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Life-history traits of the common snook *Centropomus undecimalis* in a Caribbean estuary and large-scale biogeographic patterns relevant to management

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The ecology of common snook *Centropomus undecimalis* in Amatique Bay, a tropical estuary in eastern Guatemala, was investigated and life-history traits were used to conduct a meta-analysis of the species from Florida to Brazil. The reproduction cycle of *C. undecimalis* in Amatique was strongly related to the precipitation cycle, with a lag of 2 months. Spawning occurred from April to November with a peak spawning after the onset of the summer rains. Protandric sex reversal occurred early in the dry season (December) before somatic recovery from spawning. The growth cycle preceded that of body condition by *c.* 1 month, and was out of phase with the reproductive cycle. Growth was fast, as many individuals reached >70% of the maximum observed total length (L_T , 102 cm) after 3 years. Sex transition occurred within a relatively narrow L_T range (70–79 cm), but over a wide range of ages, indicating plasticity in this respect. The meta-analysis indicated a latitudinal-temperature gradient in life-history traits, as well as different seasonal patterns relative to temperature and hydrographical cycles. *Centropomus undecimalis* from cooler winter waters (*e.g.* Florida) reach larger maximum L_T and L_T at sex change, as well as greater gonado-somatic indices and longer life spans. Further, increased fishing mortality results in younger age at sex reversal and male predominance in the populations compared. Recognition of large-scale biogeographic patterns in this important, but little studied, fish species helps in the formulation of management advice in other areas of its occurrence.

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INTRODUCTION

The common snook, or robalo *Centropomus undecimalis* (Bloch 1792) is a large euryhaline protandrous fish widely distributed in estuaries of the western-central Atlantic Ocean, from Florida, U.S.A., to Brazil, and supports extensive sport and commercial fisheries (Taylor *et al.*, 2000; FAO, 2011). This widespread distribution makes it a relevant candidate for the analysis of life-history variation in tropical estuaries, a topic that is not well understood (Blaber, 2002). Traits related to growth and sex reversal of *C. undecimalis* are still poorly known in locales outside its northern

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distribution and are not considered in population management (Taylor *et al.*, 2000; Muller & Taylor, 2006). Considerable differences in these variables have, however, been observed between the two close stocks on the east and west coasts of Florida (Taylor *et al.*, 2000). These variations have been partially attributed to genetic differences resulting from strong site fidelity to their natal estuaries and spawning grounds. This segregation of spawning groups ultimately results in biologically separable stocks (Tringali & Bert, 1996; Tringali *et al.*, 2008; Adams *et al.*, 2009, 2011; Barbour & Adams, 2012). Similar local segregation has also been shown for another estuarine centropomid, the barramundi *Lates calcarifer* (Bloch 1790) in northern Australia (Salini & Shaklee, 1988). Thus, inter-estuary differences in key life-history variables, even at small geographic scales, may have implications for the population and for the dynamics of local fisheries. The magnitude of variation in vital variables of *C. undecimalis* at larger scales has not been elucidated so far.

Amatique Bay, located on the Caribbean coast of Guatemala (Fig. 1), lies in the middle of the range of *C. undecimalis* distribution. *Centropomus undecimalis* has been a traditional target of specialized groups of small-scale fishers who pursue the fishery from the bay into Lake Izabal and Punta de Manabique (Brinson *et al.*, 1974; Andrade & Midré, 2011; B. R. García-Hernández, unpubl. data; J. E. Martínez, unpubl. data). Recent studies have described the semi-open access management regime and the rotational spatial system enforced by the communities in Amatique to minimize gear interference between fisher groups (Andrade & Midré, 2011; Heyman & Granados-Dieseldorff, 2012). There are no historical records of occurrence or catch statistics for most aquatic resources in the area. Locals, however, describe the gillnet fishery as increasingly unprofitable, except during seasons of increased *C. undecimalis* abundance (Andrade & Midré, 2011). The complex life history of *C. undecimalis* presents a challenge to develop efficient and sustainable exploitation strategies. A better understanding of local life-history traits is necessary for successful management practices (King & McFarlane, 2003; Caselle *et al.*, 2011).

Sequential hermaphroditism provides additional challenges to population management. Previous attempts to account for sex change in the development of exploitation strategies have often been restricted to specific protogynous species, which are more common (Sadovy & Shapiro, 1987; Molloy *et al.*, 2007; Alonzo *et al.*, 2008). For *L. calcarifer*, simulations have shown that reducing mesh size results in increased female survival to maximum age and total egg production (Milton *et al.*, 1998). Thus, management measures should focus on the protection of both smaller male *L. calcarifer* at sizes just prior to sex reversal and on large spawning females (Blaber *et al.*, 2009). The implementation of these selection slots, an unconventional input control, requires some knowledge of the extent of plasticity in life-history traits. One way such information can be obtained is from large-scale geographic analyses.

A realistic population model reflects the trade-offs in the allocation of resources channelled into growth and reproduction (Roff, 1983; Charnov, 2008). In this paper, a coupled growth-sex change function that can be easily understood and applied in fishery models was developed for *C. undecimalis*. Given the uneven growth patterns and other features observed in sequential hermaphrodites, the introduction of sex change into growth models may markedly improve the estimates of fish production and parental biomass in dynamic-pool fishery models (Buxton, 1992, 1993; Garratt *et al.*, 1993; Punt *et al.*, 1993; Coulson *et al.*, 2009). Further, general aspects of



FIG. 1. Location of study area, Amatique Bay, Guatemala.

the physiology of *C. undecimalis* were studied in Amatique Bay. This included analyses of the seasonal patterns of growth and reproduction, and their relation to local meteorological and hydrographic variables over a 14 month sampling period. An attempt to put these findings into a broader geographic perspective and make a latitudinal comparison of published life-history traits was also performed. The goal was to elucidate the processes influencing the ecology of *C. undecimalis* and other tropical estuarine species and provide advice to stakeholder and fishery managers, particularly in less-studied areas.

MATERIALS AND METHODS

STUDY SITE

Amatique Bay (Fig. 1) is a semi-enclosed estuarine ecosystem of 542 km² with an average depth of <10 m (Yañez-Arancibia *et al.*, 1999). Its physico-chemical variables are strongly influenced by the precipitation regime and river runoff. The warmer rainy season extends from June to September while the cooler dry season lasts from October to May. Water temperature and salinity vary seasonally between 20 and 33° C and from 10 to 30, respectively (Yañez-Arancibia *et al.*, 1999; Fig. 2). The bay receives large amounts of sediment and nutrients transported by a number of rivers (Thattai *et al.*, 2003; Burke & Sugg, 2006). One of the most important rivers is the Río Dulce that flows from Lake Izabal, the largest freshwater lake in Guatemala, c. 42 km upstream (Brinson *et al.*, 1974; Pérez *et al.*, 2011).

Livingston, home to more than 600 fishers and the largest fishing settlement of the Guatemalan Caribbean (Heyman & Graham, 2000), is located at the mouth of the Dulce. It is unknown how many local fishers target *C. undecimalis*, but > 24 fibre-glass and wooden

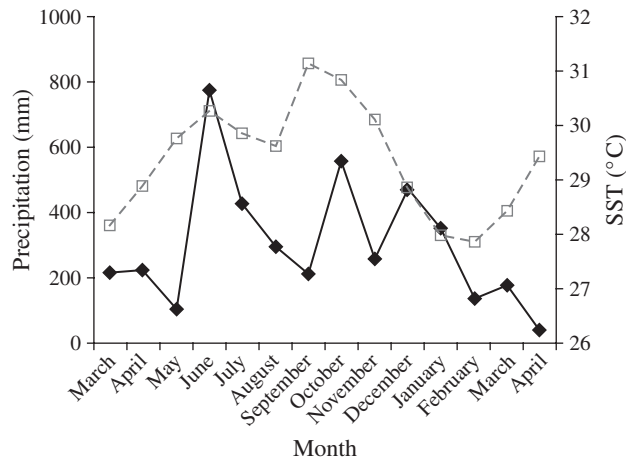


FIG. 2. Precipitation (—◆—; www.insivumeh.gob.gt) and sea-surface temperature (SST; -□-; <http://poet.jpl.nasa.gov/>) cycles from March 2006 to April 2007 in Amatique Bay.

boats have been registered (Jolon-Morales *et al.*, 2005). These boats are small outboard powered skiffs that deploy gillnets from noon until sunrise the following day. A typical gillnet section is 100 m long, 7.5 m deep, with stretched mesh sizes varying from 127 to 152 mm, and twine thickness of 0.95 mm. There are, however, no size restrictions or mesh size regulations for *C. undecimalis*, and there is no evidence that the fishery is size-selective. The fish are landed whole and ungutted, but the quantities delivered for processing are not routinely recorded. Fishers state that the *C. undecimalis* fishery has a strong seasonal component, with a peak in October. The total annual landings of *C. undecimalis* in the area have recently been estimated at 133 t (Heyman & Granados-Dieseldorff, 2012). In the Western Central Atlantic landings accounted for 1500 t in 2009 (FAO 2011).

FIELD SAMPLING AND LABORATORY ANALYSES

Biological sampling of *C. undecimalis* was undertaken from March 2006 to April 2007 at one of the largest landing compounds in Livingston. Because *C. undecimalis* were destined for processing and consumption, there were limitations to sample manipulation. Total lengths (L_T , cm) of 598 *C. undecimalis* were recorded along with their total (W_T) and gonadal (W_G) masses (± 0.1 g). Fresh gonads were inspected macroscopically and scored for sex and maturity determination. The allocation of sex in *C. undecimalis* is straightforward when the sex is obviously male or female; transitional fish can only be diagnosed by histological observation, in part, because of the brevity of sex reversal (Taylor *et al.*, 2000). Maturity classes were defined according to the criteria of gonadal appearance and size described by Perera-García *et al.* (2011) but using a simplified key of four classes: class: I immature, II developing, III mature and IV resting. To obtain an approximate estimate of the fecundity of *C. undecimalis*, egg counts from mature females in the L_T range 67–115 cm were available from Florida (R. Taylor, unpubl. data).

The left otolith was collected for age determination and processed as described by Taylor *et al.* (2000). A single reader aged the otoliths four times. When discrepancies occurred, annuli determinations were validated by experienced members of the technical staff of the Florida Wildlife Research Institute otolith processing centre. A subset of 64 otoliths were read by two of the authors to assess ageing consistency between readers. The percentage of agreement was 40% and the mean \pm s.d. disagreement between readings was low (1.42 ± 0.79 years). An annulus was comprised of one translucent band plus an adjacent opaque band

(Taylor *et al.*, 2000). To confirm annual deposition of increments and assess their seasonal formation, an edge-type analysis was conducted, following Rhodes *et al.* (2011).

DATA ANALYSIS

The relationships between W_T (g) or W_G (g) and L_T of individual fish were described and tested for homogeneity across sexes (f=female, m=male) and maturity stages by means of analysis of covariance (Zar, 1999). The linearized model assumed normal additive error and had the following general structure:

$$\ln W_T = b_0 + b_1 \ln L_T + X_{(2)} + Q_{(4)} \quad (1)$$

where b_0 is a constant, b_1 a regression coefficient, X is sex and Q is maturity stage, and the numbers in parentheses indicate the levels of the factors. For the analysis of egg count, only female L_T was taken into account as a predictive variable as the observations were made in fish predominantly at stage III. For the analysis of the seasonal variation in body condition, the condition factor (C_F) of the individual fish was calculated as $C_F = 100W_T L_T^{-b}$, where the power b corresponds to the coefficient of the L_T and W_T relationship. Similarly, the gonado-somatic index (I_G) was calculated as the individual $W_G:W_T$ ratio, expressed as a percentage. These indices were averaged across individuals, and the spawning months were defined as those with a clear mode of mean I_G if these were in agreement with the macroscopic gonadal classification. The sex change was modelled as the probability of a fish i (F_i) at a given age (A) or at L_T becoming female. The sex reversal can be described by a generalized cumulative function like a Richards curve (Wileman *et al.*, 1996), which in the age-dependent form would be represented as: $F_i(A) = (1 + e^{-b_2 - b_3 A})^{b_4^{-1}}$. When the sex change curve is symmetric, the shape parameter equals unity ($b_4 = 1$) and the function reduces to the logistic, which is described by the two usual parameters (b_2 and b_3). These parameters allow the estimation of the age (or length) of sex change, A_{50} , as well as the ages comprising the range A_{25} – A_{75} for sex reversal using the inverse logit transform. A general function for fish of either sex combining aspects of the von Bertalanffy growth function (VBGF) (Beverton, 1954) and sex change in the sampled population was utilized. Previous growth models for sequential hermaphrodites have differed on the utilization of terminal ages of cohorts of fishes or individual growth profiles, on whether or not a sex change sub-model is explicit in the growth model and on the simplicity of approach (Garratt *et al.*, 1993; Coulson *et al.*, 2009; Linde *et al.*, 2011). The model employed here relies on the terminal ages and on the main assumptions that both males and females grow according to the VBGF and share the growth patterns in early ages. Further, sex change is assumed permanent, that change in growth pattern is most noticeable during sex transition (Walker *et al.*, 2007), and that the probability of change from one sex to another in the population, or from a growth pattern to the next, is ruled by the logistic. In the full model, females and males have independent growth coefficients (K) and asymptotic lengths (L_∞), but share the t_0 , the theoretical time (years) at zero length (cm) of males: $L_i(A) = L_\infty(X)[1 - e^{-K(X)(A-t_0)}]$, where sex (X) is male if $F(A) < 0.5$ and female otherwise. Thus, in the general statistical model, the change from one growth stanza to the next, or from male to female, is ruled by the expected sex category, given by $F(A)$, rather than the observed sex of individual fish. The loss function maximized in the fit was the sum of the binomial log-likelihood (Y), for the sex change process (summation term on the left), and the normal log-likelihood, for the growth process (term on the right side): $Y = \sum_i \{m_i \ln F_i(A) + f_i \ln [1 - F_i(A)]\} + \ln z[L_i(A), \sigma]$, where m and f are binary (0, 1) dummy variables to code for the observed sex of each fish i , L the respective L_T , σ the s.d. and z the Gaussian probability density function (Haddon, 2011). In a reduced model, the assumption of different growth coefficients was relaxed ($K_{\text{male}} = K_{\text{female}}$). Additional simplification (L_∞ is same for both sexes) resulted in a pooled growth model for both sexes decoupled from sex change. To ensure a biologically meaningful magnitude for t_0 , this parameter was set to zero in the fit. The fits were performed to individual observations using a

non-linear search algorithm. The models were nested and comparison of fits took into consideration the Akaike information criterion (AIC) and the Bayesian information criterion (BIC). The S.E. of the parameters and functions of parameters were obtained after bootstrapping with replacement of the original observations and repeating the fit 1000 times (Haddon, 2011).

The instantaneous rate of total mortality (Z) was estimated by the catch-curve method (Ricker, 1975). Several independent methods provided coarse estimates of the instantaneous rate of natural mortality (M) consistent with the magnitude of Z . The observed maximum age (A_{\max}) was used as an approximation to longevity, following Hewitt & Hoening (2005), and this provided an upper estimate to M . Alternative estimates were derived from the spawning age, following Rikhter & Evanov (1976) and Charnov (1993), or physical reproductive investment (I_G) (Lester *et al.*, 2004). The A_{50} and $I_{G\text{female}}$ were considered to be the most meaningful surrogates of spawning age and physical reproductive investment, respectively. The instantaneous rate of fishing mortality (F) was computed as $F = Z - M$, and the exploitation rate (E) as $E = FZ^{-1}$, using mean values.

To identify associations in the seasonal cycles of environmental and physiological variables of *C. undecimalis* within Amatique Bay, principal component analysis (PCA) was utilized. The data consisted of biological time series of monthly averages of I_G , C_F and the frequency of occurrence of opaque bands in otoliths, which denote slow growth (Taylor *et al.*, 2000; Fowler, 2009). Environmental variables included a time series of precipitation, river runoff, sea-surface temperature (SST), air temperature and chlorophyll *a*. Precipitation and air temperature data for 2006–2007 were obtained from the nearest meteorological station located in Puerto Barrios, Department of Izabal (Fig. 1) (available at www.insivumeh.gob.gt). Estimates of monthly runoff ($\text{m}^3 \times 10^9$) were derived by Burke & Sugg (2006) using modelled results for 2003–2004. Average monthly SST ($^{\circ}\text{C}$) from March 2006 to April 2007 was derived from satellite imagery and processed by NOAA–NASA's AVHRR Oceans Pathfinder global (available at <http://poet.jpl.nasa.gov/>) for the Amatique Bay area. Chlorophyll *a* concentrations (mg m^{-3}) were obtained through NASA's Giovanni Ocean Color Radiometry data product visualization using SeaWiFS and MODIS databases (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_8day/). The temporal and spatial resolutions were 8 days and 4 km, respectively, from March 2006 to April 2007. The satellite data were not ground-truthed and are therefore more suitable for describing the relative concentration of chlorophyll *a* and the timing of the production cycle (Dierssen, 2010).

The biological and environmental time series were explored in the same reduced space of PCA (van den Brink *et al.*, 2009). PCA was conducted on ln or arc-sine-transformed observations with pair-wise deletion of samples when necessary. Good distribution of factor loadings was obtained after oblique (oblimin) or varimax rotation. To account for autocorrelation and to identify dynamic linkages between variables in the time series, cross-correlation analyses (CCAs) and plots were used. This technique allows the identification of time delays between pairs of environmental and biological variables (El-Gohary & McNames, 2007; Wilkinson *et al.*, 2009). Whenever necessary, the monthly series were ln or arc-sine-transformed and (first order or monthly) differenced prior to analysis to ensure stability of variance and stationarity in the CCAs (*i.e.* to remove temporal dependencies that affect the assumptions of statistical inference in correlation). The number of time lags (months) analysed in any instance was limited to five to avoid the excessive likelihood of type I error in multiple comparisons of series (Olden & Neff, 2001). Raleigh's test for circular distributions (Zar, 1999) was employed to examine the presence of seasonal and monthly trends in different indices.

PCA was also used in a geographic analysis of estuaries to investigate how life-history traits of *C. undecimalis* populations differed with latitude, ambient temperature and total mortality. Biological and environmental information were also available for the east and west coasts of Florida (Taylor *et al.*, 2000; Muller & Taylor, 2006), Laguna de Términos and Tabasco, Mexico (Carvajal-Rojas, 1975; Perera-García *et al.*, 2011), Isla de Margarita, Venezuela (Osorio & Gonzalez, 1986) and Cabo Frio, Brazil (Carvalho, 2006). The main environmental variables were the absolute value of latitude and average and minimum monthly SST, which prior to transformation spanned from 23.0°S to 27.5°N , and 15.0 – 27.9°C , respectively. The SST in Isla de Margarita and Cabo Frio were also recovered from NOAA–NASA's AVHRR Oceans Pathfinder Global, using 1985 and 1999–2000 as reference years, respectively. The variables describing biological traits were extracted from the literature whenever possible.

This included the maximum sex-specific I_G ($I_{G\text{female}}$ and $I_{G\text{male}}$), sex ratio male:female, A_{max} , L_{∞} , A_{50} , L_{50} , the relative size at sex change (R_{SSC}) expressed as $R_{\text{SSC}} = L_{50}L_{\infty}^{-1}$ (Molloy *et al.*, 2011) and the relative life span (R_{LS}) expressed as $R_{\text{LS}} = A_{\text{max}} - A_{50}$. When the maximum monthly I_G , interpreted here as reproductive allocation, was not mentioned in the original texts or tables, it was extracted from the averaged time series plotted in the original papers after smoothing the data. Z was also considered to have a strong environmental (exogenous) influence in the form of fishing mortality. The data matrix was small, however, and some variables, such as Z , contained only three observations or sites (see Table SI, Supporting Information). All statistical analyses were performed using the Systat 13.0 (www.systat.com) and R 2.15.1(www.r-project.org) software, and statistical significance was assessed at the $P < 0.05$ level.

RESULTS

SIZE, CONDITION AND REPRODUCTION

All *C. undecimalis* sampled from the landings of Amatique were either male ($n = 347$) or female ($n = 226$). No intersex fish were observed. Females were generally larger than males and ranged from 50 to 102 cm L_T , and weighed 1650–9230 g. Males ranged in L_T from 31 to 83 cm, and weighed 190–5800 g. Mean $\pm L_T$ and W_T were 72.0 ± 9.0 cm and 3700 ± 1300 g, respectively (Fig. 3). The overall sex ratio favoured males (1.5:1) and showed large and periodic seasonal variations (Fig. 4). From high values of 4.0 in June, the ratio decreased to 1.0 and below from November to April, with a minimum of 0.3 in January. This may be indicative not only of local aggregation of females, emigration of males, but also of sex change. Most smaller-sized males were detected during the dry cold period of December to March, and this is indicative of recruitment to the coastal fishery. In contrast, the average L_T of female *C. undecimalis* did not vary by >5 cm throughout the year. Most small females (<70 cm), however, were caught during the dry cold period. This indicates that sex reversal may occur during this season. The largest females were also caught in January.

Average W_T was higher for females than for males of the same L_T , and was highest during the maturation period (class II) regardless of sex (Table I). The factors, sex and maturity stage, showed an interaction, but additional effects on the fit of the W_T model (equation 1) were very modest. The seasonal trends in C_F were also similar for both sexes (Fig. 5). It was generally low during May to October with some recovery in July at the onset of the rainy season. A sustained improvement of the C_F in both sexes occurred, however, early in the dry season (November to March). A seasonal reproductive cycle was also discernible (Fig. 6) and W_G differed significantly between sexes and maturity classes (Table I). W_G was higher for females than males and peaked during the spawning periods (class III). Although developed gonads could be observed in both sexes throughout the year, females presented a high percentage of maturing and mature gonads (classes II–III) from April to October, in the transition to the rainy season. Immature and spent individuals were more frequent during November to February (early dry season). The I_G was highest during April to October ($I_{G\text{female}} = 1.5\text{--}2.4\%$) and then declined during November to February ($I_{G\text{female}} = 1.3$ to 0.9%). There was a strong allometry between L_T , W_T and egg counts which showed that larger females have disproportionately larger gonads that contain more eggs (Table I). This could have introduced bias into the calculation

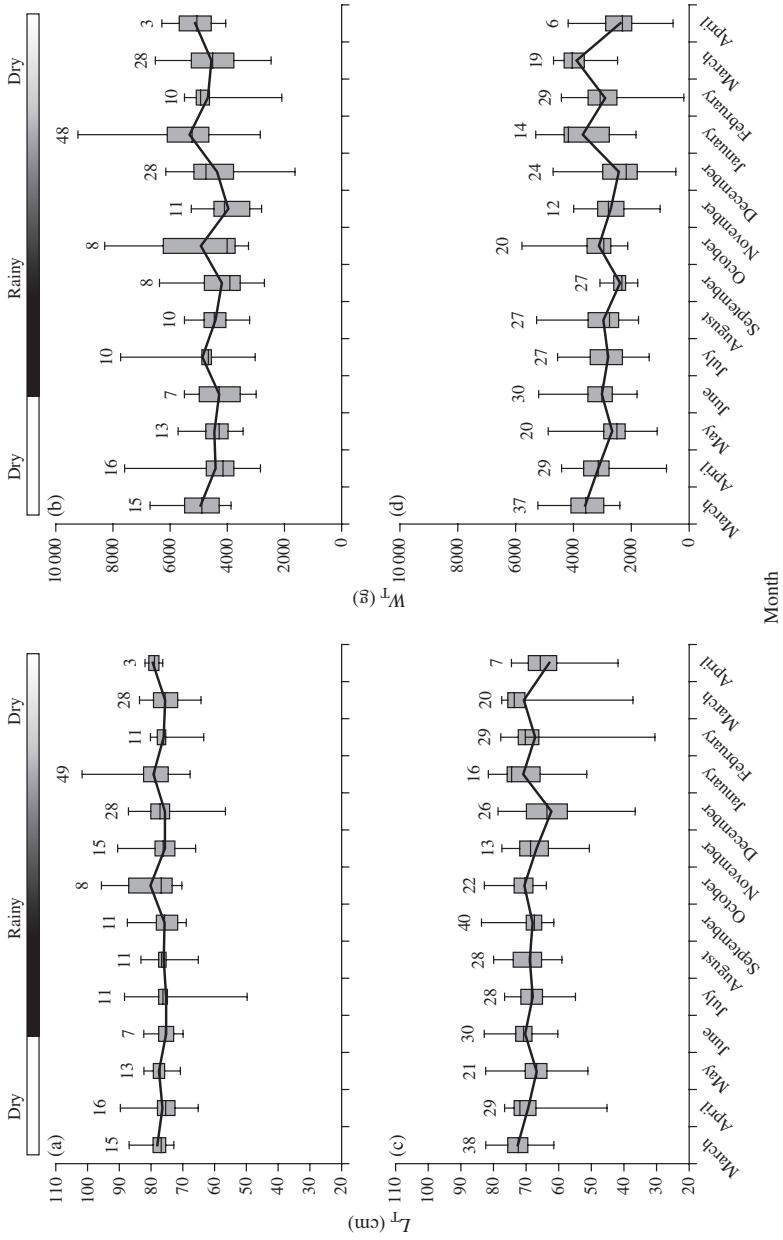


FIG. 3. Box and whisker plot diagrams of *Centropomus undecimalis* (a, c) total lengths (L_T) and (b, d) total masses (W_T) by month for (a, b) females and (c, d) males in the catches from March 2006 to April 2007. Numbers above data points indicate sample size, and the full line connects the mean values. A hydrological cycle is given with a horizontal bar.

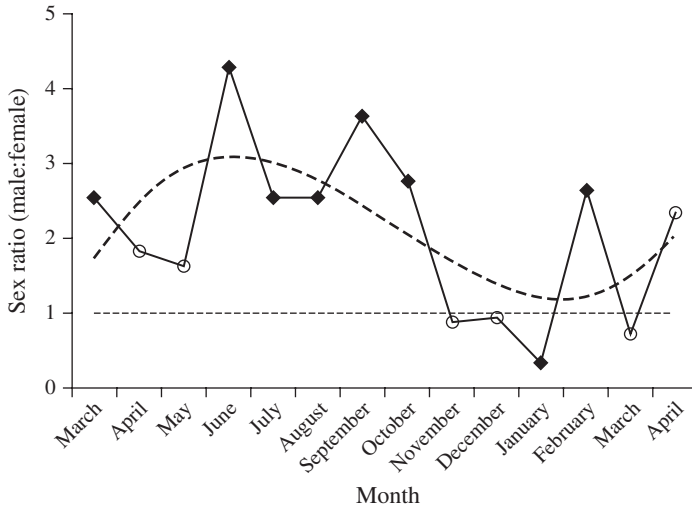


FIG. 4. Monthly trends in the sex ratio of *Centropomus undecimalis* sampled in Amatique Bay from March 2006 to April 2007. Some observations (○) did not differ significantly from the 1:1 sex ratio (----) (χ^2 -test, d.f. = 1, $\alpha = 0.05$). A third degree polynomial (---) was fitted to the monthly observations to suggest an annual cycle.

of the I_G variable if females had varied strongly in size, but because females had similar average L_T throughout the year the bias in the estimates of $I_{G\text{female}}$ is probably negligible.

Males, similar to females, also presented a high percentage of mature gonads throughout the year, except in December when 63% were classified as spent. Although the relative size of the testes was small throughout the year (Table I), the gonado-somatic cycle of males reflected that of the females. The highest

TABLE I. Allometric relationships of *Centropomus undecimalis* in Amatique Bay. Parameters (S.E.) of the general linearized (ln–ln) model (equation 1) relating body mass (W_T , g), gonadal mass (W_G , g) and egg count (E_C) to total length (L_T , cm), maturity class and sex. All regression models and variables displayed were significant ($P < 0.01$)

Factor	Level	$\ln W_T$	$\ln W_G$	$\ln E$
b_0		-5.88 (0.33)	-13.46 (1.47)	-4.55 (1.69)
b_1		3.30 (0.07)	3.83 (0.34)	4.19 (0.39)
Sex	f	0	0	
	m	-0.09 (0.02)	-1.07 (0.07)	
Maturity stage	I	0	0	
	II	0.03 (0.03)	0.46 (0.13)	
	III	-0.03 (0.02)	1.09 (0.11)	
	IV	-0.03 (0.03)	0.17 (0.13)	
n		f = 198 m = 278	f = 198 m = 278	f = 35
r^2		0.87	0.68	0.77

n , the number of observations (f, females; m, males).

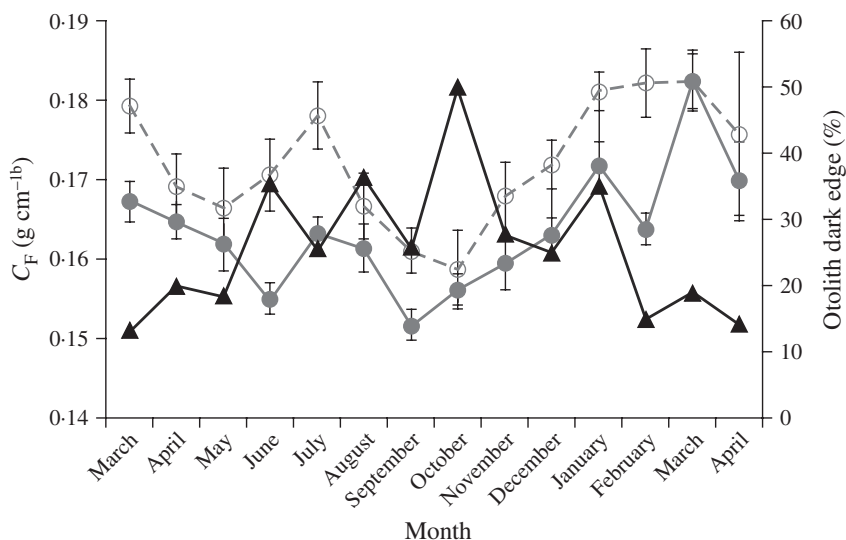


FIG. 5. Condition factor (C_F) cycle for female ($-\circ-$) and male ($-\bullet-$) *Centropomus undecimalis*, as well as frequency of occurrence of opaque edges ($-\blacktriangle$) in the otoliths (slow growth) from March 2006 to April 2007 in Amatique Bay.

$I_{G\text{male}}$ values were observed from February to October (0.4–0.7%), and a marked decline occurred from November to January ($I_{G\text{male}}$ c. 0.2–0.3%). Males seem to become mature at <40 cm, and thus, all but the smallest males in the collection were adult fish. There are indications that the maturation cycle of females slightly precedes that of males because $I_{G\text{female}}$ was significantly cross-correlated with $I_{G\text{male}}$ at a time lag of -1 month ($r = 0.72$). Further, the spawning cycle was highly correlated to the sex ratio cycle. The I_G series for both males and females was coincident or slightly preceded the sex ratio cycle (cross-correlation, lags 0 and -1 , $r = 0.57$). This indicates that mating takes place in periods of high concentration of males.

The first axis of PCA (Fig. 7) explained 44% of the variance in the biological and environmental data for Amatique and contrasted the somatic variables ($C_{F\text{female}}$, $C_{F\text{male}}$, left) with the indicators of spawning, slow growth (OPAQ) and male dominance (high m:f), on the right side. The latter indicators are associated with the warm season, characterized by high precipitation, high SST, runoff and chlorophyll *a* density. The second principal axis (vertical), which accounted for 27% of the variance, contrasted months of high I_G and m:f in the period of high SST (June to October), with the following months of increased runoff and lowest growth rate (August to December). CCAs indicated that the precipitation cycle precedes $I_{G\text{female}}$ cycle by 2 months (lag -2 , $r = 0.58$) and that the SST cycle coincided with or followed the I_G cycle by 0–1 month ($r > 0.58$). In contrast, I_G and C_F cycles were strongly negatively correlated ($r = -0.4$ to -0.5) at short time lags (0–2 months) irrespective of sex. In general, the cycles of body condition ($C_{F\text{male}}$ and $C_{F\text{female}}$) were strongly negatively correlated ($r = -0.4$ to -0.65), at short time lags, with the cycles of precipitation, air temperature and chlorophyll *a*.

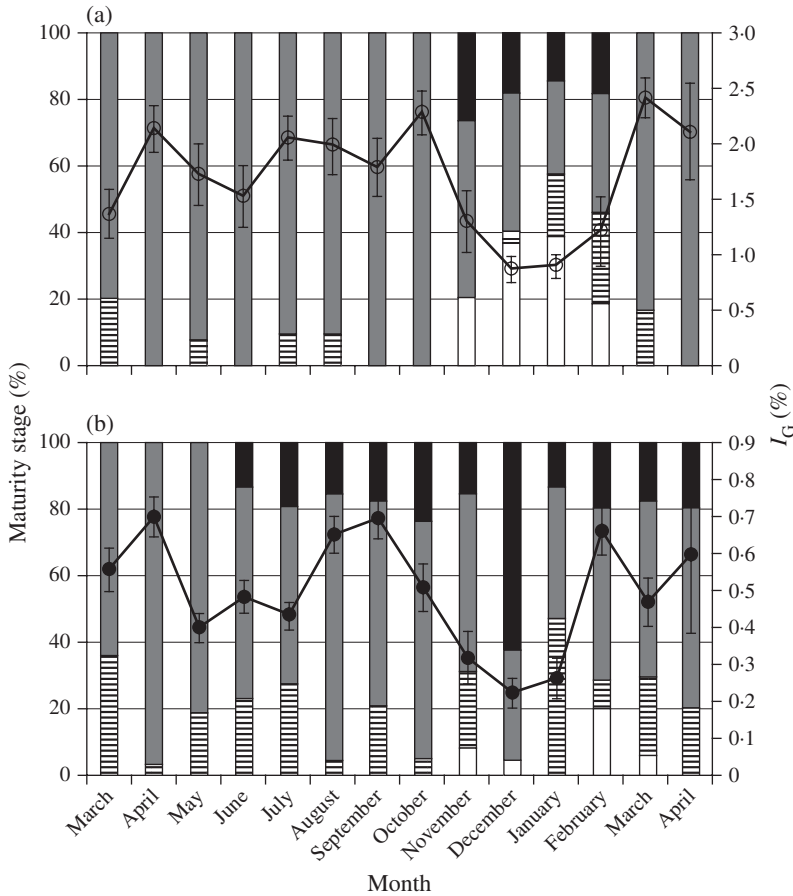


FIG. 6. Observed maturation cycle [stages I (\square), II (\equiv), III (\blacksquare) and IV (\blacksquare)] of (a) female and (b) male *Centropomus undecimalis* and their gonado-somatic index [I_G , mean \pm S.E. (\circ —, \bullet —)] in Amatique Bay, from March 2006 to April 2007.

GROWTH, SEX CHANGE AND MORTALITY

The youngest fish analysed was 2 years of age and the oldest 10 years, but most of the 456 ages determined from otoliths were between 3 and 4 years old. Growth rates are apparently high, and many individuals had already attained $>70\%$ of the maximum observed L_T (102 cm) by age 3 years (Table SII, Supporting Information). Opaque bands on the otolith edge were recorded throughout the year with the highest frequency occurring in October (50%) and the lowest ($<20\%$) from February to May (Fig. 5). Raleigh's test indicated that the monthly trends in deposition and frequency of opaque margins were clearly non-random ($r=0.99$, $P<0.001$). The cycle of opaque band deposition (annuli) was in phase (lag 0) and strongly cross-correlated with precipitation and chlorophyll *a* cycles ($r=0.72$ and 0.55). Annuli formation was out of phase, and preceded by 1–2 months, the C_F cycle in both males and females ($r=-0.64$ and -0.35). The timing and synchronism of these relationships suggest

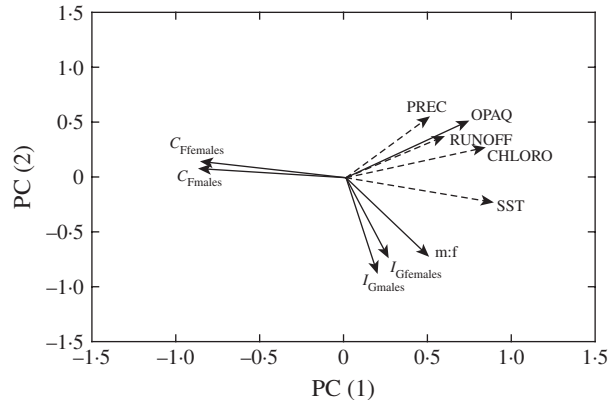


FIG. 7. Principal components' plot of ecological and physiological variables of *Centropomus undecimalis* in Amatique Bay, 2006–2007. The variables plotted are chlorophyll *a* (CHLORO), condition factor of females ($C_{F\text{females}}$) and males ($C_{M\text{males}}$), gonado-somatic index of females ($I_{G\text{females}}$) and males ($I_{G\text{males}}$), sex ratio males:females (m:f), frequency of opaque zones (OPAQ), precipitation (PREC), sea-surface temperature (SST), river runoff (RUNOFF). The exogenous variables are indicated (---).

that the fastest growth in *C. undecimalis* occurs outside the peak reproduction season (rainy season), during the time of greatest nutrient storage (dry season).

Logistic models indicated that, on average, sex reversal of *C. undecimalis* occurred when fish reached an L_T of 74.7 cm (L_{50}) or 6.8 years of age (A_{50}) (Table II, models 5 and 6). Irrespective of formulation, however, the sex reversal (logistic) curve was very flat, as indicated by the large maturation range, *i.e.* the difference between A_{75} and A_{25} . In contrast, sex reversal occurred over a short range of sizes ($L_{25} - L_{75}$). These symmetric models provided a similar good fit to sex change data as a more complex general (Richards) model, which was penalized by a higher BIC owing to the additional shape parameter (models 4 and 5). In contrast, a simple VBGF (model 3) that omits both the effect of sex change and sex-linked growth patterns fitted the observations poorly, particularly the increased size of females in relation to males of the same age. The full combined function (model 1) and the reduced combined function (model 2) performed better in terms of general fit to observations, distribution of residuals and statistics of fit. For instance, the log likelihoods (loss) of the integrated models are smaller than the sum of the losses in separated models. The reduced model performed, however, better than the full model in most respects. Despite an increase in the s.e. of parameters such as A_{50} and the common K , the important parameters $L_{\infty\text{male}}$ and $L_{\infty\text{female}}$ became more precise and consistent with the observations (Fig. 8). Also the A_{50} (7.9 years), became more consistent, and well within the standard range of the estimates obtained in simpler models. Not all parameters of this model were independent in the bootstrapped fits: the A_{50} was significantly correlated with both $L_{\infty\text{male}}$ and $L_{\infty\text{female}}$ ($r = 0.12$ and 0.20), and the latter was correlated with both the common K ($r = -0.28$) and $L_{\infty\text{male}}$ ($r = 0.07$).

Centropomus undecimalis aged 4–10 years were assumed to be fully recruited so that the Z calculated from the catch curve method averaged 0.62 year^{-1} (95% c.i.: 0.39 and 0.84 year^{-1}). Empirical and theoretical methods with different foundations provided somewhat different estimates of M . The method of Hewitt & Hoenig

TABLE II. Parameters (S.E.) of the von Bertalanffy growth function (VBGF) and maturation curve in their separated and combined versions, as well as statistics of the fit for *Centropomus undecimalis* in Amatique Bay. All models fitted in terms of fish age (years), with exception of model 6 where parameters refer to total length (L_T , cm)

Model	Processes modelled	$L_{\infty m}$	$L_{\infty f}$	L_{∞}	K_m	K_f	K	$A_{2.5}$	A_{50}	A_{75}	Loss	AIC	BIC
1	Combined growth-sex change; sex-dependent VBGF (L_{∞} , K); symmetric logistic sex change	73.7 (0.6)	106.0 (31.3)		1.2 (0.1)	0.9 (0.7)		-5.0 (3.7)	8.7 (1.6)	22.3 (6.1)	-1801	3614	3638
2	Combined growth-sex change; sex-dependent VBGF (L_{∞}) with common K ; symmetric logistic sex change	71.9 (0.3)	93.2 (24.1)				1.1 (1.0)	-4.0 (4.5)	7.9 (2.3)	19.9 (8.5)	-1791	3592	3612
3	Separated VBGF; sex-independent			74.1 (1.1)			1.1 (0.2)				-1562	3128	3136
4	Separated sex change; asymmetric logistic (Roberts)							-1.1 (3.2)	6.8 (2.0)	16.8 (8.2)	-287	578	592
5	Separated sex change; symmetric logistic							-1.8 (3.7)	6.8 (2.0)	15.4 (7.1)	-287	578	586
6	Separated sex change; symmetric logistic (function of length)							*70.3 (0.6)	*74.7 (0.5)	*79.1 (0.7)	-205	414	422

L_{∞} , asymptotic length; K , growth coefficient; m, males; f, females; 25, 50 and 75 are quartiles of the logistic curve; AIC, Akaike information criterion; BIC, Bayesian information criterion; *, L_{25} , L_{50} , L_{75} .

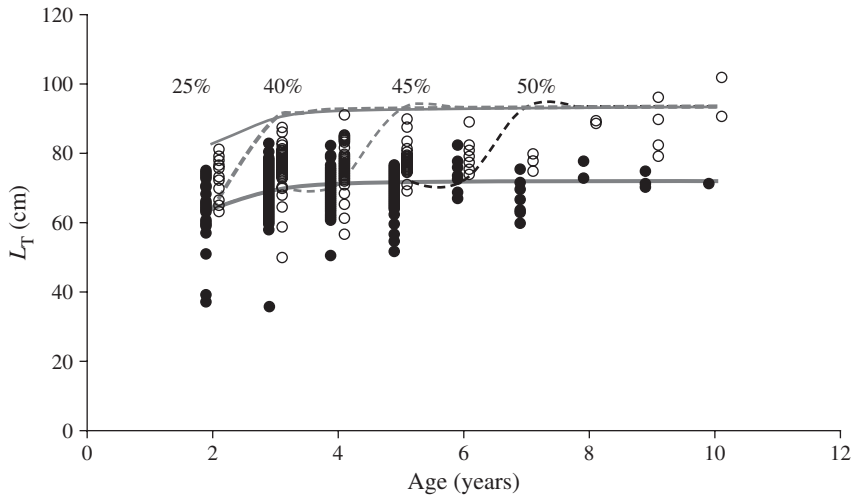


FIG. 8. von Bertalanffy growth curves (—) for different probabilities of sex change, as given by the transition lines (---), in Amatique Bay *Centropomus undecimalis*. Males (●) and females (○) are denoted. The female observations are slightly jittered. The functions fitted are based on the parameters of the sex-coupled growth (model 2; see Table II).

(2005), based on species longevity or maximum observed age, provided a maximum M of 0.4. Estimation with regard to age at maturity (sex reversal), following the methods of Rikhter & Evanov (1976) and Charnov (1993), or with regard to reproductive investment ($I_{G\text{female}}$) (Lester *et al.*, 2004), resulted in all estimates of M of *c.* 0.2. Thus, the estimates of F obtained by the two approaches varied between 0.2 and 0.4 (average 0.35), and the resulting estimates of E in Amatique were wide, ranging from 0.3 to 0.7 (average *c.* 0.6).

BIOGEOGRAPHIC TRENDS

The cross-sectional analysis of life-history traits suggested the presence of strong gradients related to geography and biology. The first axis of the rotated PCA explained 56% of the total variance and the second axis explained 39% (Fig. 9). There was no change in configuration of the life-history variables upon the introduction of exogenous variables in the same space. The first axis contrasted geographic variables, with high positive loadings of latitude and high negative loadings of minimum monthly SST. Although the correlation between (absolute) latitude and SST was not very strong, because of particular oceanographic features on the east coast of Florida and in Isla de Margarita, the first axis roughly separated populations from high latitudes and colder locales on the right side of the chart to those from warmer winter waters at lower latitudes on the left side. Whilst traits such as longevity, R_{LS} , L_{50} and high L_{∞} were associated with high latitudes, maximum I_G was more clearly associated with cold winter waters, *i.e.* diagonally opposed to high scores of minimum monthly SST. In fact, for the five populations, the maximum observed monthly I_G tended to decrease by 6–8% for every 1° C increase in SST in winter. The exponential relationship between maximum monthly

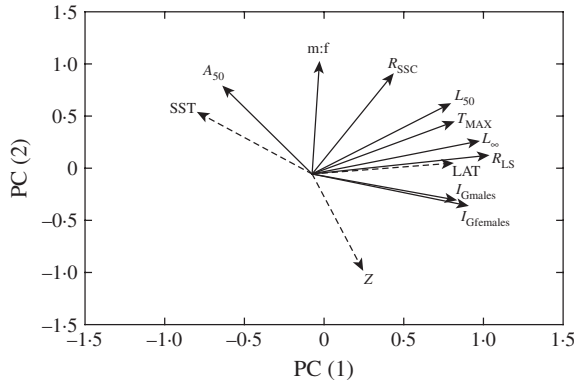


FIG. 9. Principal components' plot of life-history traits and exogenous variables in five populations of *Centropomus undecimalis* in Florida, Mexico, Guatemala, Venezuela and Brazil. The variables plotted are age at sex change (A_{50}), gonado-somatic index for females ($I_{Gfemales}$) and males (I_{Gmales}), length at sex change (L_{50}), latitude north (LAT), asymptotic length (L_{∞}), sex ratio (m:f), average minimum monthly sea-surface temperature (SST), relative size at sex change (R_{SSC}), reproductive life span (R_{LS}), observed longevity (A_{MAX}) and instantaneous rate of total mortality (Z). The exogenous variables are indicated (---).

I_G and minimum monthly SST (S) could be described by $I_G = 11.0$ (males) or 15.5 (females) $e^{-0.07S}$ ($n = 9$, $r^2 = 0.85$). This corresponds to a 60% decline in I_G along the observed range of winter temperatures ($15\text{--}28^\circ\text{C}$). The second axis was dominated by the partially exogenous biological variable Z . Populations under low mortality regimes showed greater age-at-sex reversal, their sex ratios were more clearly dominated by males and the relative size at sex reversal was also larger.

DISCUSSION

ENVIRONMENTAL VARIABLES AND *C. UNDECIMALIS* LIFE HISTORY

An apparent controversy has existed for many years about whether the existence of cycles of growth, reproduction and recruitment found in temperate species also occurs in tropical fishes (Longhurst & Pauly, 1987; Fowler, 2009). Early authors had difficulties in finding the sharp divides in physiological and ecological processes, reflected in, *e.g.* otolith ring formation, gonad maturation and recrudescence, and recruitment of juveniles to the fishery. In temperate areas, these cycles are often correlated to the controlling cycles of light, temperature and primary production. These contributions, however, are often obscured in tropical estuaries (Blaber, 2000; Staunton-Smith *et al.*, 2004). The study in Amatique Bay tends to confirm both views. For example, the patterns of ring deposition in otoliths from Amatique were far less distinct than those otoliths from Florida. Further, reproduction, growth and storage did not seem to be immediately related to cycles of light and temperature. Thus, the sometimes subtle but dynamic temporal linkages with other environmental and physiological variables required more powerful tools like CCA to be identified. Further,

the broad latitudinal distribution of *C. undecimalis* was important for the elucidation of the periodic patterns and life-history adaptations of tropical and sub-tropical fishes.

The abundant rains of June (c. 800 mm), and the slight warming (c. 1° C) of the sea water from June to September, marked the onset of spawning in the Amatique area. This is also the start of the most important fishing season for *C. undecimalis* (Heyman & Granados-Dieseldorff, 2012), a time when males are very abundant, particularly those of larger size. Present observations indicate that river runoff in the region and the chlorophyll *a* concentration in the Bay are in phase, and peak at the end of August to October period, *i.e.* late in the rainy season. It is likely that the increased runoff and primary production following spawning give the appropriate conditions for larval and juvenile growth and survival that has been reported for early juvenile *C. undecimalis* in the estuaries of Puerto Rico (Aliaume *et al.*, 2000). This is, however, not the most suitable period for adult growth. By September to October, adult fish undergo poor growth (frequent opaque zones in otoliths), which results in poor body condition. Nevertheless, it is also during this post-spawning period that a reversal of the sex ratio occurs and smaller fish, both males and females, make up the fishery. Further, this is the only period when immature females were observed. A combination of different mechanisms can account for this: new small fish (males) may have drifted downriver with the runoff and larger males may have migrated upriver to as far as Lake Izabal where they have been observed by earlier authors (Brinson *et al.*, 1974; J. E. Martínez, unpubl. data). It is also possible that these immature, newly recruited, females had recently spawned as males, based on earlier evidence suggesting that sex reversal occurs shortly after spawning (Taylor *et al.*, 2000). Whilst these suggested processes match what is known of the life cycle of *L. calcarifer*, a related species in Australasia (Balston, 2009), little is known about the migration of *C. undecimalis* in all areas of its distribution. Less uncertain seem to be the processes taking place during the dry season of January to May. This is a period of recovery, with adults showing first an increased growth rate, closely followed (lag of c. 1 month) by storage of body reserves. This is reflected in the increase of C_F and in the development of early reproductive tissue in the gonads. No information is available regarding the extent and seasonality of secondary and higher production in the marine environment of Amatique, but it is likely that there is a lag of a few months relative to the peaks of primary production measured by remote sensing in September to October. This would be coincident with the fast growing period of adult *C. undecimalis* observed in the dry season. The annual cycle in Amatique Bays closes in April, before the onset of a new spawning season, with the probable arrival of large males from upriver. This could explain the restoration of the skewed sex ratio during the spawning season, a factor that suggests a strong competition for females. Some of the processes suggested are amenable to hypothesis testing in future work. The existence of sex- and size-specific migrations could be investigated by simultaneous sampling of fish in the estuary, along the Dulce River and its creeks, preferably using non-selective gear. Further investigations, including *e.g.* RNA:DNA ratios or diet studies of *C. undecimalis* could bring new information on the production and growth cycle at higher levels in the food chain.

The annual growth and reproduction cycle of *C. undecimalis* in Amatique seem to be lagged, and differently linked to environmental variables than in *C. undecimalis* from higher latitudes, particularly Florida. Opaque, thin bands in the annuli formation have been related to slow growth in tropical fishes. For the

C. undecimalis populations in Florida, these are formed during the late winter and spring (March to May) (Taylor *et al.*, 2000). In contrast, in Amatique Bay, peak formation of opaque zones occurs during the October rainy season. Fast growth occurs during the dry season, February to May, when SST was at its yearly minimum (27° C). It is therefore likely that the life cycle in tropical *C. undecimalis* is more closely related to the hydrological regime than to the temperature regime as in Florida where water temperature minima control egg production and juvenile and adult survival (Adams *et al.*, 2012). The concept of the hydrological cycle as a limiting factor for growth and reproduction in warm areas has also been suggested by earlier authors working with tropical fishes (Jepsen *et al.*, 1999; Morales-Nin & Panfili, 2005; Fowler, 2009).

AGE, GROWTH AND SEX-CHANGE MODEL

The age and growth relationship of *C. undecimalis* in Amatique Bay was determined, although age interpretation was not as precise as previously experienced in *C. undecimalis* from Florida. This phenomenon has been reported for other tropical species with a wide distribution where increment clarity improves with latitude (Choat *et al.*, 2009; Fowler, 2009; Berumen *et al.*, 2012). This is normally associated with latitudinal gradients in environmental factors such as SST or freshwater inputs. *Centropomus undecimalis* from Amatique Bay grew very rapidly during the first 3 years to *c.* 72 cm; thereafter, size reached an asymptote prior to sex reversal. In comparison, *C. undecimalis* from Florida attain those sizes between ages 5 and 7 years, but continue to grow through to age 10 years (Taylor *et al.*, 2000). Sex reversal in Amatique *C. undecimalis* occurred within a relatively narrow range of sizes (70–79 cm) and over a large range of ages, giving the impression that it is more strongly controlled by absolute size than age. Thus, the 40% sex change probability was attained at an age of 3 years while A_{50} occurred at an age of 7.9 years. This variability is not unusual in sequential hermaphrodites (Blaber *et al.*, 1999; Walker *et al.*, 2007). It may reflect the greater importance of phenotypic plasticity and social control in sex change than that of predetermined critical ages or even size (Moore *et al.*, 2011). The most parsimonious growth function, the reduced model, indicates that there may not be marked differences in K , but that females clearly attain large L_{∞} than males. The gradual change in sizes at observed ages suggests that females, unlike males, may have an indeterminate growth pattern. Thus, it follows that both male and female *C. undecimalis* have similar physical, but not necessarily behavioural, investment in reproduction, and that females have a larger and increasing ratio of net production to reproductive investment (Lester *et al.*, 2004). The model employed here describing growth and sex reversal is simple and contains parameters that can be easily calculated from field studies or extracted from biogeographic analyses. Further, the reported estimates of variance and covariance of the various parameters enable a more realistic simulation of growth patterns and fishery production.

BIOGEOGRAPHIC TRENDS

Apart from reproductive studies, there is scant information regarding the biology of *C. undecimalis* despite its wide distribution and commercial importance. The patterns disclosed in the meta-analysis have in many cases, however, theoretical

foundations. The main pattern that emerges from the studies analysed along a latitudinal–temperature gradient is that the populations of *C. undecimalis* from higher latitudes with normally cooler winter waters attain larger sizes at given ages, greater longevity, have greater I_G and larger sizes at sex reversal. This is in agreement with the negative relationship between longevity, asymptotic length and temperature reported for better investigated species (Choat & Robertson, 2002; Robertson *et al.*, 2005; Ruttenberg *et al.*, 2005; Trip *et al.*, 2008; Berumen *et al.*, 2012), which finds support in the metabolic theory of ecology (Brown *et al.*, 2004; Munch & Salinas, 2009; Caselle *et al.*, 2011). Greater asymptotic lengths and increased fecundity at colder temperatures have been attributed to the selection pressure of winter mortality against the smallest fishes (Angilletta *et al.*, 2004; Hurst, 2007). Thus, some of the differences in life-history traits between neighbouring populations of *C. undecimalis* in Florida may be partially explained by these temperature-related processes and phenotypic influences (Tringali & Bert, 1996; Taylor *et al.*, 2000).

The second major trend identified in the present biogeographic survey was the negative relationship between Z , A_{50} and male predominance. Several other fish species present a negative relationship between Z and A_{50} (Hawkins & Roberts, 2003; Götz *et al.*, 2008; Rhodes *et al.*, 2011), which has been attributed to an adaptive response by individuals to increase their reproductive value (Munday *et al.*, 2006; Caselle *et al.*, 2011; Molloy *et al.*, 2011). The size advantage hypothesis predicts that sex change will occur earlier in populations with slower growth rates and higher mortality rates (Munday *et al.*, 2006). The negative relationship between A_{50} , R_{SSC} , m:f ratio and Z suggest that *C. undecimalis* might present some capacity to adapt the length at sex change. If a species is inflexible with respect to changing sex, removing the largest fish by selective fishing will result in lower asymptotic lengths and increasing R_{SSC} (Molloy *et al.*, 2011). Sex ratios in sex reversing populations have been shown to be biased towards the smaller sex in high mortality regimes (Molloy *et al.*, 2012). Only a few studies employed in this meta-analysis, however, contain sufficient information regarding the decline in m:f ratio, and the suggested trend is thereby subject to sampling error and, therefore, uncertain. This is an issue of importance for management that calls for further testing in either longitudinal (time series within estuaries) or cross-sectional (inter-estuary) studies.

Little is known about the reproductive physiology and behaviour of *C. undecimalis*, but the investigation along a latitudinal gradient may shed some light on the subject. The analysis of trends in fish size and sex ratios in Amatique Bay show that there is a strong deficit of females, which may suggest a strong competition among mature males during the spawning season. The reproductive investment of *C. undecimalis*, particularly by males is, however, apparently very small. Thus, despite the positive allometry in gonad mass in relation to body mass, the maximum monthly I_G of males is markedly below 1%. An I_G of this size is typical of species with internal fertilization or paired spawning, *i.e.* regimes of low sperm competition (Stockley *et al.*, 1997). Only part of this discrepancy may be explained by the temperature and I_G relationship divulged by the cross-sectional analysis. The relative size of the gonad may increase by 7% with a decrease of 1° C in winter water temperature, or by a factor of 2.5 along the observed range of temperatures. Low sperm production combined with the determinate growth pattern suggests that unknown behavioural mechanisms in males may be more costly than the physical investment in gonad products. Knowledge of the reproductive strategy of individuals and of the formation

of spawning aggregations are also important issues for population management and call for dedicated field work and individual modelling of *C. undecimalis* populations.

IMPORTANCE FOR MANAGEMENT

The voluntary management of effort in gillnet fisheries in Amatique Bay restricts operations in different areas on a weekly rotation basis in combination with a 1 month closed season, usually in May–June (Andrade & Midré, 2011). The system was agreed to and implemented by the different ethnic groups that used unique gear to avoid gear interference and conflict, and as a hiatus in the harvest. In this context, and in other remote areas of *C. undecimalis* distribution, management rules should be simple and build on existing rules and institutions to gain voluntary support for compliance. The estimate of exploitation rate of *c.* 60% suggests that, for a fish with a medium life span (Beverton, 1998), fishing mortality may be too high in Amatique and Dulce River. If growth overfishing is the cause, an extension of the closed season or preferably a change in the rotational practices may be favoured. This would result in reduction of fishing mortality without altering the established fishing pattern. If, however, the objective is to avoid recruitment overfishing, the task may be more challenging because of the poorly understood dynamics of protandric species. Seasonal closures to protect spawning aggregations may be more effective in colder waters, as *e.g.* Florida (Taylor *et al.*, 1998), where the spawning period is shorter and more pronounced than in tropical areas. Changes in the selectivity of the fishing gear must, however, be made with care. Selective fisheries that target the largest individuals can be compensated by earlier sex reversal in males. The full reproductive potential of stock is diminished, however, when large females are replaced by smaller females because of the strong allometry in fecundity. Thus, in both Florida and Papua New Guinea, the fisheries for centropomids are managed by slot-limits to protect both small fishes and large spawning females (Blaber *et al.*, 2009; Muller & Taylor, 2012). The optimal management regime for *C. undecimalis*, regardless of location, should be optimized by intense research that describes local stock dynamics delineated with the use of genetic models. Restricted harvest during periods of high availability of large females in combination with special gear selectivity may offer partial solutions, but should be tested for both efficacy and ease of implementation and acceptance.

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Supporting Information

Supporting Information may be found in the online version of this paper:

Table SI. *Centropomus undecimalis* life-history traits and exogenous variables employed in principal component analysis for the locations Amatique Bay,

Guatemala (GT); East (FLE) and West (FLW) Florida Coasts, U.S.A.; Laguna de Términos, Mexico (MX); Isla de Margarita, Venezuela (VZ) and Cabo Frio, Brazil (BZ, southern latitude). The variables are absolute latitude (LAT), average minimum monthly sea-surface temperature (LSST), asymptotic length (L_{∞}), age at sex change (A_{50}), length at sex change (L_{50}), gonado-somatic index for females ($I_{Gfemale}$) and males (I_{Gmale}), sex ratio (m:f), observed longevity (A_{MAX}), instantaneous rate of total mortality (Z), relative size at sex change (R_{SSC}) and reproductive life span (R_{LS}).

Table SII. Mean total length (L_T) at age of *Centropomus undecimalis* in Amatique Bay. Numbers in parentheses indicate s.d. and sample size

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