009).

The formation of bi-annual growth marks is rare in calcified structures. However, it has been already reported for some tropical species in several African lakes (Willoughby, 1974; Blake and Blake, 1978; Admassu and Casselman, 2000; Bwanika et al., 2007; Winker et al., 2010) and in South American rivers (Lecomte et al., 1989). Some authors linked this phenomenon to seasonal change (Bwanika et al., 2007) while others suggested that these double marks were due to spawning combined with seasonal changes (Admassu and Casselman, 2000). In Terminos, as the mark was

Table 3
Results of the effect of the date of birth on the increment width in each period: the statistic (Test value), the degree of freedom (df), the *p*-value (*p*) and the adjusted *p*-value (*P*_{adjusted}) with a Bonferroni correction of each test (Welch's *t*-tests or Mann–Whitney tests depending on the data). I1, I2, I3 represent respectively the first, second and third increment observed on otolith section. N Ind. indicates the number of individuals for each group. Past period (1980–1981) and present period (2006–2011).

Present period	I1	I2	I3	I4	I5	I6
N Ind. born in May	39	37	36	35	24	14
N Ind. born in November	51	51	47	44	24	13
Test	Welch's <i>t</i> -test	Welch's <i>t</i> -test	Welch's <i>t</i> -test	Welch's test	Mann–Whitney	Mann–Whitney
Test's value	0.52	0.38	1.28	2.4	256	77.5
df	76.53	85.11	71.81	74.5		
<i>p</i>	0.60	0.70	0.20	0.02	0.52	0.53
<i>P</i> _{adjusted}	1	1	1	0.12	1	1
Past period	I1	I2	I3	I4	I5	I6
N Ind. born in May	13	13	11	6	3	
N Ind. born in November	19	13	9	7	5	
Test	Welch's <i>t</i> -test	Mann–Whitney	Mann–Whitney	Mann–Whitney	Mann–Whitney	Mann–Whitney
Test's value	0.03	55	46	14	11.5	
Df	25.02					
<i>p</i> value	0.97	0.13	0.82	0.36	0.29	
<i>P</i> _{adjusted}	1	0.65	1	1	1	

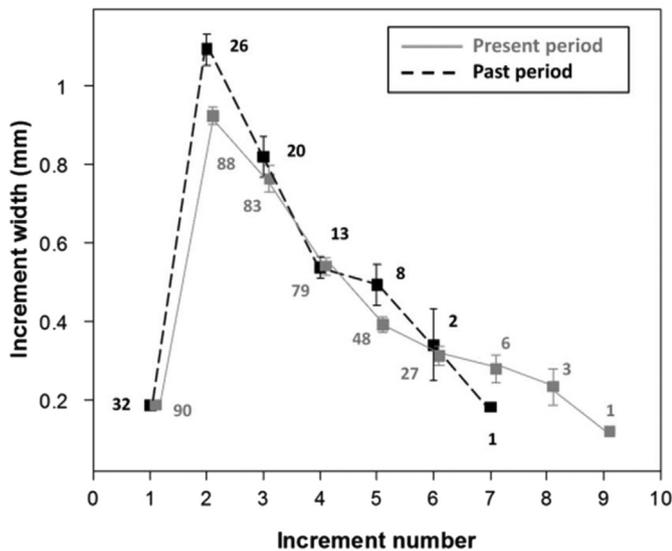


Fig. 6. Widths of the successive growth increments (mean \pm standard error in mm, number of individuals above each mean) identified in the otoliths of *B. chrysoura* analyzed for the two periods. The curve for 2006–2011 (present) has been slightly offset to the right for clearer comparison.

formed at a different time from the spawning period and occurred almost exactly at the beginning of the wet and dry seasons, it would appear that formation of the growth mark was directly controlled by seasonal changes. Fluorescent otolith labeling (e.g. with tetracycline) and/or mesocosm studies could be undertaken to confirm this.

Different values for the growth parameters were recorded in the literature for *B. chrysoura* (Chavance, 1984; Ayala-Pérez et al., 2006; Grammer et al., 2009). Even for the Terminos lagoon, estimated values for the theoretical maximum asymptotic length (L_{∞}) differed between studies: 163 mm SL (Chavance, 1984), 244 mm SL (estimated using equation (3) for the 297 mm total length proposed by Ayala-Pérez et al., 2006), and 113 mm SL in this study. These values should be compared with caution as neither Ayala-Pérez et al. (2006) nor Chavance (1984) gave information on the performances of their respective models (e.g. R^2 , AIC or AICc). The logarithm model used by Grammer et al. (2009) in the Sound of the Mississippi cannot be used to estimate L_{∞} and had a much lower coefficient of determination ($R^2 = 0.39$ – 0.56) than the logistic model used for Terminos ($R^2 = 0.66$), which seemed to be more suitable for describing growth in *B. chrysoura*. The differences in the theoretical asymptotic length could also be explained by geographic differences between populations: North (Grammer et al., 2009) versus South (present study).

Although the same logistic equation gave an accurate description of individual growth (for individuals between 27 and 143 mm SL) in the *B. chrysoura* population of the Terminos lagoon in both periods, analysis of the otolith increment width revealed that early juvenile growth, from settlement to the fourth month of life (i.e. before reaching 42 mm SL), has decreased by 15% since 1980–1981. Furthermore, there has been a significant reduction in the proportion of these smallest juveniles in the lagoon population since 1980–1981. As seagrass beds are considered as the main nursery grounds for *B. chrysoura* juveniles (Rooper et al., 1998) and as all these areas have been comprehensively sampled during past and present periods with the same standardized protocol, the most probable hypothesis is that young juveniles vanished from the lagoon. This decrease in juvenile proportion seems quite recent as this phenomenon was not observed in sampling campaigns

conducted in the area in 1997 (Ayala-Pérez et al., 2006). This is surprising because fishing has been strongly restricted in the lagoon since 1994 (Bach et al., 2005) and it follows that the fishery pressure is not the cause of the demographic changes observed in this study. There are different possible mechanisms explaining the disappearance of juveniles smaller than 60 mm, associated with a decrease of early growth, but only two hypotheses seemed consistent with our results: a selective mortality of juvenile within the lagoon since the 1980s, or a change in habitat for juveniles, outside of the lagoon itself in 2010–2011. These two mechanisms may not be mutually exclusive in explaining the species decline, and could have a common explanation: a destruction of nursery grounds coupled with changes in abiotic conditions within the lagoon since the 1980s. First, seagrass beds experienced a drastic decrease of their area since the 1980s (Ramos-Miranda et al., 2005b). Second, strong abiotic shifts (e.g. pollution by pesticides, increase in salinity) have occurred in the lagoon since the 1980s (Botello and Mendelwewicz, 1988; Carvalho et al., 2009; Villéger et al., 2010; Sirot et al., 2015). These main environmental perturbations are known to affect juvenile growth rate and habitat settlement. Abiotic factors, in particular salinity, have already been shown to have a major effect on growth during the early life stage of *B. chrysoura* (Hales and Hurley, 1991). Moreover, the degradation or loss of nursery habitats might also explain the decrease in early life growth as they provide food for early life stages and allow higher growth rates during this stage (Gibson, 1994). This decrease in early growth may lead to an increase in early life mortality, linked to 'bigger is better' (Shepherd and Cushing, 1980; Houde, 1987; Miller et al., 1988), aggravated by the destruction of the protection provided by the natural habitat against predators (Gibson, 1994; Joyeux and Ward, 1998). In addition to lead to juvenile mortality, the abiotic perturbations and the seagrass beds destruction could also constrain juveniles to change the location of their nursery outside the lagoon itself. This change in behavior could explain the disappearance of juveniles in some areas, and lead also to a growth reduction linked with reduced adaptive capacities in different conditions. This hypothesis highlights the importance to locate geographically and to assess the quality of the new nursery areas. To this end, an analysis of the otolith elemental composition might provide essential information about the location of the former and the new nurseries, but also assess their contribution to the adult stock (Vasconcelos et al., 2011). However, both hypotheses, i.e. juvenile mortality or modification of the nursery location, could lead to a low recruitment rate which may in turn explain the decline of the *B. chrysoura* population in this region since the 1980s.

Finally, the study of connectivity between populations within the Gulf of Mexico, and in particular around the Terminos lagoon, is especially important for understanding the long term effects of nursery degradation and abiotic perturbations on *B. chrysoura*'s population. Information on *B. chrysoura* ecology and especially on its movements between habitats within its geographic range is very scarce. The natural distribution of this species was reported to span the Gulf of Mexico and some studies reported that *B. chrysoura* was exclusively an estuarine species (Grammer et al., 2009). However, during our sampling campaigns, adults were caught off the Carmen Island, demonstrating that the species can live at sea and that adult population in the lagoon could be mixed with other. Moreover, Waggy et al. (2007) reported larvae from this species in the marine plankton in the north-central Gulf of Mexico, suggesting a possible marine larval stage thus reinforcing the hypothesis of a possible connectivity with other populations in the region. More comparisons of migration patterns using otolith microchemistry are required to validate the possible connectivity for the species at the Gulf of Mexico scale or between different periods.

5. Conclusion

Environmental perturbations with the resulting degradation of nursery habitats appear to be the major causes for the decline of *B. chrysoura* in the Terminos lagoon since the 1980s. Young juveniles which were very abundant in captures in the 1980–1981 campaign have now vanished from the lagoon. This probably occurred after the turn of the century and calls for urgent identification of the nursery habitats for the species in the region and their restoration to encourage the growth of juveniles. In-depth studies of the connectivity between the populations of *B. chrysoura* in the Gulf of Mexico are therefore needed in order to understand the exact mechanisms for the decline of *B. chrysoura* in Terminos. Poor connectivity between habitats could have serious consequences for the present-day population unless appropriate measures are taken by authorities to restore the nursery areas in Terminos.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2015.05.012>.

References

- Admassu, D., Casselman, J.M., 2000. Otolith age determination for adult tilapia, *Oreochromis niloticus* L. from Lake Awassa (Ethiopian Rift Valley) by interpreting biannuli and differentiating biannual recruitment. *Hydrobiologia* 418, 15–24. <http://dx.doi.org/10.1023/A:1003883419105>.
- Amara, R., Meziane, T., Gilliers, C., Hermel, G., Laffargue, P., 2007. Growth and condition indices in juvenile sole, *Hemle solea* measured to assess the quality of essential fish habitat. *Mar. Ecol. Prog. Ser.* 351, 201–208. <http://dx.doi.org/10.3354/meps07154>.
- Ashfield, L.A., Pottinger, T.G., Sumpter, J.P., 1998. Exposure of female juvenile rainbow trout to alkylphenolic compounds results in modifications to growth and ovosomatic index. *Environ. Toxicol. Chem.* 17, 679–686. <http://dx.doi.org/10.1002/etc.5620170423>.
- Ayala-Pérez, L.A., Campos, J., Tapia-García, M., 2006. Distribution, abundance and population parameters of silver perch “*Bairdiella chrysoura*” (Lacepede, 1802) (Pisces: Sciaenidae) in Terminos lagoon, Campeche, Mexico. *Thalass. Int. J. Mar. Sci.* 22, 9–18.
- Bach, L., Calderon, R., Cepeda, M.F., Oczkowski, A., Olsen, S., Robadue, D., 2005. Managing Freshwater Inflows to Estuaries, Level One Site Profile: Laguna de Terminos and its Watershed. Coastal Resources Center, University of Rhode Island, Mexico, RI.
- Blake, C., Blake, B.F., 1978. The use of opercular bones in the study of age and growth in *Labeo senegalensis* from Lake Kainji, Nigeria. *J. Fish. Biol.* 13, 287–295. <http://dx.doi.org/10.1111/j.1095-8649.1978.tb03436.x>.
- Blewett, D.A., Hensley, R.A., Stevens, P.W., 2006. Feeding habits of common snook, *Centropomus undecimalis*, in Charlotte Harbor, Florida. *Gulf Caribb. Res.* 18, 1–13.
- Botello, A.V., Mendelwewicz, M., 1988. La contaminación y los contaminantes en la región de la laguna de Término. In: Yanez-Arancibia, A., Day Jr., J.W. (Eds.), *Ecología de Los Ecosistemas Costeros En El Sur Del Golfo de México: La Región de La Laguna de Términos*, pp. 415–430.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*. Springer-Verlag, New-York.
- Bwanika, G.N., Murie, D.J., Chapman, L.J., 2007. Comparative age and growth of Nile tilapia (*Oreochromis niloticus* L.) in lakes Nabugabo and Wamala, Uganda. *Hydrobiologia* 589, 287–301. <http://dx.doi.org/10.1007/s10750-007-0746-y>.
- Campana, S.E., 1990. How reliable are growth back-calculations based on otoliths? *Can. J. Fish. Aquat. Sci.* 47, 2219–2227. <http://dx.doi.org/10.1139/f90-246>.
- Campana, S.E., Neilson, J.D., 1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* 42, 1014–1032. <http://dx.doi.org/10.1139/f85-127>.
- Carvalho, F.P., Villeneuve, J.-P., Cattini, C., Rondón, J., Mota de Oliveira, J., 2009. Pesticide and PCB residues in the aquatic ecosystems of Laguna de Terminos, a protected area of the coast of Campeche, Mexico. *Chemosphere* 74, 988–995. <http://dx.doi.org/10.1016/j.chemosphere.2008.09.092>.
- Chao, L., Musick, J., 1977. Life-history, feeding-habits, and functional-morphology of juvenile sciaenid fishes in York River estuary, Virginia. *Fish. Bull.* 75, 657–702.
- Chavance, P., 1984. *Ecología, biológica y dinámica de las poblaciones de Bairdiella chrysoura en la laguna de Terminos sur del Golfo de México (Pisces: Sciaenidae)*. Anales del Instituto de ciencias del mar y limnología.
- Chen, Y., Jackson, D.A., Harvey, H.H., 1992. A comparison of von bertalanffy and polynomial functions in modelling fish growth data. *Can. J. Fish. Aquat. Sci.* 49, 1228–1235. <http://dx.doi.org/10.1139/f92-138>.
- Chessman, B.C., 2013. Identifying species at risk from climate change: traits predict the drought vulnerability of freshwater fishes. *Biol. Conserv.* 160, 40–49. <http://dx.doi.org/10.1016/j.biocon.2012.12.032>.
- Costanza, R., D’Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O’Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world’s ecosystem services and natural capital. *Nature* 387, 253–260. <http://dx.doi.org/10.1038/387253a0>.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the Match/Mismatch hypothesis. *Adv. Mar. Biol.* 26, 249–293.
- Diouf, K., Guilhaumon, F., Aliaume, C., Ndiaye, P., Chi, T.D., Panfili, J., 2009. Effects of the environment on fish juvenile growth in West African stressful estuaries. *Estuar. Coast. Shelf Sci.* 83, 115–125. <http://dx.doi.org/10.1016/j.ecss.2009.02.031>.
- Fonseca, V.F., Cabral, H.N., 2007. Are fish early growth and condition patterns related to life-history strategies? *Rev. Fish. Biol. Fish.* 17, 545–564. <http://dx.doi.org/10.1007/s11160-007-9054-x>.
- Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Neth. J. Sea Res.* 32, 191–206. [http://dx.doi.org/10.1016/0077-7579\(94\)90040-X](http://dx.doi.org/10.1016/0077-7579(94)90040-X).
- Grammer, G.L., Brown-Peterson, N., Peterson, M.S., Comyns, B.H., 2009. Life history of Silver Perch *Bairdiella chrysoura* (Lacepede, 1803) in north-central Gulf of Mexico estuaries. *Gulf Mex. Sci.* 1, 62–73.
- Hales, L.S., Hurley, D.H., 1991. Validation of daily increment formation in the otoliths of juvenile silver perch, *Bairdiella chrysoura*. *Estuaries* 14, 199–206. <http://dx.doi.org/10.2307/1351694>.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D’Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. *Science* 319, 948–952. <http://dx.doi.org/10.1126/science.1149345>.
- Heupel, M.R., Hueter, R.E., 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. *Mar. Freshw. Res.* 53, 543–550.
- Houde, E.D., 1987. Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* 2, 17–29.
- Hutchings, J.A., 1993. Adaptive life histories effected by age-specific survival and growth rate. *Ecology* 74, 673–684. <http://dx.doi.org/10.2307/1940795>.
- Hutchings, J.A., Baum, J.K., 2005. Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 315–338. <http://dx.doi.org/10.1098/rstb.2004.1586>.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637. <http://dx.doi.org/10.1126/science.1059199>.
- Joyeux, J.-C., Ward, A.B., 1998. Constraints on coastal lagoon fisheries. In: Blaxter, J.H.S., S., A.J., T., P.A. (Eds.), *Advances in Marine Biology*. Academic Press, pp. 73–199.
- Kvålseth, T.O., 1985. Cautionary note about R^2 . *Am. Stat.* 39, 279–285.
- Layman, C.A., Allgeier, J.E., Rosemond, A.D., Dahlgren, C.P., Yeager, L.A., 2011. Marine fisheries declines viewed upside down: human impacts on consumer-driven nutrient recycling. *Ecol. Appl.* 21, 343–349. <http://dx.doi.org/10.1890/10-1339.1>.
- Lecomte, F., Meunier, F.J., Rojas-Beltran, R., 1989. Some data on the growth of Arius proops (Ariidae, Siluriforme) in the estuaries of French Guyana. *Aquat. Living Resour.* 2, 63–68. <http://dx.doi.org/10.1051/alr:1989007>.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312, 1806–1809. <http://dx.doi.org/10.1126/science.1128035>.
- Lotze, H.K., Worm, B., 2009. Historical baselines for large marine animals. *Trends Ecol. Evol.* 24, 254–262. <http://dx.doi.org/10.1016/j.tree.2008.12.004>.
- Luczkovich, J.J., Daniel, H.J., Hutchinson, M., Jenkins, T., Johnson, S.E., Pullinger, C.R., Sprague, M.W., 2000. Sounds of sex and death in the sea: bottlenose dolphin whistles suppress mating choruses of silver perch. *Bioacoustics* 10, 323–334. <http://dx.doi.org/10.1080/09524622.2000.9753441>.
- Mercier, L., Panfili, J., Paillon, C., N’diaye, A., Mouillot, D., Darnaude, A.M., 2011. Otolith reading and multi-model inference for improved estimation of age and growth in the gilthead seabream *Sparus aurata* (L.). *Estuar. Coast. Shelf Sci.* 92, 534–545. <http://dx.doi.org/10.1016/j.ecss.2011.02.001>.
- Miller, T.J., Crowder, L.B., Rice, J.A., Marschall, E.A., 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45, 1657–1670. <http://dx.doi.org/10.1139/f88-197>.

- Ramos-Miranda, J., Quiniou, L., Flores-Hernandez, D., Do-Chi, T., Ayala-Perez, L., Sosa-Lopez, A., 2005a. Spatial and temporal changes in the nekton of the Terminos Lagoon, Campeche, Mexico. *J. Fish. Biol.* 66, 513–530. <http://dx.doi.org/10.1111/j.0022-1112.2005.00619.x>.
- Ramos-Miranda, J.R., Mouillot, D., Hernandez, D.F., Lopez, A.S., Chi, T.D., Perez, L.A., 2005b. Changes in four complementary facets of fish diversity in a tropical coastal lagoon after 18 years: a functional interpretation. *Mar. Ecol. Prog. Ser.* 304, 1–13. <http://dx.doi.org/10.3354/meps304001>.
- R Development Core Team, 2014. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ricker, W.E., 1975. *Computation and Interpretation of Biological Statistics of Fish Populations*. Bulletin of the Fisheries Research Board of Canada.
- Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., Le Pape, O., 2010. Effect of nursery habitat degradation on flatfish population: application to *Solea solea* in the Eastern Channel (Western Europe). *J. Sea Res.* 64, 34–44. <http://dx.doi.org/10.1016/j.seares.2009.08.003>.
- Rooker, J.R., Holt, S.A., Soto, M.A., Holt, G.J., 1998. Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries* 21, 318–327. <http://dx.doi.org/10.2307/1352478>.
- Shepherd, J.G., Cushing, D.H., 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *J. Cons.* 39, 160–167. <http://dx.doi.org/10.1093/icesjms/39.2.160>.
- Sirot, C., Villéger, S., Mouillot, D., Darnaude, A.M., Ramos-Miranda, J., Flores-Hernandez, D., Panfili, J., 2015. Biological traits for understanding the demographic responses of lagoon fishes to environmental pressures. *Ecol. Indicator* 48, 147–156.
- Smith, A.C., Shima, J.S., 2011. Variation in the effects of larval history on juvenile performance of a temperate reef fish. *Austral Ecol.* 36, 830–838. <http://dx.doi.org/10.1111/j.1442-9993.2010.02223.x>.
- Vasconcelos, R.P., Reis-Santos, P., Costa, M.J., Cabral, H.N., 2011. Connectivity between estuaries and marine environment: integrating metrics to assess estuarine nursery function. *Ecol. Indic.* 11, 1123–1133. <http://dx.doi.org/10.1016/j.ecolind.2010.12.012>.
- Villéger, S., 2008. *Dynamique de la diversité fonctionnelle des communautés de poissons (Lagune de Terminos, Mexique)*. Montpellier SupAgro.
- Villéger, S., Ramos-Miranda, J., Hernández, D.F., Mouillot, D., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.* 20, 1512–1522. <http://dx.doi.org/10.1890/09-1310.1>.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892. <http://dx.doi.org/10.1111/j.0030-1299.2007.15559.x>.
- Waggy, G.L., Brown-Peterson, N., Petersen, M.S., 2006. Evaluation of the reproductive life history of the sciaenidae in the Gulf of Mexico and Caribbean sea: “greater” versus “lesser” strategies?. In: *57th Gulf Caribb. Fish Inst.*
- Waggy, G.L., Peterson, M., Comyns, B.H., 2007. Feeding habits and mouth morphology of young silver perch (*Bairdiella chrysoura*) from the north-central Gulf of Mexico. *Southeast. Nat.* 743–751.
- Willoughby, N.G., 1974. *The Ecology of the Genus Synodontis (Pisces: Silluroidei) in Lake Kainji, Nigeria*. University of Southampton, U.K.
- Winemiller, K.O., 2005. Life history strategies, population regulation, and implications for fisheries management. *Can. J. Fish. Aquat. Sci.* 62, 872–885. <http://dx.doi.org/10.1139/f05-040>.
- Winker, H., Weyl, O.L.F., Booth, A.J., Ellender, B.R., 2010. Validating and corroborating the deposition of two annual growth zones in asteriscus otoliths of common carp *Cyprinus carpio* from South Africa's largest impoundment. *J. Fish. Biol.* 77, 2210–2228. <http://dx.doi.org/10.1111/j.1095-8649.2010.02797.x>.
- Yañez-Arancibia, A., Day, J.W.J., 1982. *Ecological characterization of Términos Lagoon, a tropical lagoon-estuarine system in the Southern Gulf of Mexico*. *Oceanol. Acta V*.
- Zar, J.H., 1999. *Biostatistical Analysis*, fourth ed. TBS.